New insights into the Weddell Sea ecosystem applying a network approach

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## Abstract

Network approaches can shed light on the structure and stability of complex marine communities. In recent years, such approaches have been successfully applied to study polar ecosystems, improving our knowledge on how they might respond to ongoing environmental changes. The Weddell Sea is one of the most studied marine ecosystems outside the Antarctic Peninsula in the Southern Ocean. Yet, few studies consider the known complexity of the Weddell Sea food web which in its current form comprises 490 species and 16041 predator-prey interactions. Here we analyzed the Weddell Sea food web, focusing on trophic interactions that underpin ecosystem structure and stability. We estimated the strength for each interaction in the food web, characterized species position in the food web using unweighted and weighted properties, and analysed species’ roles with respect to in the stability of the food web. On the one hand, we found that the distribution of the interaction strength at the food web level is asymmetric, where weak interactions are prevalent. Including such information as a (weighted) property for species we detected a positive relationship between species mean interaction strength and two unweighted properties, trophic level and the total number of interactions. We also found that only few species are key in terms of food web stability, presenting particular weighted and unweighted properties. In the same analysis we have integrated food web and species information, enabling a more complete assessment of the ecosystem structure and function, likely highlighting the ecological processes at play in the Weddell Sea. We consider that our results provide new insights important for the development of effective policies and management strategies, particularly given the ongoing initiative to implement a Marine Protected Area (MPA) in the Weddell Sea.

## Introduction

The objective of this work was threefold: 1) estimate the strength for each interaction in the Weddell Sea food web, 2) characterise species considering weighted and unweighted properties, and 3) analyse the species’ role in the stability of the food web.

## Methodology

### Study area

The high Antarctic Weddell Sea shelf is situated between 74 and 78ºS stretching approximately 450 km from South to North (Figure 1). Water depth varies between 200 and 500 meters, and shallower areas are covered by continental ice, which forms the coastline along the eastern and southern part of the Weddell Sea. The shelf area contains a complex three-dimensional habitat with large biomass, intermediate to high diversity in comparison to benthic boreal communities and a spatially patchy distribution of organisms (Dayton 1990; Teixidó, Garrabou, and Arntz 2002).

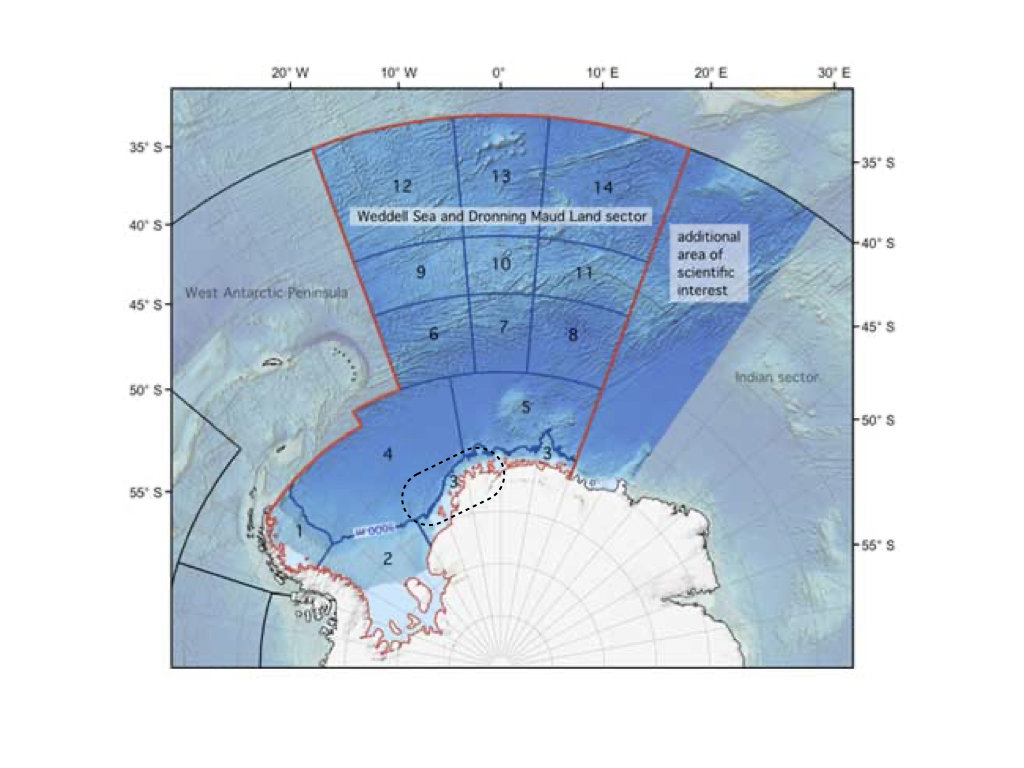


Figure 1. Map of the Weddell Sea and Dronning Maud Land sector highlighting the high Antarctic shelf as a dashed-line contour. Modified from www.soos.aq.

### Weddell Sea food web dataset

The Weddell Sea food web was retrieved from the GlobAL daTabasE of traits and food Web Architecture (GATEWAy, version 1.0) of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (Brose 2018). In addition to predator-prey interactions, the data base contains information on other biological data such as the mean body mass and movement type for each species in the food web. Furthermore, it incorporates information about the interaction itself, such as the dimensionality (2 or 3 dimensions). In its current form the Weddell Sea food web comprises 490 species and 16041 predator-prey interactions and constitutes one of the most resolved food webs constructed to date (REF).

This marine food web compiles all the trophic data available for the high Antarctic Weddell Sea collected since 1983, and is one of the most highly-resolved marine food webs documented to date. It’s noteworthy that it is a summary network that ignores seasonal changes (Jacob et al. 2011).

### Dataset analyses

We analysed the food web of the Weddell Sea by: a) estimating the strength of each interaction; b) studying the species properties in a network framework; and c) comparing the stability of the food web after performing species extinction in silico simulations.

### Interaction strength estimation and distribution

To estimate the strength of each pairwise interaction in the food web we followed the methodology proposed by Pawar et al. (2012). The minimum data requirements are body mass of the consumer (predator) and resource (prey), and the interaction dimensionality classified as 2 or 3 dimensions. [DEFINTION OF 2 and 3 dimension] GATEWAy v.1.0 provides information on the mean body mass for consumers and resources, except for ‘detritus’ and ‘sediment’, and the dimensionality for the majority of the interactions, though the latter is missing in some cases (924 interactions). To complete the missing data on species ‘dimensionality’, we used information about the movement type of consumers and resources. Thus, we classified the interaction as ‘2D’ if both consumer and resource move in 2D (e.g., if both are sessile or moving laterally on the seafloor) or if a consumer moves in 3D and a resource in 2D (e.g., swimming consumer and sessile resource). The interaction was classified as 3D if both consumer and resource move in 3D (e.g., both swimming) or if the consumer moves in 2D and the resource in 3D (e.g., sessile/walking consumer, swimming resource) (Pawar, Dell, and Van M. Savage 2012).

The main equation we used for estimating the interaction strength IS was:

where is the search rate, is the resource density, and and are the body mass for the resource and the consumer, respectively (Pawar, Dell, and Van M. Savage 2012).

We obtained estimates for resource density and the search rate from the scaling relationships with the resource and the consumer mass, respectively (Pawar, Dell, and Van M. Savage 2012). The coefficients of such relationships, determined by ordinary least squares regression, vary with the interaction dimensionality. On one hand, resource density scales with resource mass as power-law with exponents in 2D and in 3D. Since mean mass for resources ‘phytodetritus’ and ‘sediment’ were not available in GATEWAy, we considered the body mass of the smallest phytoplankton species (‘Fragilariopsis cylindrus’) as a proxy. This is justified by the fact that ‘phytodetritus’ and ‘sediment’ are mainly composed by dead or senescent phytoplankton reaching the seabed (Wolanski et al. (2011)). On the other hand, search rate scales with consumer mass as power-law with exponents in 2D and in 3D.

We fitted six candidate models (Exponential, Gamma, log-Normal, Normal, Power-law and Uniform) the interaction strength distribution using maximum likelihood (McCallum 2008), and selected the best fitting model by computing the Akaike Information Criterion AIC (Burnham and Anderson 2002).

### Species properties

To characterize the role of each species in the food web, we considered unweighted and weighted food web properties (Figure 2). Unweighted properties are related to properties commonly used in qualitative food web studies and only describe the presence or absence of interactions without any information on strength between a pairwise species link (Martinez 1991; Dunne, Williams, and Martinez 2002b; Borrelli and Ginzburg 2014). In contract, weighted properties capture the strength of interactions and thus differentiate importance of a link based on the procedure described above.

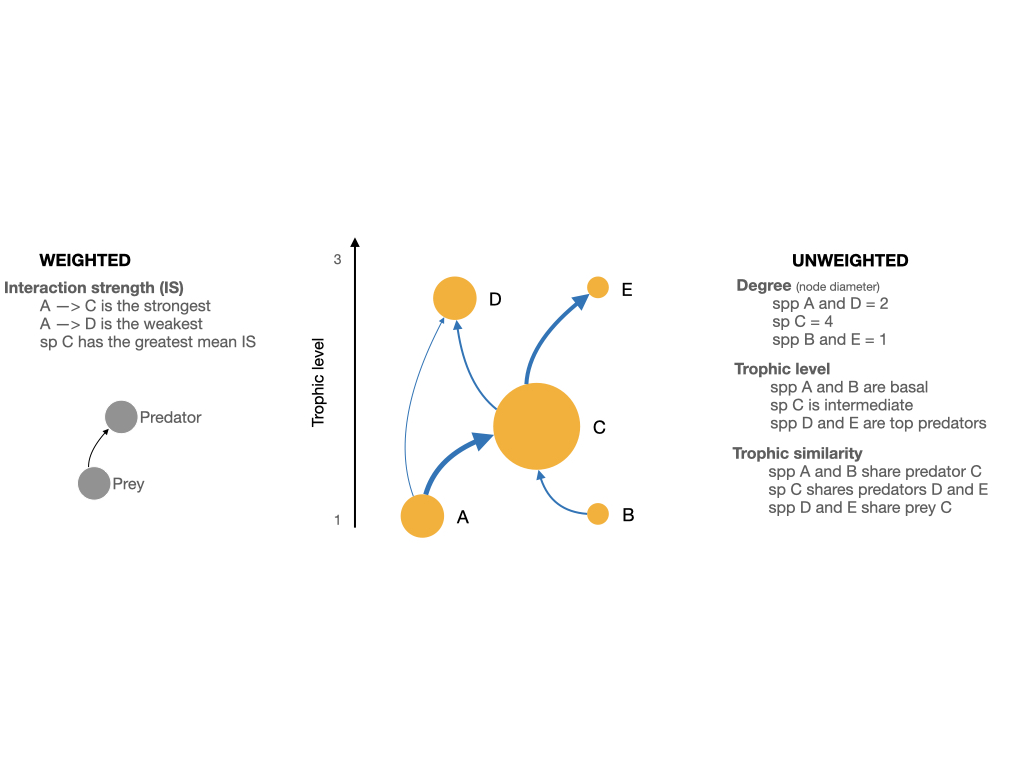


Figure 2. Illustration of a network showing the weighted and unweighted properties we used to characterize the species of the Weddell Sea food web.

To assess species roles based on the weighted food web, we focused on mean interaction strength defined as the average strength of all a species’ interactions. Further we calculated three unweighted species properties: a) species degree, i.e., the sum of in- and out-going interactions (REF); b) trophic level (REF); and c) trophic similarity, i.e., the trophic overlap based on shared and unique resources and consumers (REF). These metrics were chosen to asses a species role based on the unweighted food web. A species degree has often been equated with a species importance to the structure and functioning within a food web, i.e. perturbations to high-degree species may have larger effects on the food web robustness to perturbations than low-degree species (Dunne, Williams, and Martinez 2002a; references in Cirtwill et al. 2018). The trophic level offers information about how important a species is to its biotic community, i.e., top predators and primary producers are expected to have particularly large effects on the rest of their communities through top-down and bottom-up control, respectively (references in Cirtwill et al. 2018). Trophic similarity is an index of trophic overlap considering the set of prey and predators for a pair of species; it measures one of the most important aspects of species’ niches, the trophic niche, and functional aspects of biodiversity (Martinez 1991; Williams and Martinez 2000).

Furthermore, we took a species’ habitat into account, which describes the physical position of a species within the ecosystem. Species were categorized as: 1) benthic, if a species lives on the seafloor; 2) pelagic, if a species lives close to the surface; 3) benthopelagic, if it moves between and connects the mentioned environments; 4) demersal, if it lives and feeds on or near the bottom of the sea; and 5) land-based, if the consumer is not strictly aquatic but feeds predominantly on marine species. Species habitat affiliation were retrieved from Jacob et al. (2011).

### Extinction simulations and stability

To analyze the impact of species on food web stability, we performed extinction simulations deleting one species at a time, that is for every extinction, network size was reduced by one species only. After each extinction, we calculated the stability of the network minus the targeted species (489 nodes) and compared it with that of the whole network (490 nodes in total). To, we used anqssestimatesequals We performed 1000 simulations for each species extinction and obtained a mean QSS and a maximum eigenvalue for each species. At last we statistically analysed such difference with an Anderson-Darling test considering a p-value < 0.01 (Scholz and Stephens 1987). If this difference is positive, then the stability of the food web is higher if a species was removed, and vice versa. A detailed description on the stability calculations can be found in Supplementary Material.

**Data analyses?**

With the aim of studying the relationship between the interaction strength of the species (weighted property) and its unweighted properties we performed linear regression analyses between the log(mean interaction strength) and each of the mentioned unweighted properties. We also explored such weighted property with species habitat.

Formulas used to obtain the above species properties are described in Supplementary Material.

Once we had the results for the impact on stability for each species extinction, we plotted them considering weighted (interaction strength) and unweighted properties, and species habitat. With this we aim to characterize those species with a relatively high effect on the stability of the food web.

All analyses were performed in R software, using the R packages igraph (Csardi and Nepusz 2005) and cheddar (Hudson et al. 2013), and multiweb (Saravia 2019). The source code and data are available at <https://github.com/EcoComplex/WeddellSea>.

## Results

### Interaction strength distribution

The statistical distribution that best fitted the empirical interaction strength distribution was a ‘log-normal’ due to the skew towards weaker interactions (Figure 3, Table 1).

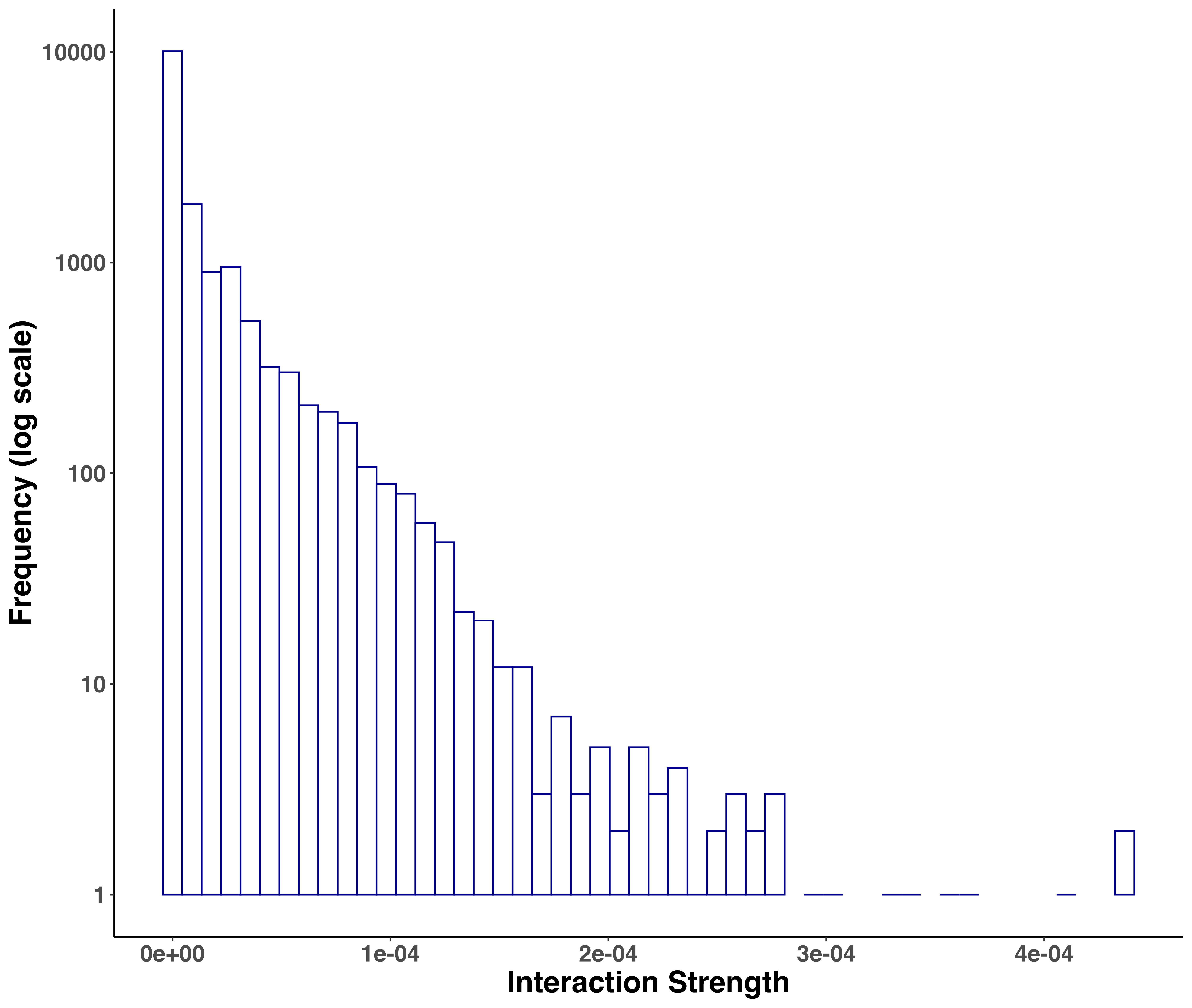


Figure 3. Frequency distribution of interaction strengths for the Weddell Sea food web. Total number of interactions = 16041.

Model comparison for the distribution of interaction strengths of the Weddell Sea food web. Order by best fit. References: df = degrees of freedom, AIC = Akaike Information Criterion, deltaAIC = difference with best fit. Log-Normal is the best model.

| Model | df | AIC | deltaAIC |
| --- | --- | --- | --- |
| Gamma | 2 | -362028.3 | 0.00 |
| log-Normal | 2 | -361975.5 | 52.86 |
| Power-law | 2 | -353270.2 | 8758.15 |
| Exponential | 1 | -327785.1 | 34243.23 |
| Normal | 2 | -291497.0 | 70531.30 |
| Uniform | 2 | -248179.0 | 113849.31 |
|  |  |  |  |

**Species’ network role related to their mean interaction strength**

Following the above results for the distribution of the interaction strengths, we found that the species mean interaction strength was different. We also found that such weighted property is related more or less with unweighted properties (Figure 4A-D). There is a positive relationship between interaction strength and trophic level showed, i.e., the higher the trophic level of the species, the higher its mean interaction strength. We also found a significant but less evident positive relationship with a species degree. Contrary, there was no significant relationship between mean interaction strength and trophic similarity. Considering species habitat affiliation, the “Benthopelagic” and “Pelagic” categories contained the two species with the highest mean interaction strength, the killer whale *Orcinus orca* and the XXXX *Mesonychoteuthis hamiltoni*, respectively. However, the majority of the species with relatively higher interaction strength belonged to the “Demersal” and “Land-based” habitats groups. Species inhabiting the benthic realm showed the lowest mean interaction strength (Figure 4D).

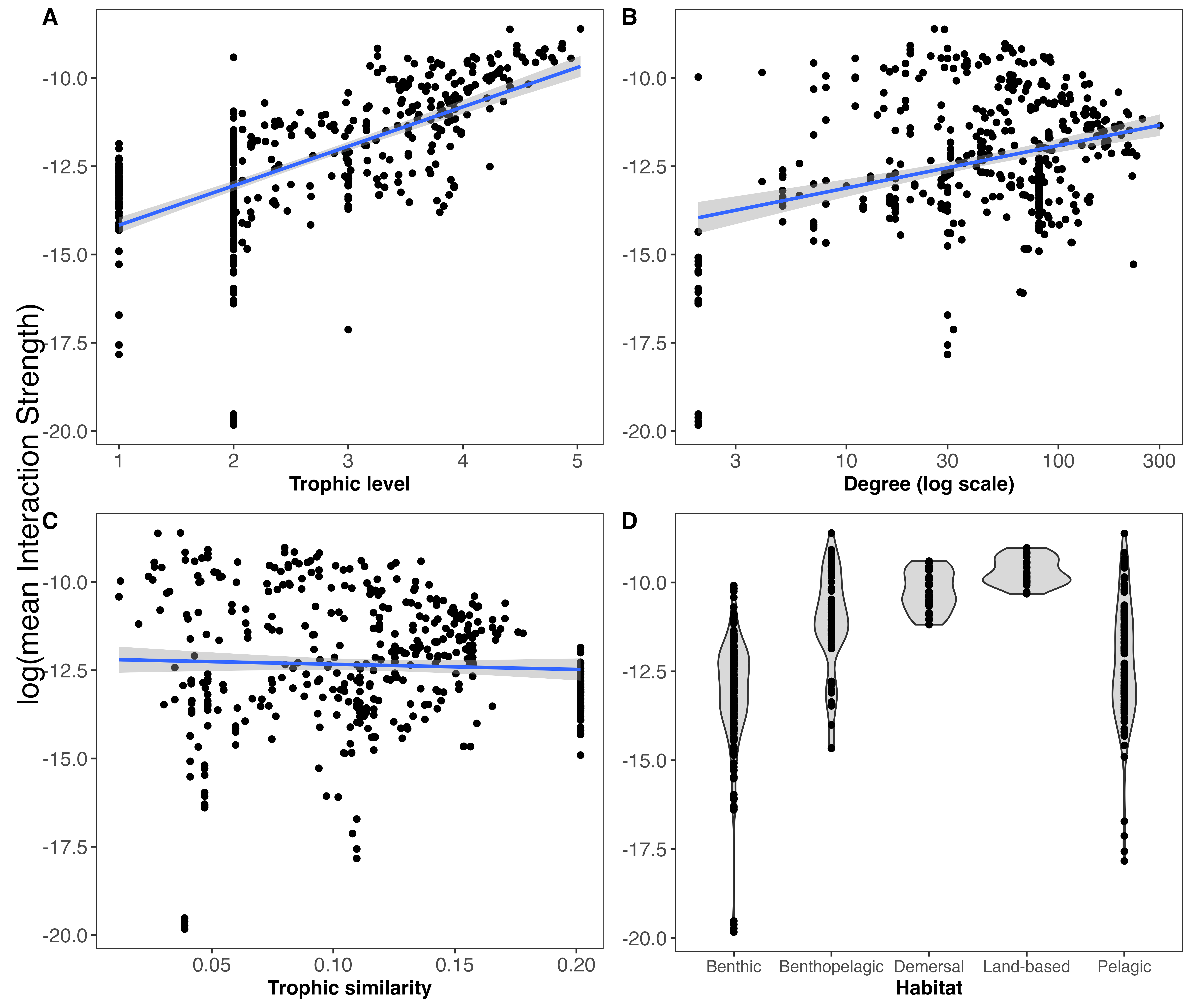


Figure 4. Relationships between weighted (mean Interaction Strength) and unweighted properties including habitat. Linear regressions are shown between log(mean interaction strength) and trophic level (A), degree (B) and trophic similarity (C). Linear regressions for trophic level (), degree () and trophic similarity ().

**Species impact on food web stability**

It’s important to note that since the proportion of Jacobians that were locally stable or QSS was zero for the Weddell Sea food web, we considered the mean maximum eigenvalue as the stability index.

Our extinction analyses showed that the majority of species had no significant impact on food web stability after being removed (Figure 5). Most of the species (black points in figure 5) do not change stability of the network considerably after being removed. Except for a few species. Only 15 out of 490 species (3.06%) gave rise to significant changes in the food web’s stability after their removal (Table 2). Most of these species had a positive impact on food web stability, i.e., network stability increased after their removal. Only two species significantly decreased network stability after being removed, the demersal fish *Pagetopsis macropterus* and the benthopelagic amphipod *Maxilliphimedia longipes*.

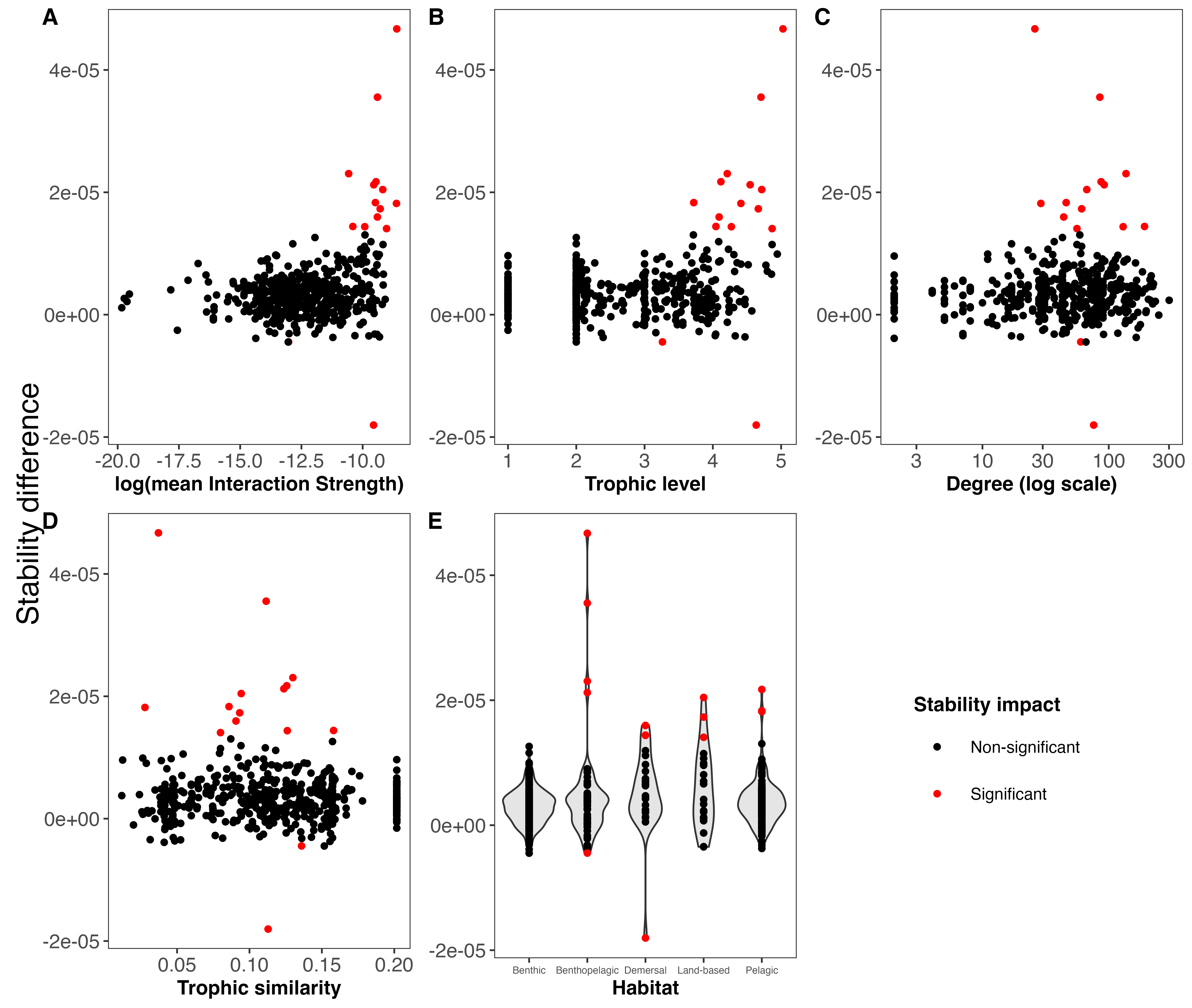


Figure 5. Quasi-Sign Stability (QSS) difference between the whole Weddell Sea food web (n = 490) and the food web without one species (n = 489) for weighted (interaction strength) and unweighted species properties, and habitat. Point color indicates the impact on the QSS; if significant the extinction of that species altered the stability (QSS) of the food web.

After exploring the stability difference against the species properties (Figure 5), we found that those species that generated a significant impact on the stability of the food web were characterized by: 1) high mean interaction strength; 2) mid to high trophic levels (TL > 3.2); 3) relatively high number of interactions (Degree > 25); and 4) mid to low trophic similarity (TS < 0.16). Habitat wise, species with a significant impact on the stability were present in all habitats, except for the benthic realm. Table 2 shows these results for such species.

Properties of the species that when become extinct generated a significant impact on the stability of the Weddell Sea food web, ordered by significance (Anderson-Darling p-value). References: meanIS = mean interaction strength, TL = trophic level, Deg = degree, TS = trophic similarity, StabDif = stability difference, ADvalue = Anderson-Darling p-value.

| Species | MeanIS | TL | Deg | TS | Habitat | StabDif | ADvalue |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Orcinus orca | 0.0001825 | 5.03 | 26 | 0.037 | Benthopelagic | 4.67e-05 | 2.0000e-41 |
| Macrourus holotrachys | 0.0000830 | 4.70 | 85 | 0.112 | Benthopelagic | 3.55e-05 | 2.7314e-23 |
| Pagetopsis macropterus | 0.0000708 | 4.64 | 76 | 0.113 | Demersal | -1.80e-05 | 2.3777e-12 |
| Abyssorchomene nodimanus | 0.0000256 | 4.21 | 137 | 0.130 | Benthopelagic | 2.30e-05 | 8.5197e-10 |
| Dissostichus mawsoni | 0.0000782 | 4.12 | 87 | 0.126 | Pelagic | 2.17e-05 | 1.5670e-09 |
| Macrourus whitsoni | 0.0000714 | 4.55 | 92 | 0.124 | Benthopelagic | 2.12e-05 | 3.3043e-08 |
| Hydrurga leptonyx | 0.0001031 | 4.72 | 67 | 0.094 | Land-based | 2.04e-05 | 9.6647e-06 |
| Mesonychoteuthis hamiltoni | 0.0001802 | 4.41 | 29 | 0.028 | Pelagic | 1.82e-05 | 4.5869e-05 |
| Champsocephalus gunnari | 0.0000762 | 3.72 | 46 | 0.086 | Pelagic | 1.83e-05 | 6.7872e-05 |
| Notothenia marmorata | 0.0000827 | 4.09 | 44 | 0.091 | Demersal | 1.60e-05 | 1.2256e-04 |
| Arctocephalus gazella | 0.0000928 | 4.67 | 61 | 0.093 | Land-based | 1.73e-05 | 2.0857e-04 |
| Trematomus pennellii | 0.0000304 | 4.04 | 192 | 0.158 | Demersal | 1.44e-05 | 1.0022e-03 |
| Mirounga leonina | 0.0001203 | 4.87 | 56 | 0.080 | Land-based | 1.41e-05 | 1.2783e-03 |
| Notothenia coriiceps | 0.0000494 | 4.27 | 130 | 0.126 | Demersal | 1.44e-05 | 1.6612e-03 |
| Maxilliphimedia longipes | 0.0000022 | 3.26 | 60 | 0.136 | Benthopelagic | -4.50e-06 | 9.7397e-03 |

## Discussion

**Many weak and a few strong interactions**

Our analyses show that the distribution of species interaction strength at the network level is asymmetric, i.e., the Weddell Sea food web contains many weak interactions and only a few strong ones. This finding is many evious, Kortsch et al. 2021Te asymmetric in food webscommunities()to date comprising . This finding reinforces the call for the inclusion of interaction strength in food web studies to better understand the ecosystem functioning, and species and whole network responses to environmental perturbations.

**Species network role related to their mean interaction strength**

We employed a range of descriptors using both unweighted and weighted food web properties to characterise the dynamic and multifaceted nature of the Weddell Sea food web. Our results show a positive relationship between interaction strength and trophic level, and between interaction strength and species degree. Mean interaction strength increases with trophic level and species degree. The former relationship might contradict those studies that suggest that mid-trophic level species are involved in the major pathways of energy flow in high-latitude marine ecosystems (**Pinkerton2014?**; Murphy et al. 2016; **McCormack2020?**; Riccialdelli et al. 2020). This could be explained by the lack of species biomass data in our interaction strength estimations; the methodology we applied here (Pawar, Dell, and Van M. Savage 2012) allows to include empirical data for the density of the resource, though not for all food web species. Unfortunately, the lack of individual data for the entire Weddell Sea food web hampers any alternative approach. On the other hand, the positive relationship between interaction strength and degree reinforces the importance of species with many interactions: species with high degree (hubs) have a large impact on overall food web structure and functioning (Dunne, Williams, and Martinez 2002a; Kortsch et al. 2015). In the Weddell Sea, species with high degree also tend to have high mean interaction strengths. This information on the quantity and quality of interactions and its relationship enables a robust assessment of the species’ role in the stability of the food web (Cirtwill et al. 2018).

**Species impact on food web stability**

According to the quasi-sign stability index employed in this study, only a few species play a key role with respect to food web stability. other n These are characterized bya set of food webs:to rIn a previous study on for the Weddell Sea food web, it was found t-sized ouldsalso was hence ed top-down This conclusion is further reinforced by the finding that have which sn a , it wascommunitiess (Murphy et al. 2016)Here we eof species impact on food web robustness by ing ( pelagic and). This suggests that the sensitivity of marine polar ecosystem to environmental perturbations is a concern also beyond the pelagic realm.

It’s also noteworthy, that our study is the first of its type to consider the dimensionality of the interaction (2 or 3 dimensions) to estimate predator-prey relationships within a food web framework. After analysing more than 2900 predator-prey interactions from several ecosystems, Pawar, Dell, and Van M. Savage (2012) concluded that interaction dimensionality is a critical factor driving consumer-resource dynamics, which will lead to better predictions of food web and ecosystem functioning. This arises as crucial to better understand how a complex system such as the Weddell Sea might respond to environmental change, which is an ongoing issue in that region of the Antarctic (Gutt et al. 2022 and references herein).

## Conclusions

Our study goes beyond the current understanding of how species influence ecosystem structure and stability in the Weddell Sea in particular and in most polar regions in general (Murphy et al. 2016; McCormack et al. 2021). In the same analysis we have integrated information about weighted (interaction strength) and unweighted species properties, enabling a more complete assessment of the food web structure and function, likely highlighting the ecological processes at play in the Weddell Sea ecosystem.

We consider that the information provided in this study is important for the development of effective policies and management strategies, particularly given the ongoing initiative to implement a Marine Protected Area (MPA) in the Weddell Sea (Teschke et al. 2021).

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