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Expanding on a marine food web using parasitological data

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ABSTRACT: Parasites comprise a significant proportion of species on Earth yet are seldom included or realistically represented in studies of food web ecology. As ecosystems continue to change in response to natural and anthropogenic pressures, it is important now more than ever to include parasites to improve our understanding of their role, now and in the future. A large-scale biodiversity survey of the coastal marine ecosystem of Otago, New Zealand, provided a unique opportunity to assess what contribution parasitological studies can make toward revealing trophic interactions between species when creating food webs. Here, we created 4 increasingly complex food web depictions of Otago and compared network properties between them to assess changes with each addition of new types of data (first excluding and then including parasite species). We also assessed how parasites influence the functioning of Otago's food web by simulating extinction scenarios for each web, estimating their robustness to biodiversity loss. The inclusion of parasites altered food web structure, such as decreasing connectance and increasing path length, modularity and species clustering. In both extinction scenarios, including parasites resulted in a lower robustness of the food webs to biodiversity loss. Our results suggest that neglecting parasite taxa in food web studies may lead to inappropriate estimates of ecosystem structure and functioning and possibly an overestimation of an ecosystem's resilience to change. Above all, we reveal the huge potential of parasitological studies to advance our understanding of predator–prey interactions.

KEY WORDS: Helminth · Cestode · Trematode · Nematode · Acanthocephalan · Food web · Trophic interactions · Trophic transmission

1. INTRODUCTION

As a result of anthropogenic and natural pressures, most of the world's ecosystems are experiencing some degree of change, including biodiversity loss (Butchart et al. 2010). To predict how natural systems might respond to ecological change, ecologists have successfully developed and employed food web analyses that provide holistic, simplified characterisations of otherwise complicated, real-world ecosystems (Cohen et al. 1990). Food web analyses have proven to be powerful tools in advancing our understanding of how ecosystems will change in response to imminent climatic pressures (Dunne et al. 2002, Bascompte & Jordano 2007, Neutel et al. 2007, Blanchard 2017).

However, before any kind of food web analysis can be performed, it is essential to have knowledge of the ecological interactions among species occurring within a given ecosystem. Considering that parasites comprise the majority of metazoan species on Earth and are present in all of the world's ecosystems (Poulin & Morand 2004), it seems reasonable to expect them to be at the forefront of food web studies, or at least be included to some degree. However, most traditional food web characterisations ignore or severely underrepresent parasitic organisms (Cohen et al. 1993, Marcogliese & Cone 1997, Lafferty et al. 2006). Not only are parasites extremely biodiverse, but combined research over the last 2 decades overwhelmingly supports the idea that parasites must be accounted for

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in order to achieve resolution of how ecosystems are structured and function (Thompson et al. 2005, Lafferty et al. 2006, 2008, Wood et al. 2007, Hernandez & Sukhdeo 2008, Kuris et al. 2008, Thieltges et al. 2008, Amundsen et al. 2009, Sato et al. 2012, Dunne et al. 2013, Morton & Lafferty 2022). The lack of parasite inclusion in ecosystem-level food webs can be attributed to the fact that parasites are smaller than and often hidden within their hosts, making their presence and trophic interactions difficult to quantify compared to those of free-living animals. Many parasites have complex life cycles, including multiple life stages within different hosts that are morphologically not comparable, making their interactions difficult to track without the use of genetic tools (Blasco-Costa & Poulin 2017, Bennett et al. 2023). Additionally, the term 'parasite' accounts for wide-ranging taxa of multiple phyla. Without significant taxonomic expertise pertaining to groups of interest, resolution of parasite biodiversity is likely to be misrepresented, leading to inappropriate assessment of trophic interactions and food web properties (Martinez 1991, Thompson & Townsend 2000). For emerging food web properties to be comparable between ecosystems and through time, a larger number of well-resolved, parasite-inclusive food webs are needed to validate current views on the structure and functioning of natural systems.

Aside from its contribution to the structure and functioning of food webs, parasitological studies can provide unique insights into what predator–prey interactions are present in ecosystems, indirectly filling the gaps in our knowledge of food web dynamics (Sukhdeo 2010, Valtonen et al. 2010, Bennett et al. 2023). For instance, the presence of a larval parasite within an intermediate host and that of an adult parasite of the same species within a definitive host provides evidence of a feeding link or transmission pathway between the 2 hosts.

The aims of this study are to (1) estimate the contribution of parasitological research in characterising trophic interactions within a coastal ecosystem and (2) characterise the structure and functioning of the ecosystem using increasingly complex versions of a food web. The ecosystem we used to explore these aims is the Otago coastal marine ecosystem (OCME), geographically defined by the Otago's Regional Council (ORC 2012). Otago has been the focus of various parasitological investigations in the past (e.g. Koehler & Poulin 2010, Bennett et al. 2022a,b). A large-scale biodiversity survey in Otago between 2019 and 2021, with a particular focus on helminth parasites (acanthocephalans, cestodes, nematodes and trematodes) infecting wide-ranging host taxa (seabirds, marine mammals, teleost fish, chondrichthyans and invertebrates), provided an opportunity to investigate how parasitology may contribute to uncovering ecological interactions, and the role of parasites in the structure and functioning of a large marine ecosystem. To achieve this goal, we created a series of increasingly complex depictions of OCME, first excluding and then including parasite taxa, and then used various food web properties to assess how parasites influence the structure of OCME. To assess how parasites influence the functioning of the food web, we compared the food web's ability to withstand biodiversity loss under different extinction scenarios, both including and excluding parasites.

2. MATERIALS AND METHODS

2.1. Parasite collection and identification

Between June 2019 and August 2021, a total of 6826 individuals from 167 animal species were dissected with the aim of characterising helminth biodiversity within Otago's coastal marine ecosystem. The OCME includes animals living in the foreshore, seabed, coastal water and air space above the water from the Waitaki River to the north of Wallace Beach as defined by the Otago Regional Council (ORC 2012). Host taxa investigated included 81 species of vertebrates (31 seabird species, 40 teleost fish species, 9 elasmobranchs species and 1 marine mammal species; see Table 1 of Bennett et al. 2022a) and 87 invertebrate species (see Bennett et al. 2022b for list of invertebrate species investigated). Vertebrates were obtained deceased as by-catch or as a by-product of other research, except for a few inter- and sub-tidal fish species collected using hand nets and euthanized under a University of Otago animal use permit (No. AUP-19-190).

Hosts were defrosted if frozen or dissected fresh. Host tissues that were dissected differed depending on taxa. For teleost fish and elasmobranchs, gills, gill arches, muscle tissue, gastrointestinal tract and internal organs were removed and dissected. For seabirds, gastrointestinal tracts and, in some cases, lungs or eyes were removed and dissected. For the single marine mammal sampled, only the gastrointestinal tract was available for dissection. Invertebrates were examined for parasites either by total dissection or by being squashed under a glass slide depending on their size.

Larval and adult parasites considered here included helminths with complex life cycles, i.e. digenean trematodes, nematodes, acanthocephalans and cestodes. Parasites were identified to the lowest taxonomic level possible with the use of molecular and morphological tools, and some of their species-level identities are or will be explored in other publications (See Bennett et al. 2022a,b, Bennett et al. 2023 for details).

2.2. Food web data sets

Four food webs of increasing complexity and resolution were created to depict the trophic interactions within Otago's coastal marine food web from different data sources, independent of Mouritsen et al. (2011)'s depiction of Otago's mudflat food web. Food webs were generated using Gephi (Bastian et al. 2009) and in R v.4.0.1 (R Core Team 2020). Here, each food web consisted of a set of entities called 'nodes', with pairs of nodes connected by 'links'. Each node represents a species, or the lowest taxonomic level possible based on available data (family or genus level in some cases), and each link represents a trophic interaction between 2 nodes (i.e. one species derives energy from another). The different life stages of parasitic helminths infect (and feed on) completely different host taxa; here, all life stages of the same species were treated together as a single node. All nodes and links included in each food web created are listed in the Supplement at www.int-res.com/articles/suppl/m727p019_supp.xlsx.

2.2.1. Food Web 1

This food web included predator–prey interactions inferred from diet studies of free-living species occurring off the coast of Otago or the surrounding area, including data from Allum & Maddigan (2012), Augé et al. (2012), Bennett & Randhawa (2019), Cruz et al. (2001), Fea et al. (1999), Flemming et al. (2013), Graham (1938), Hanchet (1991), Harcourt et al. (2002), Heather & Robertson (2015), Imber (1999), James & Stahl (2000), Lalas (1977, 1983), Lalas &Webster (2014), McKinlay et al. (2014), McKinnon (2007), Miller et al. (2013), Mills (2013), O'Driscoll (1998), Robertson (1992) and van Heezik (1990). For instance, if a species of shark was reported as having a crustacean species present in its gut contents or was observed consuming a crustacean species in nature, then we considered that a predator–prey interaction existed between the shark and crustacean. In some cases, diet data for animals studied outside Otago was included if it was considered plausible that individuals may frequent Otago in their lifetime. Some dietary links between low trophic level nodes (i.e. various invertebrates) and basal nodes (i.e. phytoplankton, plants and organic detritus) were inferred to minimise biases in the analysis regarding the disparity in links between high trophic level nodes and lower trophic level nodes, as done in previous studies (e.g. Lafferty et al. 2006). While we acknowledge that this presents an oversimplification of some trophic interaction between species (Pringle & Hutchinson 2020), it presents the first step towards a resolved food web for Otago.

2.2.2. Food Web 2

This food web included predator–prey interactions inferred from diet studies (Food Web 1), and from parasite data, excluding the parasitic taxa themselves. For instance, if the larva of a parasite species was found in one host species and the adult of the same parasite species was documented from another host species, this suggests that the second host consumes the first; there is a trophic interaction between the 2 hosts. It was not always possible to identify which free-living species serve as intermediate or paratenic hosts, and therefore any potential transmission route that revealed a feeding interaction between 2 hosts was considered real for the purpose of this study to quantify the potential that parasitological links can help infer trophic interactions. Predator–prey interactions inferred both from parasitological studies in the literature and the current biodiversity survey were included.

2.2.3. Food Web 3

This food web included predator–prey interactions inferred from diet and parasite data (Food Web 2) with the addition of parasite species as nodes themselves. Here, parasite–host interactions are depicted in the same way as predator–prey interactions (as parasites derive energy from the hosts they infect). Parasite species included those recovered from the current biodiversity survey and those already known to infect animals in Otago (except for some species either without taxonomic resolution to species level and/or without molecular data to validate their identity) (For the complete list, see Supplement 1). As it is not realistic that animals have parasite links and no prey links (except for basal species), we excluded nodes in Food Web 3 if they only had parasite–host interactions known.

2.2.4. Food Web 4

This food web included predator–prey interactions inferred from diet and parasite data, including parasites as nodes (Food Web 3), with the addition of concomitant predation interactions. Concomitant predation involves a predator–prey interaction resulting from a predator (which is not a suitable next host in a parasite's life cycle) consuming an infected host, consequently also consuming and digesting the prey's parasites. This type of trophic interaction can be important, as parasite biomass within intermediate hosts can be significant, such that when predators consume infected prey, a substantial portion of their food intake can comprise parasites (Kuris et al. 2008, Thieltges et al. 2013), and those parasites can be nutrient-rich (McKee et al. 2020). While we acknowledge that Food Web 4's depiction of Otago's food web is ultimately incomplete due to under-sampling of free-living species, lack of information on predation on free-living parasite stages and the fact that many parasites are known from only one stage of their complex life cycles, this version provides the most realistic characterisation of trophic interactions between species in Otago to date.

2.3. Contribution of parasitology to understanding food web dynamics

To estimate the contribution of parasitology to filling gaps in our knowledge of predator–prey interactions within natural systems, we calculated the proportion of interactions inferred from diet data compared to parasitological data for Food Web 2 (excluding interactions that were inferred for low trophic level and basal nodes). Next, we calculated the proportion of interactions of Food Web 4 (the most resolved food web depicting OCME) from each data source: predator–prey interactions inferred from studies on the diet of free-living animals (Food Web 1), predator–prey interactions inferred from studies on the parasitology of free-living animals (Food Web 2), parasite–host interactions inferred from studies on the parasitology of free-living animals (Food Web 3) and predator–parasite interactions inferred from studies both the diet and parasitology of free-living animals (Food Web 4).

2.4. Food web properties

To estimate the changes in food web structure with increasingly complex food web depictions of Otago, we measured and compared several network properties central to food web theory for each food web version. Each property was calculated using Gephi v.0.9.3 (Bastian et al. 2009) or in R v.4.0.1 (R Core Team 2020), using RStudio v.1.3.959 (RStudio Team 2020) implementing the packages 'foodweb' (Perdomo et al. 2012) and 'NetworkExtinction' (Corcoran et al. 2019). To test for statistically significant differences in the properties *CL*, *AD* and *EC* (defined below) among food webs, non-parametric Kruskal-Wallis rank sum and pairwise Wilcoxon rank sum tests were performed in R with the packages 'stats' and 'graphics', using default parameters (R Core Team 2020). Some network properties may be overestimated, as they are not strictly independent across food webs (i.e. many species are included in multiple food webs), although here they are treated as such.

Connectance (*C*) (Fig. 1a). *C* is a measure of the complexity of a food web estimated by the proportion of potential trophic links that actually occur within a food web: $C = L/S^2$ where *S* is the number of nodes and *L* is the number of links.

Link density (*L/S*) (Fig. 1b). *L/S* is another measure of food web complexity, measuring the overall dietary specialisation across the whole food web as the average number of incoming links per species.

Average node degree (*AD*) (Figure 1b). *AD* is the average number of species with which any node interacts, either as a consumer or resource. Unlike *L/S*, where all interactions are only counted once, *AD* accounts for the number of links that each trophic species is involved in.

Characteristic path length (*D*) (Fig. 1c). This is defined as the average number of links required to connect all pairs of nodes in a food web (Williams et al. 2002). *D* can be used as a proxy for how large a network is, with a larger value implying a longer route required for energy to be transferred from basal to top trophic levels.

Average clustering coefficient (*CL*) (Fig. 1d). This property estimates the local interconnectedness of the network, defined by the probability that 2 nodes that are connected to the same other node are also connected to each other (Watts & Strogatz 1998, Latapy 2008). *CL* is estimated for each node that has at least 2 links and is then averaged for each food web.

Modularity (*M*) (Fig. 1e). *M* measures the extent to which the food web is divided into sub-units of highly

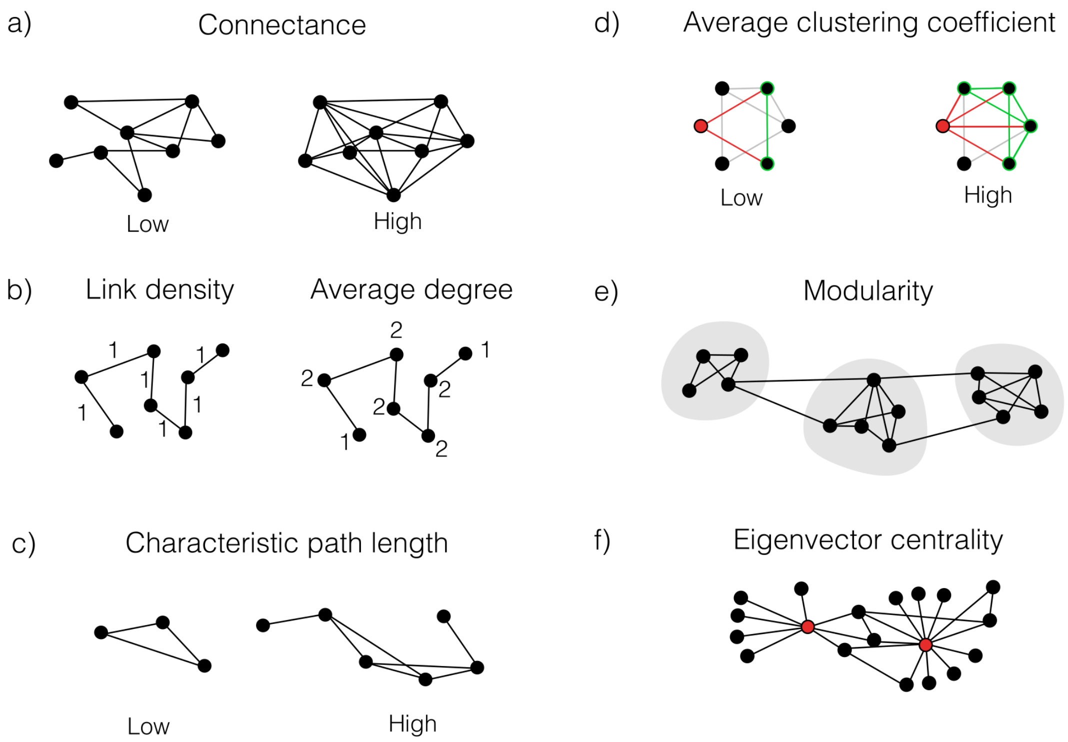


Fig. 1. Network properties (connectance, link density, average degree, characteristic path length, average clustering coefficient, modularity and eigenvector centrality) calculated for each version of Otago's coastal food web

inter-connected groups of nodes, or modules, and estimates the degree to which interactions occur more frequently within, instead of among, modules. We estimated *M* using the Louvain Modularity Algorithm as defined in Blondel et al. (2008), using a resolution parameter (Lamboitte et al. 2008) to determine the presence and number of modules in each version of OCME. Networks with high *M* values have more connections between nodes within modules and low connections between nodes among modules.

Eigenvector centrality (*EC*) (Fig. 1f). This property estimates the extent to which a node tends to occupy a central position within the food web, taking into account whether the node in question is connected to other nodes that are also highly connected themselves. Defined by Bonacich (1972) and Bonacich (1987), this measure can identify potential key nodes within the network.

Degree distribution (*DD*). *DD* describes the observed frequency distribution of the number of links per node in the food web (Estrada 2007). We fit the observed *DD* with the use of a non-linear regression using general least squares in combination with Akaike's information criterion to select the best model (power law, exponential or truncated distributions) that fit the observed *DD* for each food web version.

2.5. Extinction scenarios

To estimate how parasites contribute to the stability and functioning of the food web of which they are a component, we simulated various extinction scenarios for each version of Otago's food web using R packages 'NetworkExtinction' (Corcoran et al. 2019) and 'network' (Butts 2015) and then estimated each web version's robustness or ability to withstand species loss. Basal species were removed from each food web data set, as they are not dependent on other species for survival and their extinction is highly unlikely. Using Food Web 2 (free-living species only), Food Web 3 (including parasites as nodes) and Food Web 4 (most resolved food web including parasites and concomitant predation links), species loss was simulated by sequentially removing species under 2 scenarios: removal of species at random (50 random deletion sequences initiated for each food web) and removal of species from most connected to least connected nodes. These scenarios allow insight into the vulnerability of each food web depending on the distribution of degrees. Typically, it is expected that networks following power law distributions tend to experience higher vulnerability to the removal of the most connected nodes, whereas networks following exponential *DD* are thought to be less vulnerable to removal of the most connected species but more vulnerable to random species loss (Albert & Barabási 2002, Dunne et al. 2002, Estrada 2007, de Santana et al. 2013). In both extinction scenarios, parasites were considered as species, not as life stages, since fewer than 20% have been identified from more than one life stage within one host species.

To estimate the impact of these species' loss scenarios on food web stability, we estimated the number of potential secondary extinctions resulting from each species lost. A secondary extinction occurs when a non-basal free-living species loses all its prey items or a parasite species loses all its host species at one or more life stages. The robustness of food webs to species loss (R_{50}) was quantified as the proportion of species that had to be removed for the total loss of 50% of the species to occur (i.e. primary species removals plus secondary extinctions). R_{50} ranges from 0 to 1, with higher values representing more robust communities (i.e. the number of secondary extinctions is lower).

3. RESULTS

Otago's food web was characterised here in 4 increasingly complex depictions, first excluding (Food Web 1 and Food Web 2), and then including parasites (Food Web 3 and Food Web 4) (Figs. 2 & 3). The most resolved version of Otago's food web (Food Web 4) included 299 parasite nodes, 287 free-living nodes and almost 6000 links between species (Table 1).

3.1. Contribution of parasitology to revealing food web nodes and links

When considering only free-living species, the investigations of parasites uncovered 38% of all interactions present in Otago, compared to 62% of interactions being known due to diet studies of free-living animals (Fig. 4). This means that of the 1516 predator–prey interactions known in Food Web 4, 620 of those are only known because of parasitological investigations. When including all data in Otago's most resolved version (Food Web 4), parasite nodes were involved in 80% of all interactions between species, either as consumers or prey (Fig. 4). Of the 5937 interactions present in Food Web 4, 80% resulted from parasitological research, 15% resulted from dietary data and 5% were inferred between low trophic level species and basal nodes (Fig. 4).

3.2. Food web properties

The 4 food webs representing Otago's coastal ecosystem differed in their structural properties (Table 1, Figs. 2, 3 & 5). As more data were added to each food web, the number of species and links present increased (Figs. 2, 3 & 5). *C* was highest in Food Web 1 and Food Web 2, decreasing when parasite–host interactions were added in Food Web 3, followed by an increase when concomitant predation links were added in Food Web 4 (Table 1). *AD* (Kruskal-Wallis $\chi^2 = 133.45$, df = 3, $p < 0.001$), *CL* (Kruskal-Wallis $\chi^2 = 104.78$, df = 3, $p < 0.001$) and *EC* (Kruskal-Wallis $\chi^2 = 18.97$, df = 3, $p < 0.001$) all differed significantly between food web versions (Fig. 5). The addition of parasite–host interactions in Food Web 3 resulted in a decreased number of links between species from Food Web 1 (Wilcoxon rank-sum test, $p < 0.001$) and Food Web 2 (Wilcoxon rank-sum test, $p < 0.001$), followed by an increase in links per species observed in Food Web 4 when concomitant links were added (Wilcoxon rank-sum test, $p < 0.001$) (Fig. 5a). The *EC* measure was lower in Food Web 3 than Food Webs 1,

Table 1. Structural properties of each food web (Food Webs 1 to 4) representing Otago's coastal marine ecosystem

	Property definition	Food Web 1	Food Web 2	Food Web 3	Food Web 4
S	Number of trophic species	246	273	586	586
L	Total number of links	1202	1762	2382	5937
P_{par}	Proportion of nodes as parasites	0	0	0.51	0.51
C	Connectance	0.020	0.024	0.007	0.017
L/S	Link density	4.89	6.45	4.07	10.13
AD	Average degrees per node	9.77	12.91	8.13	20.26
D	Characteristic path length	2.47	2.44	3.03	3.34
CL	Average clustering coefficient	0.044	0.053	0.048	0.092
M	Modularity (number of modules)	0.304 (5)	0.302 (5)	0.372 (9)	0.291 (7)
EC	Average eigenvector centrality (over 100 iterations)	0.021	0.053	0.043	0.017
DD	Degree distribution	Exponential	Exponential	Power law	Exponential

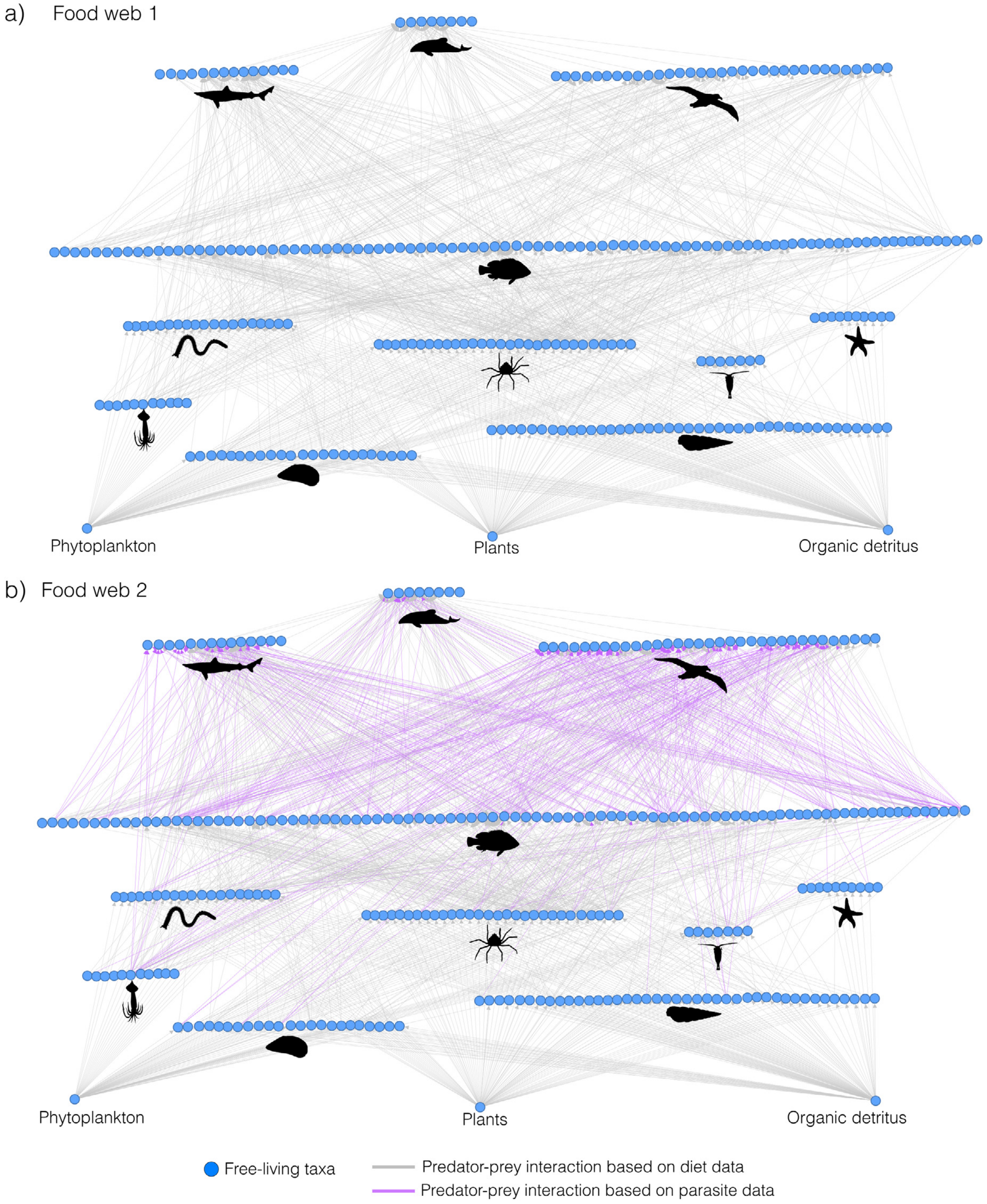
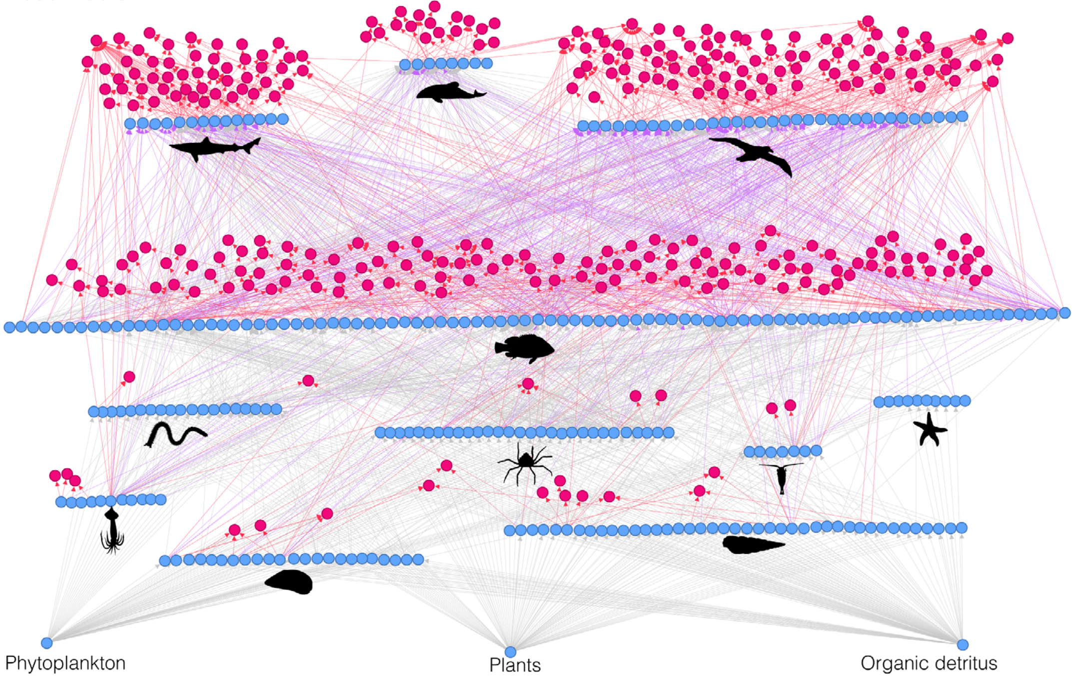


Fig. 2. (a) Food Web 1, illustrating predator–prey interactions inferred from previously published diet data (grey lines) of animals living in Otago's coastal ecosystem. (b) Food Web 2, illustrating predator–prey interactions inferred from previously published diet data and parasite data (purple lines). Blue circles: free-living taxa. Silhouettes represent host groups (left to right, top to bottom): chondrichthyans, marine mammals, seabirds, teleost fish, polychaetes, crustaceans, zooplankton, echinoderms and tunicates, cephalopods, bivalves, gastropods, phytoplankton, plants and organic detritus

2 and 4 (Wilcoxon rank-sum test, $p < 0.001$, $p = 0.045$, $p < 0.001$ respectively) (Fig. 5b). Food Web 4 had the highest clustering between species (Wilcoxon rank-sum pairwise comparisons, $p < 0.001$) (Fig. 5c). M and number of modules appeared to increase in Food Web 3, followed by a small decrease in Food Web 4.

a) Food web 3



b) Food web 4

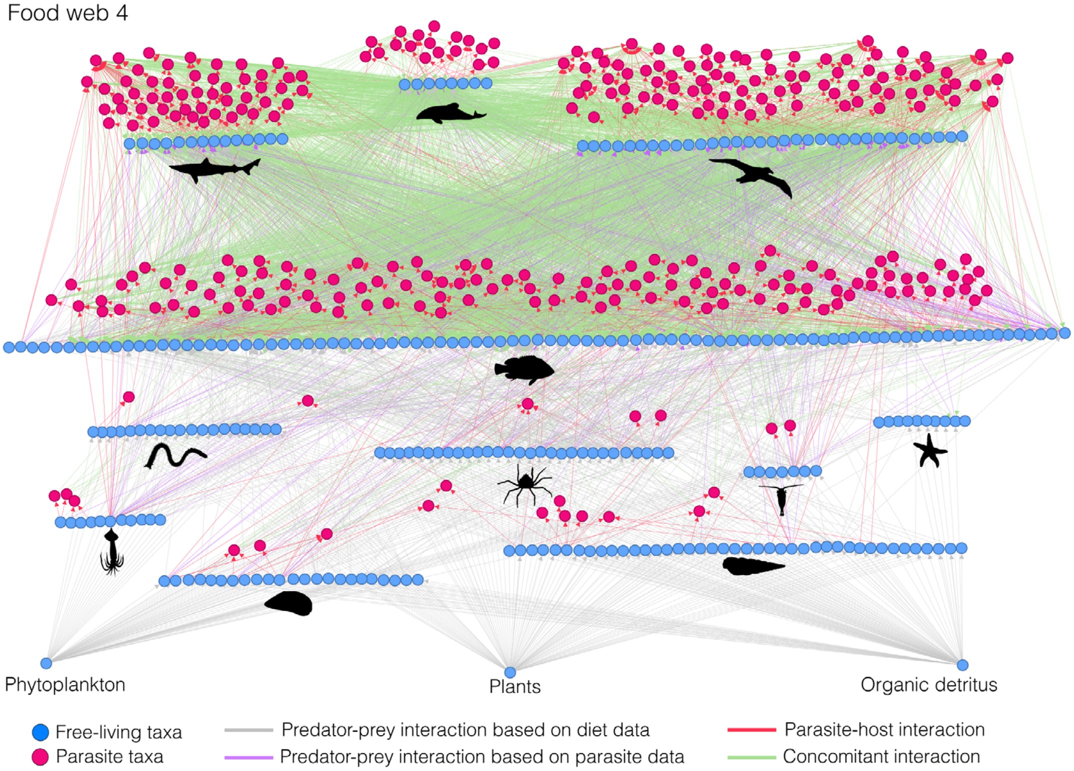


Fig. 3. (a) Food Web 3, illustrating predator–prey interactions inferred from diet (grey lines) and parasite (purple lines) data of animals living in or known to frequent Otago's coastal ecosystem and including parasites as nodes and their parasite–host interactions (pink lines). (b) Food Web 4, illustrating predator–prey interactions inferred from diet and parasite data, parasites as nodes and their host–parasite interactions, and concomitant predation links (green links). Blue circles: free-living taxa; pink circles: parasite taxa. Silhouettes represent host groups (left to right, top to bottom): chondrichthyans, marine mammals, seabirds, teleost fish, polychaetes, crustaceans, zooplankton, echinoderms and tunicates, cephalopods, bivalves, gastropods, phytoplankton, plants and organic detritus

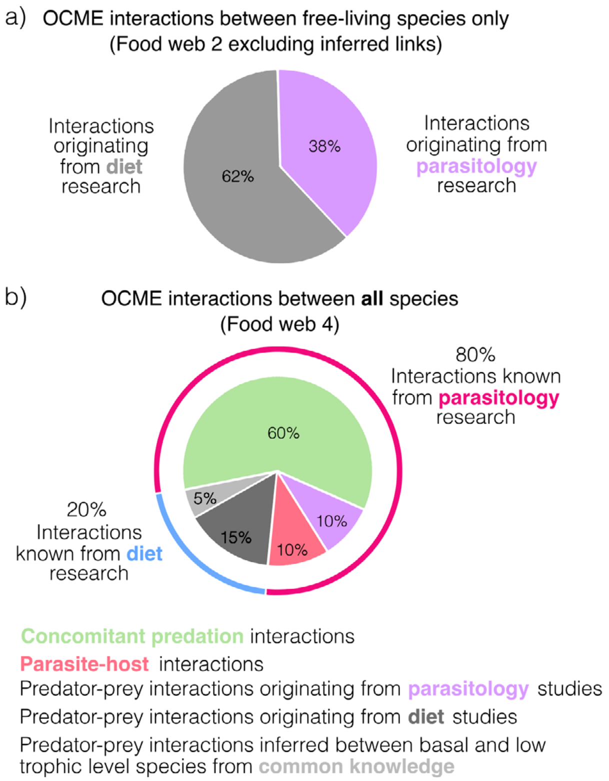


Fig. 4. Origins of interaction data obtained for Otago's coastal marine ecosystem (OCME); (a) Food Web 2 (OCME with free-living species only) and (b) Food Web 4 (parasitic and free-living species included). Colours of pie chart represent the origins of interactions

Average *D* also appeared to increase when more data and parasites were added (Table 1). Frequency distributions of links per node in Food Webs 1, 2 and 4 followed an exponential *DD*, while that of Food Web 3 followed a power law distribution (see Table A1 in the Appendix).

3.3. Extinction scenarios

In both extinction scenarios (random removal of nodes and removal from most to least connected nodes), OCME exhibited lower robustness when including parasites in Food Webs 3 and 4 compared to excluding parasites in Food Web 2 (Fig. 6). The decrease in robustness was more stark in the most-to-least connected extinction order (Fig. 6).

4. DISCUSSION

Our study achieves 3 important goals. First, it adds to the growing handful of food webs that attempt to include parasitic taxa and data. Second, our study provides a unique perspective into the structure and functioning of a food web that is relatively large in size and hosts a comparable number of parasite and free-living species. Third, our study illustrates the large extent to which parasitology can be used to further our understanding of food web dynamics in natural systems. Ultimately, we hope that this study will encourage food web ecologists to consider the use of parasitology to identify hidden trophic interactions between species and to include parasitic taxa in their own food web models.

Consistently finding an adult helminth in a vertebrate host and its larval stage in an invertebrate host reveals an existing predator–prey trophic link, even if diet studies have not uncovered it (adult helminths remain in the gastrointestinal tract of predators much longer than prey items). In Otago's coastal ecosystem, predator–prey interactions inferred from the study of parasitology accounted for almost 41% of all interactions between free-living marine animals. This is already a significant contribution in itself, but it does not even include parasite–host interactions or concomitant predation links. In total, trophic interactions inferred from parasite data (predator–prey interactions, parasite–host interactions and predator–parasite interactions) account for 80% of all links in the food web — similar to Lafferty et al. (2006), who reported parasites being involved in over 75% of all food web links. Parasites are thus deeply embedded in the ecosystem and are involved in the majority of links between species. This information would be lost in a traditional analysis that ignores the potential of parasites for inference of trophic interactions and food web construction. Parasite research focusing on trophically transmitted parasites has the potential to greatly advance our understanding of trophic interactions among species within natural systems (Valtonen et al. 2010).

The data presented here represent the currently known trophic interactions within Otago's coastal marine ecosystem but are likely not representative of the ecosystem as a whole. Our focus was on parasites; however, interactions between free-living animals recorded in the literature likely reflect only a fraction of existing trophic interactions (although there are undoubtedly links missing for parasite life cycles too). Data regarding invertebrate diet was seldom available, hence trophic interactions between basal and low trophic level species had to be inferred. Even parasite data can be hard to recover, especially for low trophic level species such as zooplankton, in which parasite prevalence can be extremely low

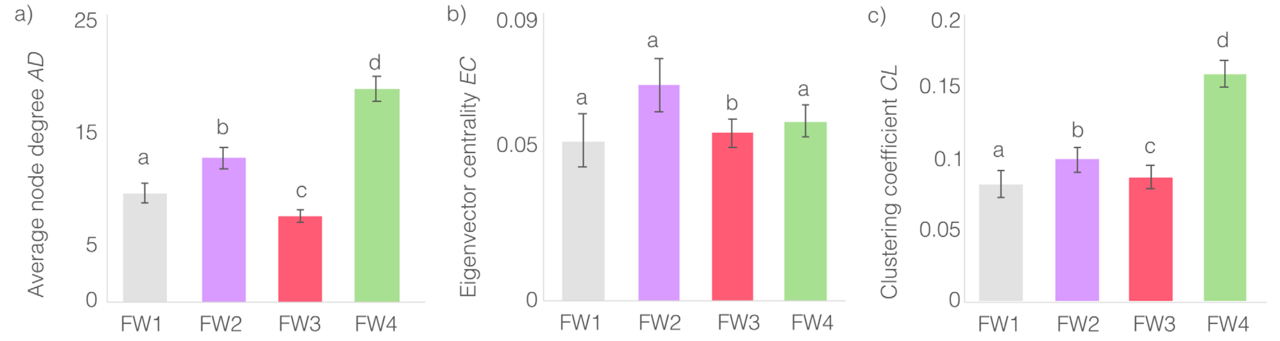


Fig. 5. Average values of (a) average node degree (*AD*), (b) eigenvector centrality (*EC*), and (c) clustering coefficient (*CL*), for each of the 4 food web (FW) versions (FW1–FW4). Lowercase letters represent significant differences in properties between food webs, as determined by non-parametric pairwise Wilcoxon tests, with $p < 0.05$. Error bars: 95% confidence intervals

(Marcogliese 1995). Additionally, parasite prevalence, intensity and presence or absence can vary in time and space (Thieltges & Reise 2007, Poulin 2020), as do trophic interactions among free-living species. This places limitations on the present study, the results of which must be interpreted cautiously. Nevertheless, the food web characterisations provided here are by far the most resolved for Otago's coastal marine ecosystem to date and act as a starting point for understanding how the food web is structured, how it functions and what roles parasites play. Intensive sampling of both free-living and parasitic taxa, such as in McLaughlin (2018) and Morton et al. (2021), may provide further resolution for Otago's ecosystem (Goldwasser & Roughgarden 1997). Although we did not give as much attention to the study of interactions between free-living species, this would greatly increase our ability to test specific hypotheses regarding how food web properties are influenced by parasitic taxa, such as in Morton & Lafferty (2022). Furthermore, although our sampling was biased towards parasites, the apparent 50:50 ratio of parasitic to free-living species present in Otago is not unrealistic. Researchers estimate that parasites make up between 30 and 70% of all metazoan species (Poulin & Morand 2004, Dobson et al. 2008, Poulin 2014), so this number should not be disregarded purely due to the sampling method employed here.

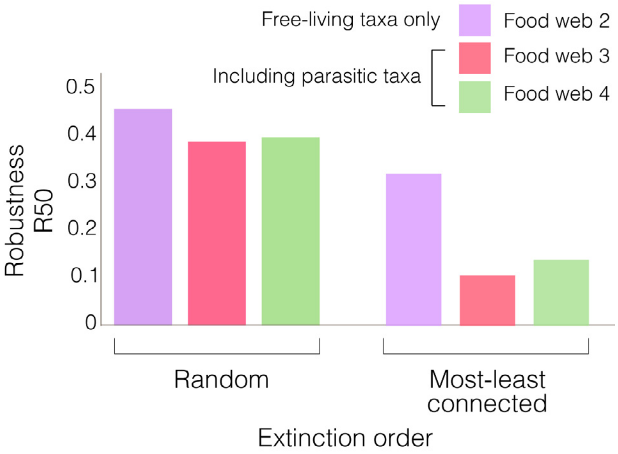


Fig. 6. Robustness of Otago's coastal marine food web (Food Web 2, Food Web 3 and Food Web 4) under 2 extinction scenarios: removal of nodes at random and removal of species from most to least connected nodes. Robustness of each food web was calculated as the proportion of primary species that had to be removed to result in a total loss of at least 50% of all species present in the food web (R_{50})

It is well documented that parasites can alter food web structure, complexity and functioning in natural systems (Lafferty et al. 2008, Lafferty & Kuris 2009, Poulin 2010, Sukhdeo 2010, Chen et al. 2011, Rudolf & Lafferty 2011, Dunne et al. 2013, Poulin et al. 2013, Runghen et al. 2021, Morton & Lafferty 2022). We found that the data from OCME compared relatively well in most metrics calculated with what has been found previously in other ecological regions (Thompson et al. 2005, Lafferty et al. 2006, 2008, Hernandez & Sukhdeo 2008, Dunne et al. 2013, Morton & Lafferty 2022). However, Otago exhibited relatively low overall *C* compared to previous food web (including parasites) analyses (Dunne et al. 2013). Species living here do not share as many interactions with each other compared to other ecological systems around the world. This fits a broader pattern: Otago is one of the most species-rich food web networks analysed to date, and *C* typically decreases exponentially with network species richness across a range of ecological interaction networks (Mouillot et al. 2008, Poulin & McDougall 2022). When parasites are included, overall food web *C* does not increase, in contrast to previous studies (Dunne et al. 2013). However, the low *C* values reported here may not be representative of the ecosystem but reflective of the under-sampling of species due to how the food web data were collected and assembled. Furthermore, Lafferty et al. (2006) proposed that *C* can be underestimated in food web analyses if specific parasite interactions are not accounted for. These include the obvious parasite–host interactions, predator–parasite concomitant predation interactions and parasite–parasite interactions, whereby parasites consume other parasites. The latter can occur actively, as in trematodes, e.g. *Philophthalmus* rediae that, in their first intermediate hosts, can consume the co-infecting parasites *Galactosomum* and *Maritrema* (Kamiya & Poulin 2013). However, these links are not accounted for in the present study, which may contribute to the particularly low *C* value observed for the system.

In the most resolved version of Otago's coastal ecosystem including parasites (Food Web 4), the inclusion of parasites as nodes and parasite-inferred predator–prey interactions increased the total path length (by almost one extra interaction step), number of species present (by almost 230%), number of trophic interactions (by almost 490%), *L/S* (by almost 5 links per species) and *AD* (by almost 10 degrees per node). These changes are quite substantial compared to those reported in previous studies: Lafferty et al. (2006) reported increases in species by ~50% and links by 100%, whereas Hernandez & Sukhdeo (2008) reported ~30% more species and 40% more links. These changes can be explained by the biology and embedded nature of the parasites studied, in that most helminths rely on trophic interactions to complete their life cycles, so while more links between species are identified using parasitology, even more are observed between those species when parasites are included as nodes.

Otago's food web consists of several unique modules, each with its own set of interacting species, more often interacting among themselves than with species from other modules. Poulin et al. (2013) analysed Otago's intertidal mud flat community as described by Mouritsen et al. (2011), identifying 3 modules from a data set containing 118 taxa (including 19 parasite taxa) and 1354 links between species. Many interactions from Mouritsen et al. (2011) are included in the present analysis, along with additional data from other habitats within Otago's marine ecosystem (i.e. tidal, sub-tidal, pelagic and benthic zones). In the most resolved version of OCME, 7 unique modules were identified, likely resulting from underlying evolutionary processes such as co-evolution and dietary similarity, which can promote the modular organisation of ecosystems (Rezende et al. 2009). When parasites were included as nodes, the overall *M* increased; however, when concomitant predation links were subsequently added, *M* decreased again. Presumably, the addition of parasite–host interactions creates more connections within sub-webs, whereas the inclusion of concomitant interactions lessens the independence of each module and creates more links between modules. Poulin et al. (2013) also found that parasites are involved in a high number of links between modules in various food webs, suggesting that they contribute significantly to the cohesion and stability of the system.

The average clustering of species increased from Food Web 1 (no input from parasitological research to create OCME) to Food Web 4, suggesting that species are more clustered together within modules than would have been thought using free-living diet data only. Species within each module contribute differently to the interconnectedness of the whole web, with some modules comprising highly interconnected nodes and others less connected nodes. Highly connected species within a modular structure may promote clusters of interactions allowing for higher transmission efficiency, something that may have favoured the evolution of trophically transmitted parasites (Anderson & Sukhdeo 2011, Rossiter & Sukhdeo 2011). Two parasites, *Corynosoma hannae* and *Hysterothylacium aduncum*, exhibiting particularly high centrality positions in the web also exhibit extremely low host specificity for both their intermediate or paratenic and definitive hosts, thus their positioning reflects this. Central species can promote energy transfer between low and high trophic levels and represent stable interactions within food webs. Identifying central species in Otago at present, whether they are parasitic or free-living, may facilitate predictions of future ecosystem stability or biodiversity loss (Stouffer et al. 2012, Roopnarine & Dineen 2018).

Links per node in all food webs except Food Web 3 followed an exponential *DD*. Even with the addition of new data, the distribution of links was skewed across species, with a few nodes having a high number of links and many having only a few. This likely reflects the range of dietary breadth and host specificity of species in the ecosystem, whether they are free-living or parasitic (Dunne et al. 2002, Stouffer et al. 2005). Exponential *DD* is common in ecological networks and can imply a vulnerability to both random losses of biodiversity and losses of highly connected nodes, resulting in community fragmentation (Albert et al. 2000, de Santana et al. 2013). Otago may be particularly vulnerable to further fragmentation, whether from random-species extinctions or highly connected-species extinctions, as it already exhibits relatively low connectivity and path lengths between species (de Santana et al. 2013).

Parasites may affect the resilience of the OCME to ecological change, specifically biodiversity loss. Similar to what has been reported previously, when including parasites, the network exhibits an overall lower robustness (e.g. Lafferty & Kuris 2009, Rudolf & Lafferty 2011, Chen et al. 2011). The underlying explanation stems from the fact that (1) parasites are reliant on the persistence of at least one suitable host species per life stage within their complex life cycles (Lafferty & Kuris 2009) and (2) parasites are more vulnerable to secondary extinctions than their hosts due to their often high host specificity (Cizauskas et al. 2017). The low robustness of the food web when accounting for parasites may further be underestimated because each parasite species was considered as a single node within the network. Hence, the analyses assumed that a parasite with, for example, a 3-host life cycle would not go extinct as long as any of the 3 hosts were still present; this is biologically implausible. As stated by Lafferty & Kuris (2009), who split their nodes into life stages, had they lumped all life stages, parasites would likely have appeared relatively invulnerable to secondary extinctions. Keeping this in mind, the robustness analyses still showed the high vulnerability of the system to species loss. This may reflect Otago's exponential *DD* of number of links per node, which makes it prone to disruption by the removal of either highly connected or random nodes (de Santana et al. 2013). Additionally, a lack of resolution regarding parasite life cycles and host feeding behaviour is also likely to result in a lower than expected robustness level. Although much effort was directed at completing the life cycle of Otago's parasites in this study, most still remain only known from one life stage, meaning that many trophic interactions connecting nodes are presently unknown. Lastly, as parasites do not occur at random within food webs; their inclusion and the subsequent decrease in robustness may be due to their host species occupying central positions, which makes them particularly vulnerable to extinction (Chen et al. 2011). All these variables probably contribute to the limited resilience of the Otago food web to withstand species losses. Regardless of the reasons, given that over half of the metazoan species in the food web are parasitic, and that parasites are particularly vulnerable to biodiversity loss compared to their hosts (Chen et al. 2011, Cizauskas et al. 2017), the present results clearly demonstrate that parasite species must be considered in future predictions pertaining to ecosystem change. If parasites are ignored or underrepresented, our ability to estimate ecosystem robustness and predict change is limited.

The analyses presented here are by no means an in-depth or comprehensive model of how the OCME will respond to ecological change, nor are the trophic interactions realistically fully resolved, and in fact they may never be. Rather, this study provides a holistic perspective on the underutilized potential that parasitology as a discipline has in uncovering unseen but real trophic interactions within ecosystems. We reveal the potential influence of parasites on the basic structure and functioning of this system. It is well known that parasite inclusion in ecological research is essential for full-picture resolution of ecosystems, something that this study strongly supports. It is important, now more than ever, to include parasitic organisms within food web prediction models, as the consequences of ignoring them potentially means an overestimation of an ecosystem's resilience to ecological pressures (Lafferty & Kuris 2009).

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Appendix.

Table A1. Degree distribution models with the best fit for each depiction of Otago's food web including Akaike Information Criterion (AIC) values and changes in AIC from next best fit model

Food web	Best fit model	AIC	AIC Δ
FW1	Exponential	−555	202
FW2	Exponential	−526	234
FW3	Power law	−469	59
FW4	Exponential	−733	231

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