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New insights into the Weddell Sea ecosystem applying a quantitative 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 analysed the Weddell Sea food web, focusing on the species and trophic interactions that underpin ecosystem structure and stability. We estimated the strength for each interaction in the food web, characterised species position in the food web using unweighted and weighted food web properties, and analysed species' roles with respect to the stability of the food web. We found that the distribution of the interaction strength (IS) at the food web level is asymmetric, with many weak interactions and few strong ones. We detected a positive relationship between species mean IS and two unweighted properties (i.e., trophic level and the total number of interactions). We also found that only a few species possess key positions in terms of food web stability. These species are characterised by high mean IS, mid to high trophic level, relatively high number of interactions, and mid to low trophic similarity. In this study, we integrated unweighted and weighted food web information, enabling a more complete assessment of the ecosystem structure and function of the Weddell Sea food web. Our results provide new insights, which are 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.

1 Introduction

Food web analysis constitutes an important framework for understanding ecological community structure and for conserving biodiversity through ecosystem management (Thompson et al., 2012). Although topological food web analysis, which considers only the presence and absence of predator-prey interactions, provides important insights into the structure and functioning of ecological communities (e.g. Pascual et al., 2006; Kortsch et al., 2015; Marina et al., 2018; Cordone et al., 2020; Rodriguez et al., 2022), more information on the nature of the trophic interactions is needed to effectively characterise ecosystem dynamics and stability (e.g. Kortsch et al., 2021; Pecuchet et al., 2022). This is a fundamental step for providing assessments on ecosystem vulnerability to environmental pressures and for prioritising management actions. In this regard, quantifying the strength of trophic interactions and species' roles within the network are of paramount importance (Carrara et al., 2015; Allesina et al., 2015; Nilsson and McCann, 2016; Cirtwill et al., 2018).

Estimating interaction strength (IS) in food webs allows differentiating the importance of species interactions. On the contrary, unweighted food web representations give equal importance to all interactions well-knowing that some species interactions are stronger than others and hence play a different role for ecosystem functioning and stability. Both empirical and theoretical studies show that interactions strength distributions in food webs are assymmetric (Paine, 1992; McCann et al., 1998; Emmerson and Raffaelli, 2004; Wootton and Emmerson, 2005; Kortsch et al., 2021), containing a few strong and many weak interactions. This asymmetric patterning of weak and strong links is crucial to food web stability (Paine, 1992; McCann et al., 1998; Neutel et al., 2002). In a recent paper on an aquatic food web it was further highlighted that temporal changes in ecosystem functioning could only be predicted using weighted food web structure (Kortsch et al., 2021). Hence, in order to assess the stability and functioning of a food web, it is important to first determine the quantitative structure of the trophic network.

Several methodologies have been applied to estimate IS in food webs, where the quantity and quality of the data mostly determines which approach is the most convenient (Berlow et al., 2004). Approaches include experimental methods combined with dynamic modelling (Emmerson and Raffaelli, 2004; Carrara et al., 2015), measurements of species abundances through time (Fahimipour and Hein, 2014; Chang et al., 2021), and estimation of metabolic rates and biomass of all species in the community (Neutel and Thorne, 2014). However, these types of methods require large experimental set-ups and parameterisations restricting the analyses to smaller networks (e.g., approximately 10 species or less). Other methods based on allometric scaling relationships and biomass information (Kortsch et al., 2021; Gauzens et al., 2019) can be applied to larger networks with less data requirements, but this comes at the expense of precision in the predictions. For even larger food webs composed of nearly 1000 species and more than 10000 interactions, only methods with even less data requirements are feasible. One of these methods, proposed by Pawar et al. (2012), combines data on consumer and resource body masses and consumer search space (interaction dimensionality) to obtain IS estimates for each pairwise predator-prey interaction. An advantage of this method is that it can be applied without information on species biomass.

Using a a network approach, different types (e.g., terrestrial, lake, marine) of food webs from various geographic locations are studied worldwide, including marine polar food webs (Carscallen and Romanuk, 2012; de Santana et al., 2013; Kortsch et al., 2019; Pecuchet et al., 2022). Some of the studies from the Arctic show how food web properties (e.g., connectance) are constrained by environmental factors such as sea ice cover and seawater temperature (Kortsch et al., 2019; Pecuchet et al., 2022). In the Southern Ocean, important insights have been gained into mechanisms of energy flow, the relative importance of individual species and their traits, and the influence of environmental variables (e.g., sea-ice) on the structure of local food webs (Cordone et al., 2020; Rossi et al., 2019). For instance, in Potter Cove (West Antarctic Peninsula) the substratum type (i.e. hard/soft or rocks/sediments) plays a significant role in the structure and stability of the food web. In Terra Nova Bay (Ross Sea), the architecture of biodiversity was reshaped by the pulsed input of sympagic food sources following sea-ice break up, with food web simplification, decreased intraguild predation, potential disturbance propagation and increased vulnerability to biodiversity loss (Rossi et al., 2019).

The Weddell Sea is expected to be one of the last regions of the Southern Ocean to experience the consequences of climate change due to its extensive ice cover and ocean currents (Teschke et al., 2021) resulting in less sea surface warming compared to other areas of the Southern Ocean. This Sea plays an important role in driving global thermohaline circulation and ventilating the global abyssal ocean because it generates a considerable part of the Antarctic Bottom Water (Fahrbach et al., 2009). Because of these environmental characteristics, the Weddell Sea may serve as a refuge for Antarctic species which depend on sea ice (e.g. krill, emperor penguin, Weddell seal) or have low heat tolerance (e.g., most notothenoid fishes) due to their adaptations to freezing temperatures (Griffiths et al., 2017). While essential large-scale hydrodynamic relationships are relatively well-known for this region (de Steur et al., 2019), information on the current distribution, abundance and sensitivity to climate change is only partially known for a few species (e.g., emperor penguin) (Houstin et al., 2022).

The network complexity of the Weddell Sea food web is high comprising 488 species and 16200 predator-prey interactions (Jacob et al., 2011). In an attempt to better understand species roles related to food web stability, Jacob et al. (2011) performed secondary extinction experiments and found that the removal of small to medium-sized, and not large, organisms caused a cascade of secondary extinctions. This findings highlighted the relative importance of predators, rather than prey, for the architecture, functioning and stability of the Weddell Sea food web, which coincides with findings from recent meta-analyses in natural complex food webs (Brose et al., 2019; Perkins et al., 2022). Other investigations considered this food web in a meta-analysis context showing that high predator-prey body-mass ratios are found for predator groups with specific trait combinations, including small vertebrates and large swimming or flying predators (Brose et al., 2019). These trait combinations generate weak interactions that stabilize communities against perturbations maintaining ecosystem functioning.

In this study, we aim to go beyond a purely topological (presence/absence) assessment of who eats whom in the Weddell Sea ecosystem by providing a quantitative analysis of the trophic interaction network. We aim to analyse the species' role for the structure and stability of the food web. To achieve this, we: 1) estimated the strength for each interaction in the Weddell Sea food web, 2) characterised species' role considering both weighted and unweighted properties, and 3) analysed the species' role related to the stability of the food web. This is the first time that interaction strengths were estimated for all pairwise trophic interactions at the species level (except for a few) for the Weddell sea food web.

2 Methodology

2.1 Study area

The high Antarctic Weddell Sea shelf is situated between 74 and 78ºS, stretching approximately 450 km from East to West (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 benthic habitat with large benthic biomasses, intermediate to high diversity in comparison to benthic boreal communities and a spatially patchy distribution of organisms (Dayton, 1990; Teixidó et al., 2002).

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2.2 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 database 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 dimension of the predator search space (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 (Jacob et al., 2011).

2.3 Dataset analyses

2.3.1 Interaction strength estimation and distribution

To estimate the strength of each pairwise interaction in the food web, we followed an approach proposed by Pawar et al. (2012). The minimum data requirements are body mass of the consumer (predator) and resource (prey), and the interaction dimensionality (ID) classified as 2 or 3 dimensions. The ID is defined as the search space dimensions of the predator, which is also equivalent to the movement space of the prey. Thus, the ID is classified as 2D when both predator and prey move in 2D (e.g., both are benthic) or if a predator moves in 3D and a prey in 2D (e.g., pelagic predator on benthic prey). The ID is classified as 3D when both predator and prey move in 3D (e.g., both pelagic) or if the predator moves in 2D and the prey in 3D (e.g., benthic predator, pelagic prey) (Pawar et al., 2012). 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 predators and prey included in GATEWAy.

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

$$IS = \alpha x_R \frac{m_R}{m_C} \qquad (1)$$

where $\boldsymbol{\alpha}$ is the search rate, $\boldsymbol{x_R}$ is the resource density, and $\boldsymbol{m_R}$ and $\boldsymbol{m_C}$ are the body mass for the resource and the consumer, respectively (Pawar et al., 2012).

We obtained estimates for resource density and the search rate from the scaling relationships with the resource and the consumer mass, respectively (Pawar et al., 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 different 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 of dead or senescent phytoplankton reaching the

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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 IS distribution using maximum likelihood (McCallum, 2008), and selected the best fitting model by computing the Akaike Information Criterion AIC (Burnham and Anderson, 2002).

2.3.2 Species properties

To characterise 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 et al., 2002a; Borrelli and Ginzburg, 2014). In contrast, weighted properties capture the importance of a trophic interaction by considering its strength.

To assess species roles as a function of the weighted food web, we focused on mean IS defined as the average strength of all interactions for a given species. Further we calculated three unweighted species properties: a) species degree, i.e., the sum of in- and out-going interactions ; b) trophic level ; and c) trophic similarity, i.e., the trophic overlap based on shared and unique resources and consumers. These metrics were chosen to assess a species role based on the unweighted network. The species degree has often been equated with species importance to the structure and functioning within a food web, i.e. perturbations to high-degree species may therefore have more significant effects on the food web robustness to perturbations than low-degree species (Dunne et al., 2002b; 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 species habitat affiliation into account, which describes the physical position of a species within the ecosystem. Species were categorised 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 aforementioned 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 affiliations were retrieved from Jacob et al. (2011).

To study the relationship between species mean IS (weighted property) and the unweighted species properties, we performed linear regression analyses between the log mean IS and each of the aforementioned unweighted properties. Thus, we considered the IS as the dependent variable and the given unweighted property as the independent variable, and obtained the coefficients (slope and intercept) for the linear model. Models were fitted using the least squares approach. We also explored the mean IS distribution with the species habitat.

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

2.3.3 Extinction simulations and stability

To analyse 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 removed species (489 nodes) and compared it with that of the whole network (490 nodes in total). To calculate stability, we used the mean of the real part of the maximum eigenvalue of the Jacobian matrix using randomized Jacobians, keeping the predator-prey sign structure fixed (Allesina and Pascual, 2008; Grilli et al., 2016). This stability index indicates a more stable food web when it is negative. We performed 1000 simulations for each species removal and obtained a mean maximum eigenvalue for each case. Finally, we statistically analysed this difference with an Anderson-Darling test considering a p-value < 0.01 (Scholz and Stephens, 1987). If the difference between the networks without and with the removed species is positive, then the stability of the whole food web is higher without the targeted species, in other words this species makes the network less stable. If the difference is negative, then the stability of the whole food web is lower without the targeted species, i.e., this species ahs a stabilizing effect. A detailed description on the stability calculations can be found in the supplementary material.

To identify the species with the highest effect on food web stability and their characteristics, we plotted the results of each species' extinction and its effect on food web stability (the stability difference) against weighted (interaction strength), and the three unweighted properties (trophic level, degree, and trophic similarity), and species habitat affiliation.

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

3 Results

3.1 Interaction strength distribution

The statistical distribution that best fitted the empirical interaction strength distribution of the Weddell Sea food web was a 'gamma' due to the high proportion of weak interactions and the existence of a few strong interactions (Figure 3, Table S3).

3.2 Species' role related to their mean interaction strength

We found that the species' mean IS (weighted property) shows different relationships with the unweighted properties analysed (Figure 4A-D). In this regard, there is a positive relationship between IS and trophic level, i.e., the higher the trophic level of the species, the higher its mean IS. We also found a significant but less evident positive relationship with species degree. Contrary, there was no significant relationship between mean IS and trophic similarity. Considering species habitat affiliation, the "Benthopelagic" and "Pelagic" categories contained the two species with the highest mean IS, the killer whale Orcinus orca and the colossal squid Mesonychoteuthis hamiltoni, respectively. However, the majority of the species with relatively higher IS belonged to the "Demersal" and "Land-based" habitats groups. Species inhabiting the benthic realm showed the lowest mean IS (Figure 4D).

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3.3 Species impact on food web stability

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) did not change the stability of the network considerably after being removed, except for a few species (red points in figure 5). Only 15 out of 490 species (3.06%) gave rise to significant changes in the food web's stability after their removal (Table 2). Network stability increased after the removal of most of these species, i.e., these species have a negative effect on stability. Only two species significantly decreased network stability after being removed, the demersal fish Pagetopsis macropterus and the benthopelagic amphipod Maxilliphimedia longipes.

After exploring the stability difference against the species properties (Figure 5), we found that the species that generated a significant impact on the stability of the food web were characterised by: 1) high mean IS; 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 the results for the species with highest impact on the food web stability.

4 Discussion

4.1 Many weak and a few strong interactions

Our analyses show that the distribution of species IS 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 consistent with many previous theoretical and empirical studies (e.g. McCann et al., 1998; Neutel et al., 2002; Emmerson and Raffaelli, 2004; Wootton and Emmerson, 2005; Kortsch et al., 2021). The asymmetric distribution of IS in food webs has been interpreted as an explanation for the persistence of complex communities in nature (Bascompte et al., 2005; Allesina et al., 2015; Nilsson and McCann, 2016). Here we show that this pattern is also prevalent in the Weddell Sea, one of the most complex food webs to date, comprising 490 species and 16041 predator-prey interactions. This finding is in someway validating the method we used, validation of allometric methods of IS estimation not including interaction dimensionality has been performed for microcosmos of relatively few species (Jonsson et al., 2018).

4.2 Species's 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 IS and trophic level, and between IS and species degree. In the Weddell Sea, species with high degree also tend to have high mean ISs. This positive relationship between IS and species degree reinforces the central role of species with many interactions: species with a high degree (hubs) have a large impact on overall food web structure and functioning (Dunne et al., 2002b; Kortsch et al., 2015). On the other hand, the positive IS-trophic level relationship contradicts studies that suggest that mid-trophic level species (e.g. krill, mesopelagic fish, squid) are involved in the major pathways of energy flow in high-latitude marine ecosystems (Pinkerton and

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Bradford-Grieve, 2014; Murphy et al., 2016; McCormack et al., 2020; Riccialdelli et al., 2020). Such contradiction could be explained by the lack of species biomass information in the calculation of IS we applied here (Pawar et al., 2012). Although this methodology allows information on species biomass or density to be included, this type of data was not available for the majority of species of the Weddell Sea food web.

Overall, the combination of 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).

4.3 Species impact on food web stability

Only a few species play a key role with respect to the Weddell Sea food web stability, according to the stability index employed in this study. This is in concordance with other studies on complex empirical food webs in marine ecosystems in the Arctic and other locations in Antarctica (Kortsch et al., 2015; Marina et al., 2018; Rodriguez et al., 2022). These key species are characterised by a particular set of food web properties: high to mean IS; mid to high trophic level; a relatively high number of interactions; and mid to low trophic similarity. In a previous study on sequential extinction simulations for the Weddell Sea food web (Jacob et al., 2011), it was found that larger bodied-sized species could be lost without causing a collapse of the network. A major caveat of this finding, also recognised by the authors, was that population dynamics were ignored and hence no top-down extinctions, or other indirect effects, could occur. In our study we considered such top-down effects by including information on the species IS, which is of paramount importance when analysing the response of perturbations in ecological communities (McCann et al., 1998; Montoya et al., 2009; Novak et al., 2011). Thus, our study suggests that species with high mean IS and high trophic levels need to be considered with particular attention when trying to predict the effects of perturbations on the Weddell Sea ecosystem. This conclusion is further reinforced by the finding that these species have mid to low trophic similarity, which means that few other species of the food web can occupy the same trophic role. In a review, it was emphasised that polar pelagic communities are particularly sensitive to changes due to a low functional redundancy at key trophic levels (Murphy et al., 2016). Here we provide a broader analysis of the species impact on food web robustness by including species from all habitats (benthic, pelagic and land-based). This suggests that the sensitivity of marine polar ecosystems to environmental perturbations is a concern also beyond the pelagic realm.

5 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 integrated information on weighted (IS) and unweighted species properties, enabling a more complete assessment of species' role with respect to food web structure and stability. Futher, tha analyses allowed us to identify species and their characteristics which can have a destabilising or stabilising effect on the food web.

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 region (Teschke et al., 2021).

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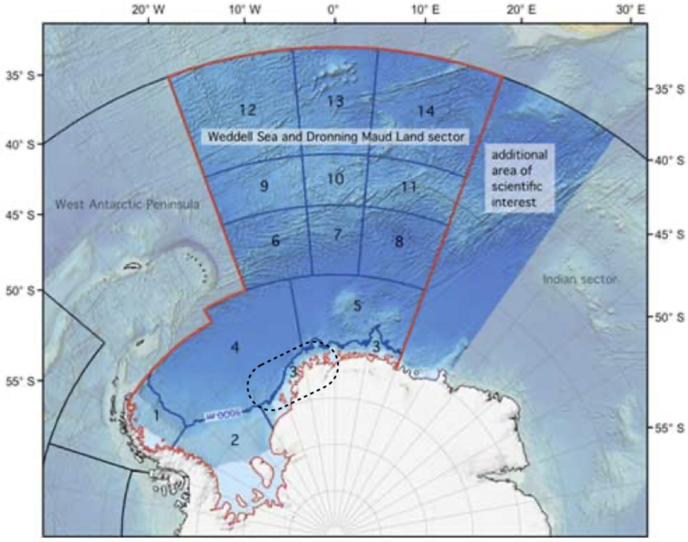

Figure 1. Map of the Weddell Sea and Dronning Maud Land sector highlighting the high Antarctic shelf as a dashed-line contour. Modified from www.soos.aq.

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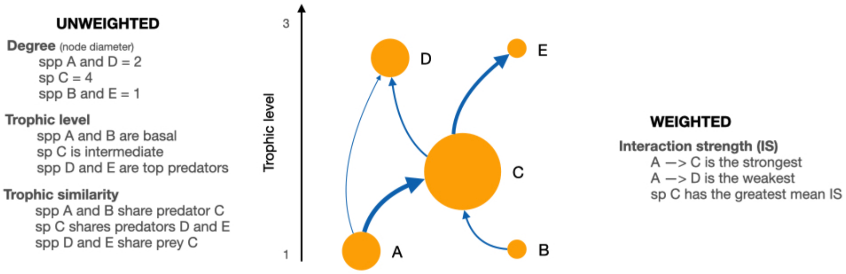

Figure 2. Scheme of a network showing the weighted and unweighted properties we used to characterize the species of the Weddell Sea food web. Directed arrows indicate the flow of energy; the width of the arrow represents the interaction strength of it.

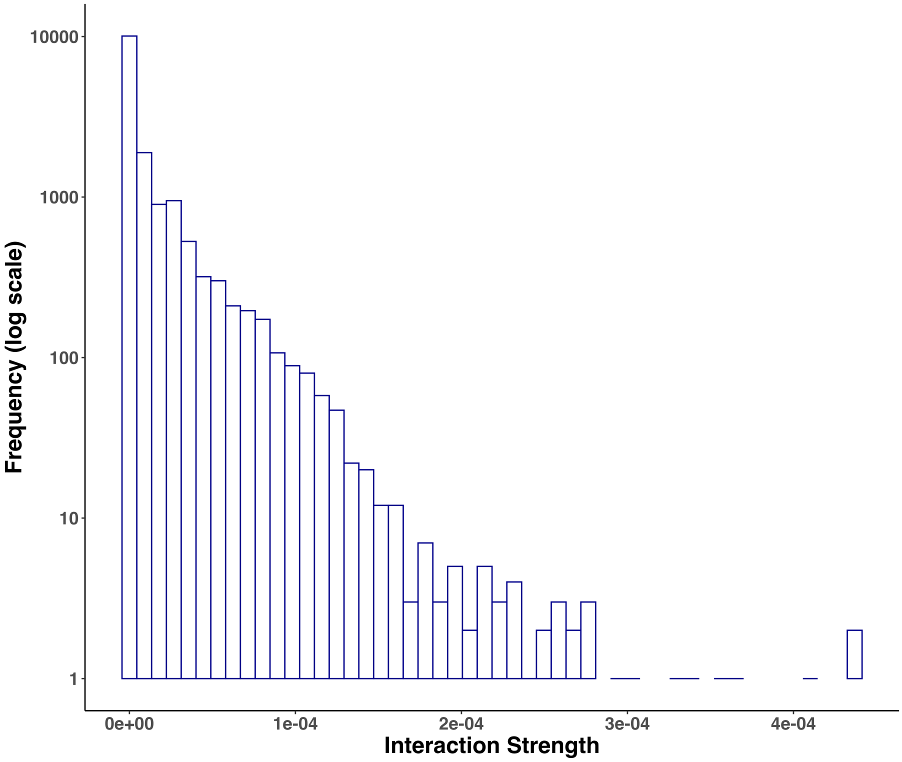

Figure 3. Frequency distribution of interaction strengths for the Weddell Sea food web. Total number of interactions = 16041. The distribution was best fitted to a 'gamma' model.

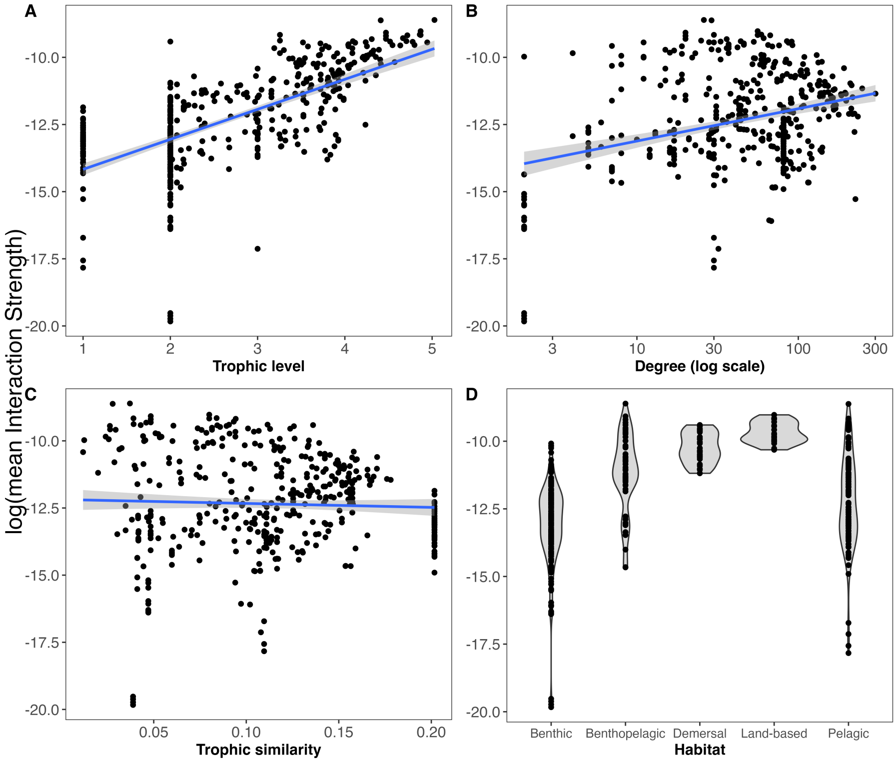

Figure 4. Relationships between weighted (mean Interaction Strength) and unweighted properties including habitat. Linear regressions are shown between log(mean interaction strength) and trophic level (A), degree (B) and trophic similarity (C). Linear regressions for trophic level ($y = 1.12x - 15.29, R^2 = 0.43, p - value < 2e - 16$), degree ($y = 0.006x - 12.77, R^2 = 0.03, p - value = 4.06e - 5$) and trophic similarity ($y = -1.46x - 12.18, R^2 = -0.0004, p - value = 0.36$).

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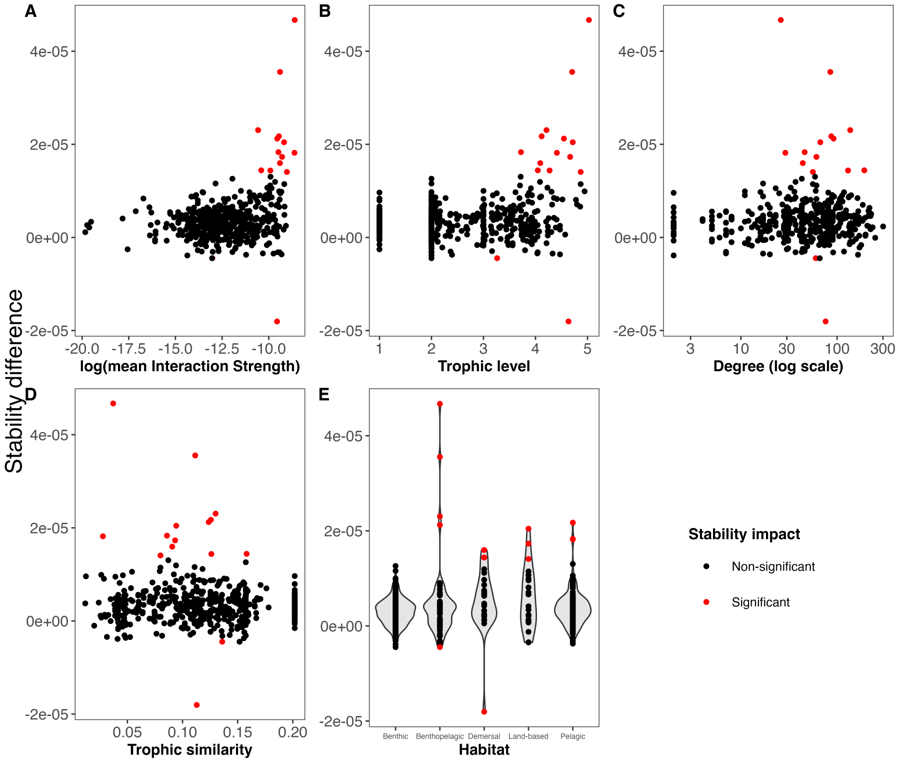

Figure 5. Stability difference (mean maximum eingenvalue) between the whole Weddell Sea food web (n = 490) and the food web minus one species (n = 489) for weighted (interaction strength) and unweighted species properties, and habitat. Point color indicates the impact on the stability; if significant the extinction of that species altered the stability of the food web.

Table 1. 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	1.83e-4	5.03	26	0.037	Benthopelagic	4.67e-5	2.28e-41
Macrourus holotrachys	8.30e-5	4.70	85	0.112	Benthopelagic	3.55e-5	2.73e-23
Pagetopsis macropterus	7.08e-5	4.64	76	0.113	Demersal	-1.80e-5	2.38e-12
Abyssorchomene nodimanus	2.56e-5	4.21	137	0.130	Benthopelagic	2.30e-5	8.52e-10
Dissostichus mawsoni	7.82e-5	4.12	87	0.126	Pelagic	2.17e-5	1.57e-9
Macrourus whitsoni	7.14e-5	4.55	92	0.124	Benthopelagic	2.12e-5	3.30e-8
Hydrurga leptonyx	1.03e-4	4.72	67	0.094	Land-based	2.04e-5	9.66e-6
Mesonychoteuthis hamiltoni	1.80e-4	4.41	29	0.028	Pelagic	1.82e-5	4.59e-5
Champsocephalus gunnari	7.62e-5	3.72	46	0.086	Pelagic	1.83e-5	6.79e-5
Notothenia marmorata	8.27e-5	4.09	44	0.091	Demersal	1.60e-5	1.23e-4
Arctocephalus gazella	9.28e-5	4.67	61	0.093	Land-based	1.17e-5	2.09e-4
Trematomus pennellii	3.04e-5	4.04	192	0.158	Demersal	1.44e-5	1.00e-3
Mirounga leonina	1.20e-4	4.87	56	0.080	Land-based	1.41e-5	1.28e-3
Notothenia coriiceps	4.94e-5	4.27	130	0.126	Demersal	1.44e-5	1.66e-3
Maxilliphimedia longipes	2.21e-6	3.26	60	0.136	Benthopelagic	-4.46e-6	9.74e-3

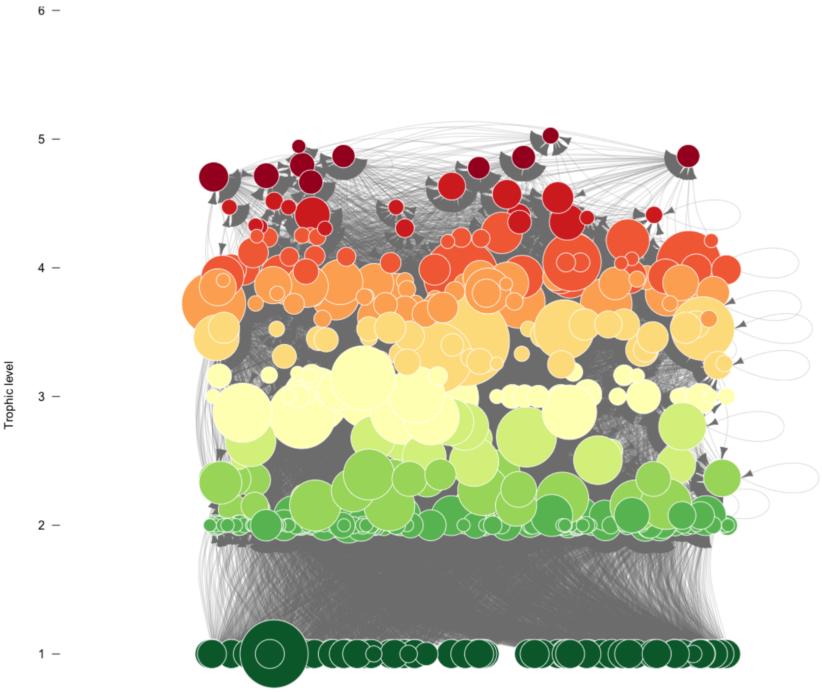

Figure A1. Graphic representation of the Weddell Sea food web. Species (nodes) are arranged vertically and colored by trophic level. The diameter of the node indicates the total number of interactions. Predator-prey interactions are represented by the arrows, from prey to predator.

. TIM and LAS: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Coding (lead); Writing – original draft (lead); Writing – review and editing (lead). SK: Conceptualization (lead); Formal analysis (supporting); Methodology (supporting); Coding (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

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