Vol. 713: 97–115, 2023
https://doi.org/10.3354/meps14336

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published June 29

Impacts of an invasion by green crab *Carcinus maenas* on the intertidal food web of a Patagonian rocky shore, Argentina

Georgina Cordone[1,*], David E. Galván[1], Fernando R. Momo[2,3]

[1]Centro Para el Estudio de Sistemas Marinos (CESIMAR), Centro Nacional Patagónico (CCT CONICET-CENPAT), Boulevard Brown 2915, U9120 Puerto Madryn, Chubut, Argentina
[2]Instituto de Ciencias (ICI), Universidad Nacional de General Sarmiento, J.M. Gutierrez 1150, B1613 Los Polvorines, Buenos Aires, Argentina
[3]Instituto de Ecología y Desarrollo Sustentable (INEDES), Universidad Nacional de Luján, CC 221, B6700 Luján, Buenos Aires, Argentina

ABSTRACT: The green crab *Carcinus maenas* (L., 1758) is a highly invasive species that has altered various coastal marine ecosystems worldwide. Green crabs were first found on the Argentinian Patagonian coast in 2001 and were detected in Golfo Nuevo (Chubut, Argentina) in 2015. In this study, we described a rocky intertidal food web in the Golfo Nuevo and evaluated the effect of green crab invasion on the network. We assembled the intertidal food web from a compilation of diet studies and compared 2 scenarios: pre-invasion (without green crab) and post-invasion (with green crab). We calculated several structural network metrics to compare the scenarios. The green crab was positioned as a top predator in the intertidal food web, consuming prey from different trophic levels and exhibiting the capacity to exert top-down control. Green crab presence altered the structure and stability of the food web. Additionally, we evaluated the effect of potential competitive interactions between native species and the green crab on the food web. Possible competitive interactions increased the effect the green crab had on the structure of the food web. Our results show that green crab invasion decreased food web stability by reducing the capacity of the food web to contain small- and long-range disturbances. These results contribute to the assessment and monitoring of the possible effects of other factors of global change. The system is less stable than before green crab invasion, and the drastic changes in community composition already recorded in rocky intertidal ecosystems in Patagonia are more likely to amplify through the food web.

KEY WORDS: Ecological networks · Invasive species · Food web stability · Modularity · Omnivory · Quasi-sign-stability · Niche overlap

1. INTRODUCTION

Biological invasions are one of the main causes of ecosystem change (Gallardo et al. 2016). Non-native species establish new ecological interactions with resident species upon arrival in colonized ecosystems. The impacts of invasions on communities are hard to predict, as direct and indirect interactions can trigger both positive and negative effects on resident species (Thomsen et al. 2011a,b, David et al. 2017). One example of a direct interaction is predation by non-native species, which typically leads to size reductions in native populations and can ultimately result in local species extinctions (e.g. Med-

---

*Corresponding author: georginacordone@gmail.com ina et al. 2011, Green et al. 2012). Indirect interactions, such as exploitation and apparent competition, may also cause native populations to decline (White et al. 2006, Dangremond et al. 2010). Simultaneously, non-native species may have positive effects on resident species (Rodríguez 2006), such as increasing food availability for resident species in high trophic positions or providing new habitats for other species (Thomsen et al. 2010). For instance, the invasive kelp *Undaria pinnatifida* (Harvey) Suringar, 1873, forms dense seasonal forests that provide refuge for different species of benthic macroinvertebrates in Golfo Nuevo (Irigoyen et al. 2011a). However, these same kelp forests interfere with the habitat of rocky reef fishes, resulting in a decrease in the abundance of these fishes (Irigoyen et al. 2011b). Therefore, biological invasions are complex phenomena that involve multiple factors and can trigger different responses in resident species. Ecological networks provide a means to study complex ecosystems and their response to changes, such as the introduction of invasive species, by considering all species and interactions in a community (Frost et al. 2019). Ecological networks consist of well-established mathematical models that can capture ecological complexity, formally describe species coexistence and interactions, and help us understand community structure, stability, and ecosystem functioning (Layman et al. 2015, Landi et al. 2018).

Ecological networks include different interactions between species: predator–prey interactions, mutualism, competition, amensalism, and commensalism (Bersier 2007). Trophic interactions are easier to recognize than other ecological interactions due to the presence of prey in the guts or feces of the predator or by direct observation of the predator feeding under field conditions. For this reason, the most extensively described and analyzed ecological networks are those that summarize trophic interactions, known as food webs (Bersier 2007). Food webs are essential descriptors for understanding ecosystem functioning, and their study can provide insights into almost all areas of ecology, ranging from population dynamics to nutrient cycles (Layman et al. 2015). The effect of an invasive species on a food web depends on 2 factors: invasiveness and invasibility (Frost et al. 2019). Invasiveness is determined by non-native species traits such as phenotypic plasticity, body size, and diet breadth (Drenovsky et al. 2012, Lurgi et al. 2014), whereas invasibility is determined by community features such as food web structure (Hui et al. 2016, Smith-Ramesh et al. 2017). Food webs with higher biodiversity are expected to be more resistant to invasions; however, more diverse communities also harbor a higher richness of invaders (Kennedy et al. 2002, Stachowicz & Byrnes 2006, Galiana et al. 2014). Knowing the food web structure and non-native species interactions is crucial to understanding how a biological invasion may affect a native ecosystem.

'A map is not the territory' (Korzybski 1933, p. 750) but it is useful to navigate through it. Similarly, the flows of matter and energy and the trophic interactions between species represent only the topological structure of the food web. While network structure is useful for many questions, it leaves out many species characteristics that are important for description and analysis. Species exhibit plasticity, respond to environmental stimuli, and show a certain degree of disturbance resilience (Miner et al. 2005, Canale & Henry 2010, Hughes et al. 2012, Norin & Metcalfe 2019). If a species loses its main prey item, it will most likely switch to an alternative prey, reducing the risk of extinction cascades in the food web (Borrvall et al. 2000; e.g. Belleggia et al. 2017). Moreover, within the same species, individuals can have variable diets depending on their life stage, sex, and environmental conditions such as prey availability (e.g. Koen Alonso et al. 2002, Gulka et al. 2017, Pasti et al. 2021). None of these factors are accounted for when analyzing the topological structure of a food web.

The representation of a food web based on its topological structure is a way to visualize the trophic relationships among species within an ecosystem. This approach is static and focuses on the presence or absence of species and their interactions in the food webs (Cohen 1977, Dunne 2006). However, there are also dynamic approaches that consider the trophic interactions and the dynamic between species (Ebenman et al. 2004, Riede et al. 2011). The dynamic approach can detect responses to disturbances that the topological approach cannot (Ebenman & Jonsson 2005). Nonetheless, the dynamic approach requires knowledge of the population dynamics of all species in the ecosystem, which makes it challenging to scale up for highly resolved food webs. In contrast, the topological approach is useful for studying highly resolved food webs since it only requires knowledge of food web structure (Eklöf et al. 2013). Allesina & Pascual (2008) demonstrated that food web topology determines food web local stability and influences stability more than interaction forces do. Studies characterizing food web topology have shown that common structure properties exist (Montoya & Solé 2003, Vermaat et al. 2009, Marina et al. 2018). These structural properties, such as motif presence, are related to population dynamics in ecosystem and food web stability (Rooney & McCann 2012, Monteiro & Faria 2016). Therefore, studying food web topology is crucial to understand how food webs respond to environmental changes. For example, analyzing food web topology can help us understand the extent of invasive species effects on an ecosystem, as invasive species can establish new trophic interactions with resident species and alter important structural food web properties (Frost et al. 2019).

Rocky intertidal ecosystems along the Argentine coasts exhibit differences from other intertidal ecosystems worldwide. The number of predator species is relatively low, and they are primarily small-bodied (Palomo et al. 2019). The intertidal ecosystems on Patagonian rocky shores are exposed to harsh physical conditions, have low consumer pressure, and community structure is mainly driven by environmental factors (Bertness et al. 2006, Hidalgo et al. 2007). Recently, the green crab *Carcinus maenas* (Linnaeus, 1758), which is native to northwestern Europe and Africa, has invaded the Patagonian rocky shore at Golfo Nuevo (Chubut, Argentina) (Torres & González-Pisani 2016). Green crabs are voracious predators that may exert strong predation pressure within intertidal ecosystems (Hidalgo et al. 2007, Rossong et al. 2012). Green crabs have damaged various populations of mollusks and crustaceans globally, making them one of the non-native marine species that have caused a significant ecological change in invaded ecosystems (Grosholz et al. 2000, Poirier et al. 2017, Anton et al. 2019). The damages caused by *C. maenas* are so severe that governments and countries are making tremendous efforts to eradicate them from invaded sites (Ens et al. 2022). Although there are 129 invasive and 72 cryptogenic species recorded on the Argentine coast, their impacts on invaded ecosystems are still relatively unknown (Orensanz et al. 2002, Palomo et al. 2019, Schwindt et al. 2020). Invasive green crabs may have negative impacts on community structure not only by increasing predation pressure but also by interfering with facilitation processes and competing with other species (e.g. McDonald et al. 2001). Green crabs have a diverse diet, consume numerous prey, and occupy the third trophic level (TL) in the intertidal at Golfo Nuevo (Cordone et al. 2022). Non-native predators at high TLs typically have larger negative impacts on resident species and food web structure (David et al. 2017). The high predation rate of green crabs on habitat formers, such as mussels, can result in a refuge loss for other intertidal species, which may ultimately lead to a marked decrease in biodiversity (Hidalgo et al. 2007). It is expected that non-native predators will trigger adverse effects at lower TLs, and the depletion of resident species is a common result of direct predation (David et al. 2017). The green crab invasion poses a serious threat to Patagonian species that live in rocky intertidal environments since it can affect them through direct predation or indirect interactions such as competition.

This study aimed to reconstruct the food web of the rocky intertidal ecosystem in Patagonia and evaluate the impact of the introduction of a non-native species, the green crab, on the food web at a recently invaded site. Since green crabs have a diverse diet, occupy a high TL, and the intertidal Patagonian rocky ecosystems lack analog native predators, we hypothesized that green crab presence will alter food web structure and decrease its stability. We anticipated that food web metrics, which are positively correlated with stability, would decrease when the green crab is included in the network description. Additionally, we expected that the mean TL and the amount of omnivory would increase with the incorporation of the green crab into the food web. Beyond predation, green crabs can also establish other interactions with resident species, such as competition for food. Therefore, we expected changes in food web structural metrics to be positively correlated with the number of potential green crab competitors affected.

2. MATERIALS AND METHODS

2.1. Food web assembly and the inclusion of the green crab

We conducted an exhaustive bibliographic search of scientific publications such as published papers, and graduate and undergraduate theses on marine species in the Patagonian intertidal rocky shore at Golfo Nuevo (Fig. 1). We used the search engine

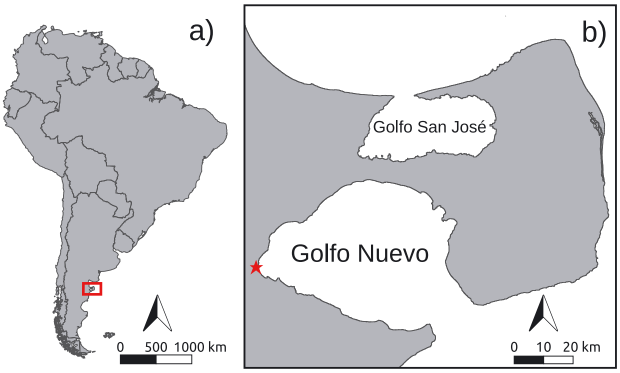

Fig. 1. (a) Location of the study site on the Argentinian coast; red box: Golfo Nuevo. (b) Golfo Nuevo; red star: the city of Puerto Madryn in Chubut, Argentina

'Google Scholar' and national repositories such as the Instituto Nacional de Investigación y Desarrollo Pesquero (https://marabierto.inidep.edu.ar/home) and Consejo Nacional de Investigaciones Científicas y Tecnicas (https://ri.conicet.gov.ar/). We selected 37 scientific publications after the bibliographic search to build the intertidal food web (see the Supplement at www.int-res.com/articles/suppl/m713p097_supp.xlsx). The scientific publications mainly comprised community composition and trophic ecology studies based on gut contents, feces, and regurgitation observations. Investigations using stable isotopes or fatty acids and studies about feeding preference under laboratory conditions were not included, as they did not provide information suitable for a qualitative and high-resolved network description. We only considered species associated with rocky intertidal ecosystems and excluded species exclusively associated with sandy intertidal ecosystems. After the first food web assembly, we consulted local experts from different laboratories at the Centro Nacional Patagónico (CCT CONICET-CENPAT) for each taxonomic group: marine invertebrates, fishes, and birds. As a result of this expert consultation, some trophic species and trophic interactions were modified, and we added new interactions not previously reported in the literature. Through this procedure, we obtained a highly resolved food web.

Food webs are composed of nodes representing trophic species and links representing trophic interactions (i.e. flow of matter and energy from resources to consumers), where S represents the number of trophic species and L represents the number of trophic interactions. Trophic species can correspond to biological species (e.g. macroalgae: *Ulva lactuca* Linnaeus, 1753; mollusks: *Trophon geversianus* (Pallas, 1774); fish: *Patagonotothen guntheri* (Norman, 1937)), groups of organisms that share the same set of predators and prey (e.g. hyperids, copepods, phytoplankton), and non-living compartments of matter and energy such as detritus. Hereafter, the term 'species' will be used as a synonym for 'trophic species' (Briand & Cohen 1984). All food webs are associated with an adjacency matrix, which is a binary square matrix with the species list in columns and rows. Trophic interactions are represented by '$a_i = 1$' in the adjacency matrix, whereby the species in column (j) consume the species in row (i).

The information generated from previous work on the diet of the green crab in the study area was used to incorporate the species into the food web description (Cordone et al. 2022). We identified 30 prey species of the green crab and added those interactions into the intertidal food web description. We also added one interaction between the green crab and the kelp gull *Larus dominicanus* Lichtenstein, 1823, as it was recently observed that kelp gulls eat green crabs (Yorio et al. 2020). In this way, the intertidal food web was constructed using information from the literature, expert consultation, and Cordone et al. (2022).

2.2. Evaluation of direct effects of the green crab on the food web

We analyzed food web structure and stability based on the following network metrics widely used in food web studies (Pimm 1982, Cohen et al. 1990, Pascual & Dunne 2006, Bascompte 2009): characteristic path length (CPL), clustering coefficient (CC), mean TL (meanTL), omnivory (Om), modularity (Mod), and quasi-sign-stability (QSS).

TL indicates a species' position in the food web (Eq. A1 in the Appendix). It summarizes a species' distance from the source of matter and energy, where basal species such as autotrophs have a TL of 1 (Lindeman 1942, Odum & Heald 1975). Food webs with low meanTL exhibit efficient energy transfer (Borrelli & Ginzburg 2014). CC measures the likelihood that 2 connected species are connected to a third one (Eq. A2). CPL represents the average distance between each pair of species in the network, as measured by the link number that joins each species pair. CPL has a complex relationship with stability (Kaunzinger & Morin 1998, Albert & Barabási 2002) (Eq. A3). Low CPL values are associated with high network stability; however, short chains can contribute to rapid disturbance propagation (Newman 2003, Borrelli & Ginzburg 2014). QSS measures the probability that a network will return to its equilibrium point after a small perturbation. This metric ranges from 0 to 1, with QSS values close to 1 indicating high stability (Allesina & Pascual 2008). Om represents the species fraction that feeds at different TLs (McCann & Hastings 1997, Kuijper et al. 2003). High Om values are generally destabilizing, but intermediate levels promote stability when weak interactions predominate (Gellner & McCann 2012, Wootton 2017). Mod reflects how strongly species subgroups interact with species in other subgroups (Krause et al. 2003, Newman & Girvan 2004) (Eq. A4). High Mod values promote stability by containing disturbances within the subgroup where they occur and preventing their transfer to the rest of the network (Stouffer & Bascompte 2011, Grilli et al. 2016).

To assess the direct impacts of the green crab on the intertidal food web, we compared 2 food-web scenarios: one simulating the pre-invasion state without the green crab and the other including the green crab as a node to simulate the post-invasion state. We used the curve-ball algorithm to generate 1000 simulated food webs per scenario. The curve-ball algorithm generates simulated networks that maintain the degree (*D*) of the species, i.e. the number of incoming and outcoming links per node (Strona et al. 2014). These simulated food webs preserve key structural properties, such as the distribution of top, intermediate, and basal species, while varying in other properties, such as CC or CPL. The curve-ball algorithm simulates ecologically meaningful food webs that can be used for comparisons (Strona et al. 2014, Kortsch et al. 2019). Recently, this approach has been successfully applied when comparing food webs across different ecosystems (Cordone et al. 2020, Rodriguez et al. 2022, Funes et al. 2022).

After generating the simulated food webs, we calculated the CPL, CC, meanTL, O, Mod, and QSS for both food web scenarios. To compare these metrics, we calculated effect size as quantile shift (Q) following Wilcox's (2018) magnitude criterion: undetectable ($Q < 0.5$), small ($Q > 0.55$), medium ($Q > 0.65$), and large ($Q > 0.7$).

2.3. Evaluation of indirect effects of the green crab on the food web

Green crabs can affect other species in the food web not only directly, but also by establishing other types of ecological interactions. One type of interaction that invasive species can establish with resident species is competition (McDonald et al. 2001, Ciancio et al. 2008, Layman & Allgeier 2012). Probable competitive interactions can be identified through secondary graphs (Lundgren 1989). All food webs are associated with 2 secondary graphs: the common enemies graph and the niche overlap graph. The first is built by linking prey that share at least one predator, and the second is built by linking predators with at least one prey species in common (Bersier 2007). These graphs are useful since they explicitly show the indirect interactions between predators and prey in an ecosystem and can serve to elucidate indirect mechanisms between species, such as apparent competition (Holt & Lawton 1994).

We constructed the niche overlap graph to establish possible competitive interactions (Fig. A1 in the Appendix). We define species susceptible to competition as those species that shared more than 75% of their prey with the green crab in the niche overlap graph. We chose a threshold of 75% because in other marine food webs, a true collapse in the system is only detected once this threshold is reached (Cordone et al. 2018). In addition, we chose a high threshold because we lack information on prey proportions in predators' diets, so we selected a conservative threshold to avoid overestimating indirect green crab effects on the food web. Detritivorous species were not considered as possible competitors. The green crab is an active carnivore that feeds especially on mollusks and crustaceans (Grosholz & Ruiz 1996, Chen et al. 2004). Our previous work on green crab diet showed that green crabs at Golfo Nuevo display a high TL and mainly consume bivalves (Cordone et al. 2022). Therefore, green crab consumption pressure over debris is probably low at the study site. Furthermore, there are large amounts of organic matter originating from another invasive species in Golfo Nuevo waters, the brown algae *U. pinnatifida*. *U. pinnatifida* has had a great impact on the ecosystem since it increased the amount of debris available considerably at the intertidal zone (Bunicontro et al. 2019). In fact, biomass values recorded in 2019–2020 were much higher than previous records obtained at the same site before the green crab invasion (Lozada et al. 2022). We identified 2 types of possible competitors: (1) mobile species and (2) sessile or sedentary species (Table 1). Mobile species correspond to organisms that can consume prey outside the intertidal zone (birds and fish with action range wider than the rocky intertidal), while sessile or sedentary species are benthic species with smaller action ranges that feed only in the intertidal zone. The effect that the green crab has on possible competitors differs depending on the species' movement capacity. The effect expected on mobile species is a range shift to areas with less competitive pressure (lower abun-

Table 1. Classification of potential competitors of green crab according to their ability of movement: mobile, sessile, or sedentary species. Potential competitors are those species that share more than 75% of their prey with the green crab

Classification	Susceptible species
Mobile	*Calidris alba* (Pallas, 1764) *Charadrius falklandicus* Latham, 1790 *Helcogrammoides cunninghami* (Smitt, 1898) *Ribeiroclinus eigenmanni* (Jordan, 1888) *Patagonotothen cornucola* (Richardson, 1844) *P. sima* (Richardson, 1845)
Sessile or sedentary	*Anthothoe chilensis* (Lesson, 1830) *Diadumene lineata* (Verrill, 1869) *Serolis* sp. Leach, 1818 *Trophon geversianus* (Pallas, 1774)

dance of green crabs), while the effect expected on sessile and sedentary species is local extinction at those sites with greater competitive pressure (greater number of crabs). Both events can occur at the same time. However, a range shift will probably happen sooner since it implies a behavioral change in the organisms in the area. Meanwhile, local extinctions involve population processes of low recruitment and high mortality.

Based on this information, we proposed 3 scenarios: (1) the removal of mobile species, (2) the removal of sessile or sedentary species, and (3) the joint removal of mobile, sessile, and sedentary species. These 3 scenarios represent the indirect effects caused by the green crab on the rocky intertidal food web and were named Case A, Case B, and Case C, respectively. We calculated and compared CPL, CC, meanTL, Om, Mod, and QSS for the 3 scenarios as described in Section 2.2.

All network metrics were calculated with the R package 'multiweb' (Saravia 2019), and effect sizes were calculated using the 'WRS2' package (Mair & Wilcox 2020). The database containing the intertidal food web is provided in the Supplement.

3. RESULTS

3.1. Food web assembly and inclusion of the green crab

The intertidal food web without the green crab, in the pre-invasion scenario, was composed of 87 trophic species and 454 trophic interactions. In the post-invasion scenario, 31 trophic interactions and one node corresponding to the invasive species were added to the intertidal food web, resulting in a food web with 88 species and 485 trophic interactions. The green crab was positioned at one of the highest TLs (TL = 3.21), preying on 35% of the species inhabiting the intertidal area (Fig. 2). The top predators in the intertidal food web were 2 bird species, *Larus dominicanus* (TL = 3.37) and *Haematopus ater* Vieillot & Oudart, 1825 (TL = 3.38), a cephalopod species *Octopus tehuelchus* d'Orbigny [in Férussac & d'Orbigny], 1834 (TL = 3.44), and a gastropod species *Epitonium fabrizioi* Pastorino & Penchaszadeh, 1998 (TL = 4.15). In addition, the green crab was found to be among the most connected species, with a high degree (D_{crab} = 31), being surpassed only by detritus (D_{detritus} = 36).

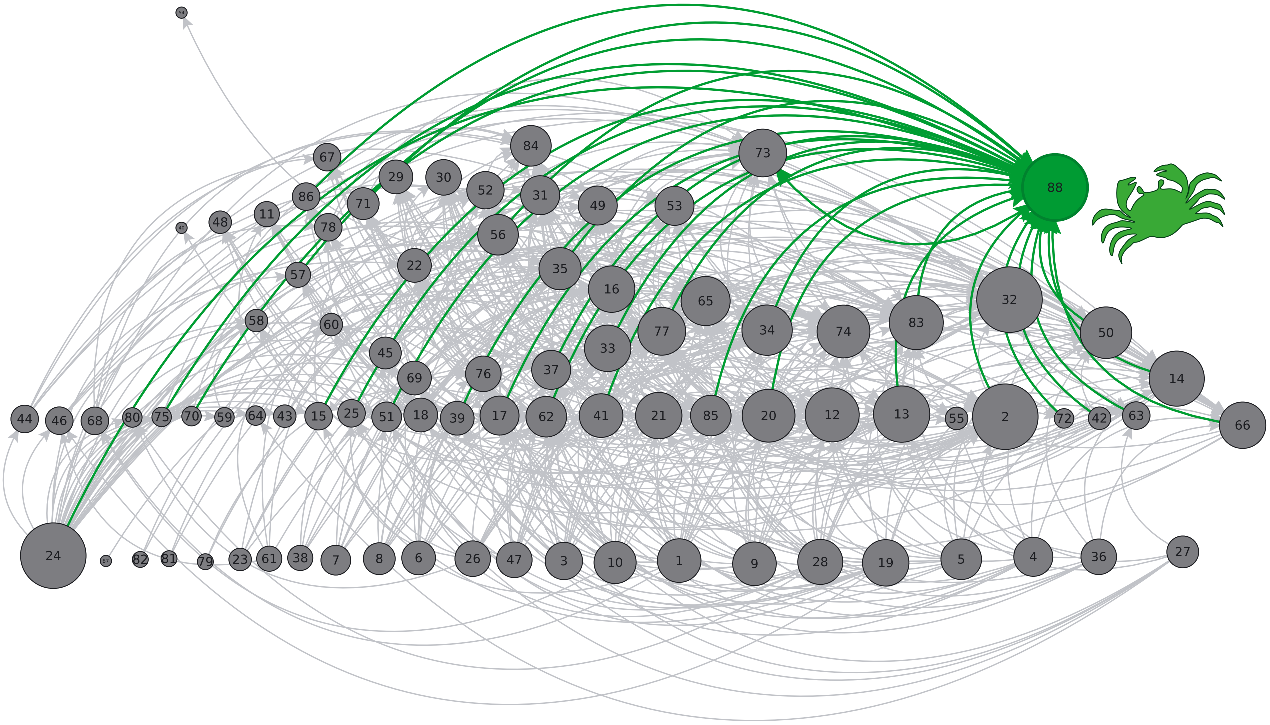

Fig. 2. Representation of the rocky intertidal food web of Puerto Madryn (Golfo Nuevo, Argentina). Each node represents a species and each arrow represents a trophic interaction, which indicates the flow of matter and energy from resources to consumers. The size of each node is relative to the species degree (sensu Strona et al. 2014), while the vertical scale represents the trophic level. The ID is indicated within the nodes (see Table A1 in the Appendix). The green crab *Carcinus maenas* is represented as a green node, and its trophic interactions are highlighted in green

3.2. Direct effects of the green crab on the food web

We observed changes between the pre- and post-invasion scenarios in 4 out of the 6 analyzed metrics (Fig. 3, Table 2). As expected, CC and meanTL increased in the post-invasion scenario. The meanTL increased because green crabs have a high TL in the intertidal food web (fifth out of 87 species). The effect size magnitude for meanTL comparisons between the pre- and post-invasion scenarios was one of the 3 largest (0.88). An increase in meanTL implies a less efficient network in transporting energy. The increase in CC was mediated by the high degree of Om exhibited by the crab. When including the green crab in the network, the probability that 2 species that were connected to each other were also connected to the green crab was high, and the CC of the food web increased with the largest effect size (0.96). The 2 network metrics most closely related to stability (Mod and QSS) changed as predicted. Mod decreased and exhibited the second-largest magnitude of effect size between pre- and post-invasion scenario comparisons (0.91). Mod decreased because the green crab established connections between species belonging to different modules. QSS decreased

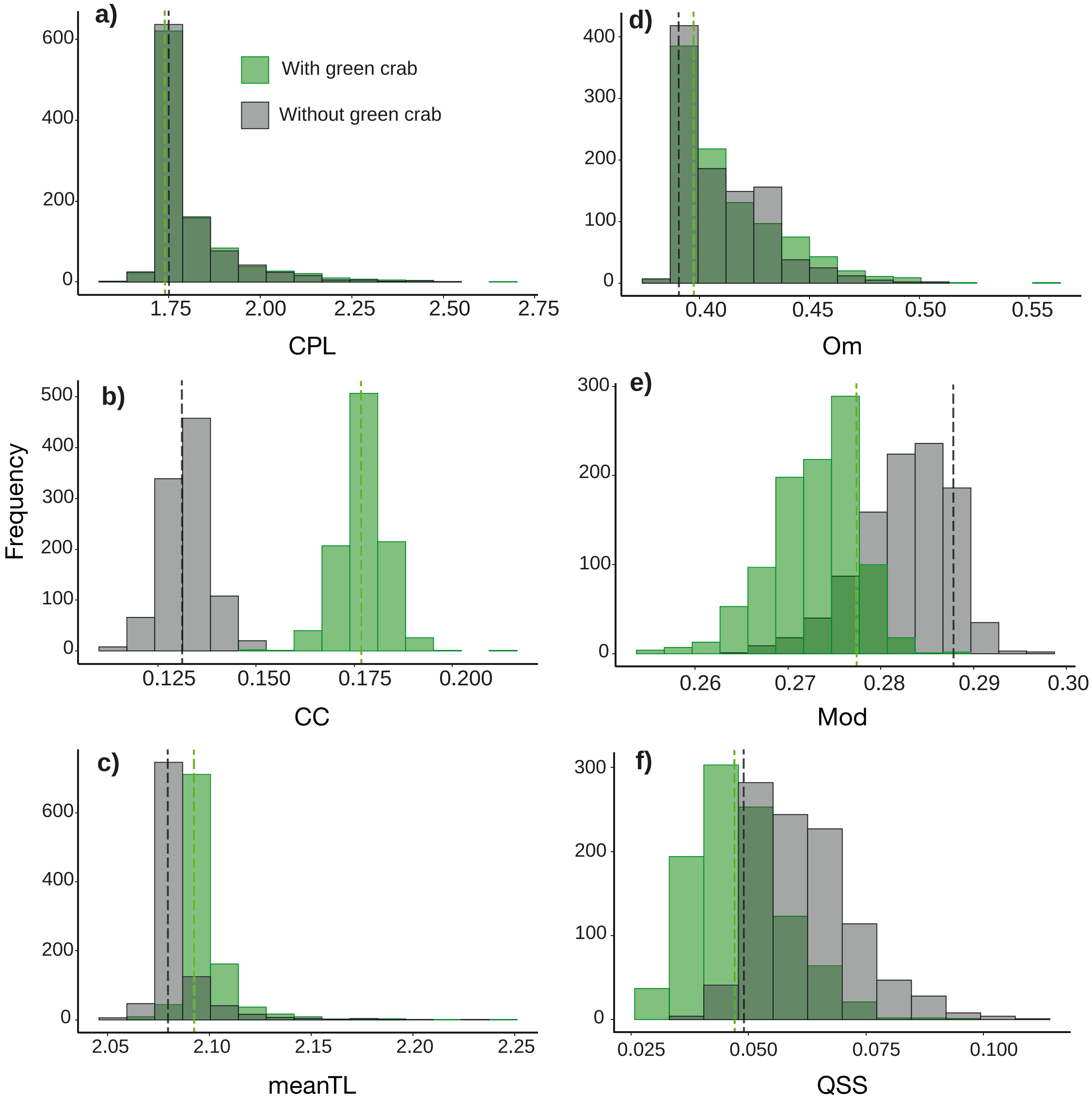

Fig. 3. Network metrics for the pre- and post-invasion scenarios in the Patagonian rocky intertidal: (a) characteristic path length (CPL), (b) clustering coefficient (CC), (c) mean trophic level (meanTL), (d) omnivory (Om), (e) modularity (Mod), and (f) quasi-sign-stability (QSS). Dotted lines: empirical values; bars: curve-ball simulations

Table 2. Effect size estimates by quantile shift (Q) for network metrics for the pre- and post-invasion scenarios in the Patagonian rocky intertidal. Effect undetectable ($Q < 0.5$), *small ($Q > 0.55$), **medium ($Q > 0.65$), ***large ($Q > 0.7$)

Network metric	Effect size (Q)
Characteristic path length	0.02 (0.00, 0.08)
Clustering coefficient	0.96 (0.95, 0.97)***
Mean trophic level	0.88 (0.85, 0.90)***
Omnivory	0.26 (0.18, 0.32)
Modularity	0.91 (0.89, 0.93)***
Quasi-sign-stability	0.76 (0.72, 0.80)***

with a magnitude of effect size of 0.76. Mod and QSS are indicators of the capacity of the food web to contain disturbances. In this sense, the food web in the post-invasion scenario was less stable than in the pre-invasion scenario. On the other hand, CPL and Om did not show differences between pre- and post-invasion and had undetectable effect size magnitudes (0.02 and 0.26, respectively).

3.3. Indirect effects of the green crab on the food web

We observed changes between the pre- and post-invasion scenarios in most of the analyzed metrics when considering indirect effects (Fig. 4, Table 3). The meanTL, Mod, and QSS decreased in the post-invasion scenario, whereas CC increased. Om decreased only in Case C, when all possible competitors were lost, and QSS did not change in this case. The magnitude of the effect size was large for CC (0.96 for Case A; 0.97 for Cases B and C), the meanTL (0.96 for Cases A and B; 0.94 for Case C), and Mod (0.98 across all 3 cases). CPL exhibited a large effect size for Case C (0.78), medium for Case A (0.69), and undetectable for Case B (0.09). Om exhibited a large effect size for Case C (0.89) and was undetectable for Cases A and B (0.45 and 0.23, respectively). QSS showed median effect sizes for Cases A and B (0.57 and 0.56, respectively) and was undetectable for Case C (0.07). It is worth noting that the effect of the green crab on network metrics had larger effect sizes when considering indirect interactions than only considering direct interactions (Section 3.2). This happened for all network metrics except QSS. Indeed, we detected changes in the 2 network metrics with previously undetectable effect sizes, Om and CPL, when we considered all the possible competitive interactions (Case C).

4. DISCUSSION

To our knowledge, this study constitutes the first published reconstruction of a rocky intertidal food web in Patagonia, Argentina. We confirmed our general hypothesis, that the presence of green crabs alters food web structure and stability, by detecting changes in the network metrics with high effect sizes. The changes triggered by green crab presence decreased food web stability, as we expected. We also identified 10 potential competitors to green crabs and observed that perturbations in these potential competitors enhanced alterations in most of the analyzed network metrics.

4.1. Food web assembly and inclusion of the green crab

Samplings conducted by the Census of Marine Life (CoML) using the Natural Geography in Shore Areas (NaGISA) protocol in the rocky intertidal of Punta Este (Puerto Madryn, Golfo Nuevo) recorded a total of 34 species of benthic invertebrates and 29 macroalgae (Rechimont et al. 2013). We reconstructed the rocky intertidal food web, considering a large number of these species (87 trophic species) and with high resolution (more than 400 interactions). Network metrics, such as the distribution of basal/intermediate/top species, Om, CPL, and mean TL, coincided with other rocky intertidal food webs (Mendonça et al. 2018). Additionally, debris was the highest degree node, as in other intertidal food webs (McMeans et al. 2013). The green crab plays a key role in the intertidal food web by directly preying on a large number of species and occupying a high TL. It was the most connected consumer, preying on 30 species and displaying a TL of 3.21. The maximum TL was 4.15 in the rocky intertidal food web at our study site. Our estimation of the TL of the green crab, obtained through food web reconstruction, was similar to the value of 3.10 obtained by stable isotope analysis of the same population (Cordone et al. 2022). Intertidal food webs are usually short, with maximum TLs between 3 and 4 (Schaal et al. 2010, McMeans et al. 2013, Vinagre et al. 2015, 2018). The maximum TL of the Patagonian intertidal rocky food web was within this range and was occupied by a specialist gastropod species that feeds on anemone, *Epitonium fabrizioi*. It is worth noting that invertebrate species, such as sea stars, act as top predators in benthic habitats (Amiraux et al. 2023). However, the Patagonian rocky intertidal ecosystems lack large invertebrates acting as top predators. In this sense, green crabs,

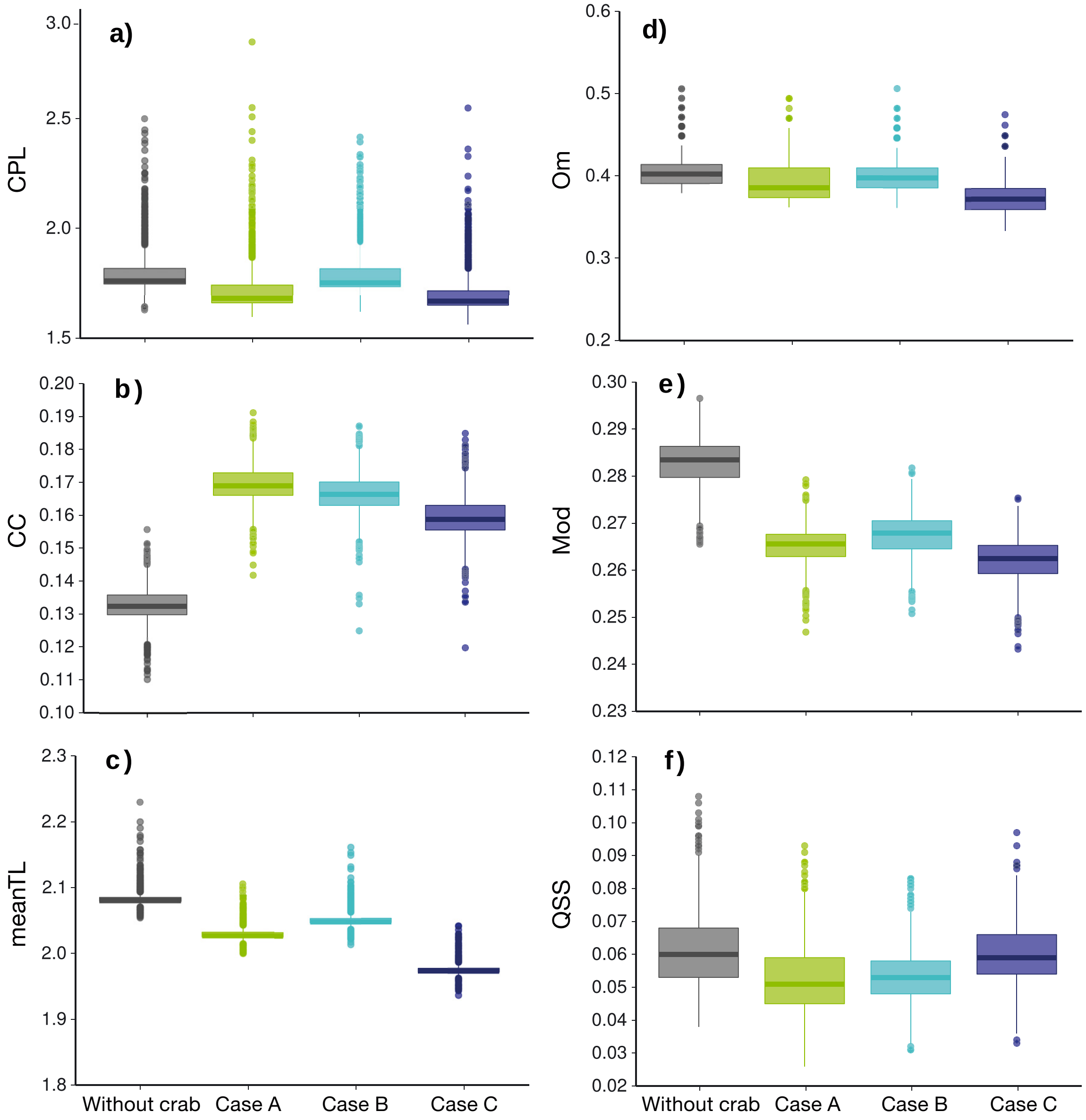

Fig. 4. Network metrics for the pre-and post-invasion scenarios in the Patagonian rocky intertidal considering indirect effects. (a) Characteristic path length, (b) clustering coefficient, (c) mean trophic level, (d) omnivory, (e) modularity, and (f) quasi-sign-stability (abbreviations as in Fig. 3). Horizontal lines: median; lower and upper hinges: first and third quartiles (25th and 75th percentiles); individual points: outliers (data > 1.5 × IQR). The 4 analyzed cases are the pre-invasion scenario (without green crabs), the removal of mobile species (Case A), the removal of sessile or sedentary species (Case B), and the joint removal of mobile, sessile, and sedentary species (Case C)

with high TLs, are occupying a new role in the intertidal ecosystem and can trigger cascading top-down effects (Moran et al. 1996, Alvarez et al. 2013, Papacostas & Freestone 2019). Trophic cascades are indirect species interactions that originate with predators and spread downward through food webs via top-down forcing (Ripple et al. 2016). Green crabs feeding on intermediate consumers allowed non-native basal and non-native low-TL species to become more abundant in estuarine communities (Locke et al. 2007, Papacostas & Freestone 2019). Grosholz et al. (2000) observed that green crabs exerted strong top-down control, significantly reducing the abundances of several invertebrate species in central California. Similarly, green crabs in Patagonia could exert top-down control, reduce intermediate consumer abundances, and favor the proliferation of non-native basal species. For example, green crabs could benefit some algae species by preying on herbivores, as observed in other sites (Trussell et al. 2017).

Table 3. Effect size estimates by quantile shift (Q) for network metrics for the pre- and post-invasion scenarios in the Patagonian rocky intertidal considering indirect effects. Effect undetectable (Q < 0.5), *small (Q > 0.55), **medium (Q > 0.65), ***large (Q > 0.7)

Network metric	Effect size (Q) Case A	Case B	Case C
Characteristic path length	0.69 (0.65, 0.73)**	0.09 (0.02, 0.16)	0.78 (0.74, 0.82)***
Clustering coefficient	0.96 (0.96, 0.97)***	0.97 (0.97, 0.98)***	0.97 (0.97, 0.98)***
Mean trophic level	0.96 (0.95, 0.97)***	0.96 (0.95, 0.97)***	0.94 (0.94, 0.95)***
Omnivory	0.45 (0.38, 0.57)	0.23 (0.17, 0.29)	0.89 (0.73, 0.94)***
Modularity	0.98 (0.97, 0.99)***	0.98 (0.97, 0.99)***	0.98 (0.97, 0.99)***
Quasi-sign-stability	0.57 (0.51, 0.61)**	0.56 (0.50, 0.60)**	0.07 (0.02, 0.13)

4.2. Direct effect of the green crab on the food web

The presence of the green crab modified the structure and stability of the intertidal food web by altering network metrics such as CC, Mod, QSS, and meanTL. We confirmed our predictions of changes in Mod, QSS, and meanTL, but we did not observe changes in Om. The inclusion of new species or interactions into a food web does not necessarily result in substantial changes in network metrics. For instance, a comparison of other marine food webs with larger differences in species number and interactions (ΔS = 5 and ΔL = 72) does not show differences in their Mod values (Q = 0.13) (Cordone 2022). However, a smaller difference, the inclusion of the green crab (ΔS = 1 and ΔL = 31) had a high effect on Mod (Q = 0.91). In this sense, the effects triggered on a food web by species addition do not depend strictly on the number of species or interactions added but on species-level network characteristics and previous food web structure (Lurgi et al. 2014, Frost et. al 2019).

Mod and the QSS are metrics related to disturbance propagation (Allesina & Pascual 2008, Stouffer & Bascompte 2011, Grilli et al. 2016). In this sense, incorporation of the green crab into the intertidal food web affected the ability of the food web to both contain small disturbances (i.e. QSS) and propagate disturbances to a greater range (i.e. Mod). This finding is particularly relevant given the recent drastic changes in the rocky intertidal ecosystem at Golfo Nuevo. At our study site, Mendez et al. (2021) observed dramatic mass mortality events of foundation species, *Perumytilus purpuratus* (Lamarck, 1819) and *Brachidontes rodriguezii* (d'Orbigny, 1842). The disturbances caused by these mass mortality events may propagate more extensively or at a faster pace in the intertidals of the Golfo Nuevo after the invasion of green crabs than before it. Therefore, the presence of green crabs has a significant impact on food web stability and may contribute to further amplifying future changes in the intertidal community composition. Mussels are one of the main prey items of green crabs in Golfo Nuevo (Cordone et al. 2022). Although the mussel mass mortality events were not related to green crab presence, green crabs could have affected the recovery of the mussels by preying on them. Dare & Edwards (1976) observed high mortality of mussel beds due to green crab predation on smaller individuals in North Wales. Similarly, green crab predation pressure on mussels could be one of the reasons why the mussel beds have not yet recovered in the Golfo Nuevo. In the Northwestern Atlantic, green crabs have damaged bivalves, cumaceans, amphipods, and other crab populations (Grosholz & Ruiz 1995, 1996, Grosholz et al. 2000). It is expected that green crabs would also harm species of bivalves, amphipods, and other invertebrates — especially those that are their favorite prey — in Patagonia. The drastic changes registered in the ecosystem coincide with this presumption.

Mussel losses could simultaneously trigger changes in the green crab diet. We described the green crab diet before the mussel mass mortality events happened (Cordone et al. 2022). It is well known that green crabs can adapt their diet to prey availability. For example, green crabs altered their diet from bivalves to consuming more algae in the presence of a competitor species in the northwestern Atlantic (Griffen et al. 2008). However, in Golfo Nuevo, after mussel populations declined, the number of *Buccinastrum deforme* shells with signs of predation by green crabs increased (G. Bigatti pers. comm.), and artisanal fishermen reported substantial decreases in catches of this snail (D. Galván pers. obs.). An algae-based diet or increased consumption of a scavenger such as *B. deforme* could impact food web stability differently than a bivalve-based diet, as studied here.

4.3. Indirect effects of the green crab on the food web

4.3.1. Competitive interactions for food

We observed changes in most network metrics when assessing the indirect effects caused by the competitive interactions between the green crab and intertidal species. The meanTL, Om, Mod, and QSS decreased for the 3 cases evaluated. The only metric that showed an increase was CC. This response is consistent with the results obtained when considering the direct effect on the food web (Section 4.2). The incorporation of an omnivorous consumer of a high TL such as the green crab had such a great influence on network structure that even after removing several species, it continued to influence the CC. Although the patterns were similar for mobile species (Case A) and for sessile or sedentary species (Case B), we observed differences in the responses. CPL was not affected when sessile or sedentary species were disturbed, but it was when mobile species were disturbed. We expected the magnitude of the changes to be greater when disturbing both sessile and mobile species (Case C). This occurred for all metrics except QSS. QSS did not show differences when all susceptible species were disturbed together. This result highlights the non-linear nature of food webs since, given the sum of disturbances, network response is not necessarily equal to the sum of individual responses. Non-linearity is considered an essential feature of complexity where the principle of superposition (the sum of responses) does not apply (Ladyman et al. 2013).

We observed a decrease in food web Om when disturbing both sessile and mobile species (Case C). Om has a complex relationship with stability (McCann & Hastings 1997, Kuijper et al. 2003, Gellner & McCann 2012, Wootton 2017). A decrease in Om values in a network where weak interactions predominate can cause a decrease in network stability. It is necessary to estimate interaction strengths to determine the effect of the reduction in Om on intertidal food web stability. Predation pressure in the Patagonian rocky intertidal is low (Bertness et al. 2006, Hidalgo et al. 2007). Thus, if most trophic interactions in the intertidal food web are weak, the decrease in Om will result in a loss of stability. The alterations observed in the network metrics, when considering the indirect interactions resulting from competition for food, imply that the impact of green crabs on the structure and stability of the food web is greater than that caused by predation alone (Section 4.2). Hence, green crab presence increases the likelihood of recent and potential future changes being magnified in the intertidal ecosystem.

While a decrease in abundance or biomass of resident species is an early sign of the effects of an invasion, it cannot be detected through our approach (Ebenman & Jonsson 2005). The topological approach is only capable of reproducing the complete loss of one species as a local extinction or a range shift. It is highly probable that before a species is lost, green crab invasion leads to a decrease in the abundance and biomass of native competitors. Interspecific competition between green crabs and resident species is difficult to document in the field, but under laboratory conditions green crabs can out-compete other species such as the lobster *Homarus americanus* H. Milne Edwards, 1837 or the grapsid crab *Hemigrapsus oregonensis* (Dana, 1851) (Jensen et al. 2002, Williams et al. 2006, Young & Elliott 2019). Although it is impossible to replicate the decrease in abundance or biomass with the topological approach, it is useful to know how perturbations in focal species modify the structure and stability of the global network by simulating focal species loss in the food web (Albert et al. 2000, Dunne et al. 2004). In this sense, our results showed that potential competitive interactions between the green crab and resident species alter food web structure and may trigger negative consequences for food web stability.

4.3.2. Other indirect interactions

Beyond the effects that green crabs can cause as a result of competition for food, they can also establish other types of ecological interactions in invaded sites (Fig. 5). One of these possible interactions is the spread of parasites to native species. Green crabs are infected by more microparasites than native crabs in Golfo Nuevo (Frizzera et al. 2021). In this sense, green crabs could potentially transmit parasites to birds and carcinophagus fish in the invaded sites in the Patagonia rocky shores (Cordone et al. 2022). In the Dutch Wadden Sea, mass mortalities of birds have been related to the transmission of parasites by green crabs (Camphuysen et al. 2002). Additionally, green crabs altered snail feeding behavior and triggered changes in the abundance of barnacles and fucoid algae in rocky intertidal shores in New England (Trussell et al. 2002, 2003, 2017). Species of native snails at Golfo Nuevo may undergo similar effects and trigger analogous changes in the local community. Another possible competition interaction is for

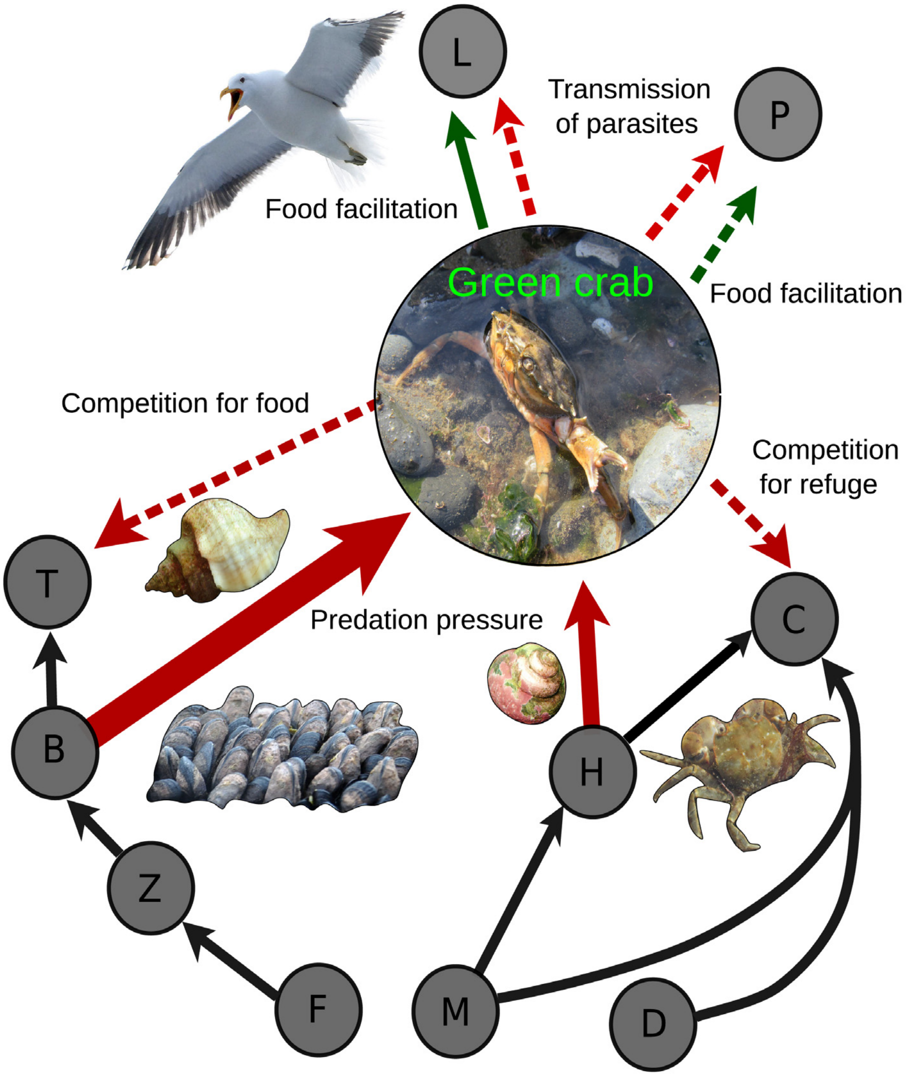

Fig. 5. Scheme of the confirmed and potential ecological interactions between the invasive green crab *Carcinus maenas* and resident species at the Atlantic Patagonian intertidal food webs. Solid lines: confirmed ecological interactions; dotted lines: potential interactions that are not yet confirmed. Solid red lines represent a direct negative relationship, which indicates predation on resident species. The width of the solid red line represents the food preference of the green crab. Dotted red lines: indirect negative relationship to resident species, which indicates competition for food or shelter and potential parasite transfer. Solid green line: a direct positive relationship to bird species through food facilitation. The dotted green line represents a possible positive relationship to carcinophagus fish by food facilitation. F: phytoplankton; M: macroalgae; D: detritus; Z: zooplankton; H: herbivores; C: native crabs such as *Cyrtograptus angulatus* or *C. altimanus*; B: bivalves; T: *Trophon geversianus*; L: *Larus dominicanus*; P: fishes. Photo credits: Antonela Leiva and Georgina Cordone

refuge. Green crabs compete with other crab species for refuge beneath rocks, shells, and other covers (Jensen et al. 2002). We observed that since green crabs arrived in Golfo Nuevo, other species of native crabs, e.g. *Cyrtograpsus* spp. Dana, 1851, are more difficult to find (G. Cordone pers. obs.). We hypothesize that green crabs compete with *Cyrtograpsus* spp. for shelter since refuges at the rocky intertidal are now largely occupied by green crabs (Fig. 5).

Green crabs can also harm native competitors by feeding on them. At our study site, the potential competitors detected by our selection criteria that were also prey for green crabs were fish. Fish were found in low frequency of occurrence in green crab guts (<2%) and could not be identified to the genus or species level (Cordone et al. 2022). The predation pressure exerted by green crabs on fish is probably low. However, prey items that are shared between fish and green crabs are the main prey of the green crabs, including amphipods, polychaetes, and bivalves. In this sense, the indirect effects of green crabs on fish species due to competitive interactions are probably more important to fish populations than the direct effect caused by green crab predation (Fig. 5).

4.4. Study limitations

One limitation of our work is the lack of information about interaction strengths. Estimating interaction strengths is not a simple task since several pieces of data on species' biology and ecology are required, such as intrinsic growth rates, carrying capacities, and predator attack rates, among others (Binzer et al. 2016). There are methods that propose that interaction strengths can be estimated from a few parameters, such as species biomass and metabolic rates (Barnes et al. 2018). We suggest that further studies be conducted to estimate the interaction strengths in the Patagonian intertidal food web based on these few-parameter methods. Interaction strengths would allow us to calculate weighted quantitative metrics and might yield new insights into the effects of green crab invasion that may go unnoticed with unweighted qualitative metrics (Bersier et al. 2002). Additionally, it would allow us to explore how changes in interaction strength may impact food web stability. As mentioned earlier, food webs with high O and weak interaction domination are more stable than those with high O and strong interaction domination. We observed that perturbations in all potential green crab competitors decreased O in the food web. If weak interactions dominate the food web with green crabs, then a reduction in O implies a loss of stability. On the other hand, if strong interactions dominate, then a decrease in O implies a gain in stability. Therefore, it is necessary to know the interaction strengths in the food web of the Patagonian rocky intertidal to clarify this issue.

Despite the aforementioned limitation, the approach used here was successful in detecting changes in the intertidal food web. Recently, green crab specimens were found in other Patagonian locations north of our study site (Müller Baigorria et al. 2022). Hidalgo et al. (2005) predicted that green crabs could colonize the eastern coast of South America from the mouth of the Magellan Strait (52° S) to southern Brazil (29° S) based on surface seawater temperature. More recently, Malvé et al. (preprint doi:10.1101/2020.11.04.368761) detected green crab presence at Puerto Lobos (42° S) and, using oceanographic variables and occurrence data, predicted a hotspot of invasibility around 40–33° S. One main limitation to green crab expansion is temperature; larvae can only develop at 10–22.5°C (de Rivera et al. 2007). Although adult green crabs can tolerate a wide range of temperatures, larvae physiological restriction may explain why green crabs were more successful in expanding towards lower latitudes than higher latitudes from the first detection point (Young & Elliott 2019, Malvé et al. preprint doi:10.1101/2020.11.04.368761). Global warming could promote the expansion of the green crab to higher latitudes. Higher temperatures increase invasion success in food webs (Sentis et al. 2021). Changes in fish assembly in Patagonia have already occurred; species from warmer waters are expanding into northern and central Patagonia, and alien species are advancing into central and southern Patagonia (Galván et al. 2022). Analogously, green crabs may expand south as a result of the temperature rise in Patagonia. Our results showed that their presence may alter the matter and energy flows of the Atlantic Patagonian intertidal assemblages by modifying food web structure and stability, particularly the capacity of the food web to recover after a disturbance. Green crabs established negative interactions with their prey and could potentially compete for food or refuge with other species, such as other crabs (Fig. 5). In addition, green crabs can become prey to species of higher TLs, birds or fishes, and potentially transmit parasites to their predators (Fig. 5). For this reason, it is of crucial importance to study and monitor rocky intertidal communities as this species continues to expand. Network studies like this allow the detection of potential resident species that are being increasingly threatened by non-native species. Species that have the potential to compete for food with green crabs at our study site could also be engaging in competition with green crabs in other Atlantic Patagonian ecosystems.

Acknowledgements. We thank Maria Martha Mendez, Juan Pablo Livore, Gregorio Bigatti, Florencia Ríos, Luciana Musmeci, and Pablo Yorio for their expert assessment of trophic interactions in the Patagonian rocky intertidal.

LITERATURE CITED

Albert R, Barabási AL (2002) Statistical mechanics of complex networks. Rev Mod Phys 74:47

Albert R, Jeong H, Barabási AL (2000) Error and attack tolerance of complex networks. Nature 406:378–382

Allesina S, Pascual M (2008) Network structure, predator–prey modules, and stability in large food webs. Theor Ecol 1:55–64

Alvarez MF, Esquius KS, Addino M, Alberti J, Iribarne O, Botto F (2013) Cascading top-down effects on estuarine intertidal meiofaunal and algal assemblages. J Exp Mar Biol Ecol 440:216–224

Amiraux R, Yurkowski DJ, Archambault P, Pierrejean M, Mundy CJ (2023) Top predator sea stars are the benthic equivalent to polar bears of the pelagic realm. Proc Natl Acad Sci USA 120:e2216701120

Anton A, Geraldi NR, Lovelock CE, Apostolaki ET and others (2019) Global ecological impacts of marine exotic species. Nat Ecol Evol 3:787–800

Barnes AD, Jochum M, Lefcheck JS, Eisenhauer N and others (2018) Energy flux: the link between multitrophic biodiversity and ecosystem functioning. Trends Ecol Evol 33: 186–197

Bascompte J (2009) Disentangling the web of life. Science 325:416–419

Belleggia M, Giberto A, Bremec C (2017) Adapting the diet in a changed environment: increased consumption of the lobster krill *Munida gregaria* (Fabricius, 1793) by Argentine hake. Mar Ecol 38:e12445

Bersier LF (2007) A history of the study of ecological networks. In: Képès F (ed) Biological networks. Complex systems and interdisciplinary science, Vol 3. World Scientific, Singapore, p 365–421

Bersier LF, Banašek-Richter C, Cattin MF (2002) Quantitative descriptors of food-web matrices. Ecology 83:2394–2407

Bertness MD, Crain CM, Silliman BR, Bazterrica MC, Reyna MV, Hildago F, Farina JK (2006) The community structure of western Atlantic Patagonian rocky shores. Ecol Monogr 76:439–460

Binzer A, Guill C, Rall BC, Brose U (2016) Interactive effects of warming, eutrophication and size structure: impacts on biodiversity and food web structure. Glob Change Biol 22:220–227

Borrelli JJ, Ginzburg LR (2014) Why there are so few trophic levels: selection against instability explains the pattern. Food Webs 1:10–17

Borrvall C, Ebenman B, Tomas Jonsson TJ (2000) Biodiversity lessens the risk of cascading extinction in model food webs. Ecol Lett 3:131–136

Briand F, Cohen JE (1984) Community food webs have scale-invariant structure. Nature 307:264–267

Bunicontro MP, Marcomini SC, Casas GN (2019) Environmental impacts of an alien kelp species (*Undaria pinnatifida*, Laminariales) along the Patagonian coasts. In: Makowski C, Finkl CW (eds) Impacts of invasive species on coastal environments. Springer, Cham, p 373–396

Camphuysen CJ, Berrevoets CM, Cremers HJWM, Dekinga A and others (2002) Mass mortality of common eiders (*Somateria mollissima*) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. Biol Conserv 106:303–317

Canale CI, Henry PY (2010) Adaptive phenotypic plasticity and resilience of vertebrates to increasing climatic unpredictability. Clim Res 43:135–147

Chen RB, Watanabe S, Yokota M (2004) Feeding habits of an exotic species, the Mediterranean green crab *Carcinus aestuarii*, in Tokyo Bay. Fish Sci 70:430–435

Ciancio JE, Pascual MA, Botto F, Frere E, Iribarne O (2008) Trophic relationships of exotic anadromous salmonids in the southern Patagonian Shelf as inferred from stable isotopes. Limnol Oceanogr 53:788–798

Cohen JE (1977) Food webs and the dimensionality of trophic niche space. Proc Natl Acad Sci USA 74:4533–4536

Cohen JE, Briand F, Newman C (1990) Community food webs: data and theory. Biomathematics, Vol 20. Springer Science & Business Media, Berlin Heidelberg

Cordone GF (2022) Respuesta de redes tróficas marinas costeras a estresores en las regiones antártica y subantártica: incremento de la temperatura y especies invasoras. PhD dissertation, Universidad de Buenos Aires

Cordone G, Marina TI, Salinas V, Doyle SR, Saravia LA, Momo FR (2018) Effects of macroalgae loss in an Antarctic marine food web: applying extinction thresholds to food web studies. PeerJ 6:e5531

Cordone G, Salinas V, Marina TI, Doyle SR, Pasotti F, Saravia LA, Momo FR (2020) Green vs brown food web: effects of habitat type on multidimensional stability proxies for a highly-resolved Antarctic food web. Food Webs 25:e00166

Cordone G, Lozada M, Vilacoba E, Thalinger B and others (2022) Metabarcoding, direct stomach observation and stable isotope analysis reveal a highly diverse diet for the invasive green crab in Atlantic Patagonia. Biol Invasions 24:505–526

Dangremond EM, Pardini EA, Knight TM (2010) Apparent competition with an invasive plant hastens the extinction of an endangered lupine. Ecology 91:2261–2271

Dare PJ, Edwards DB (1976) Experiments on the survival, growth and yield of relaid seed mussels (*Mytilus edulis* L.) in the Menai Straits, North Wales. ICES J Mar Sci 37: 16–28

David P, Thebault E, Anneville O, Duyck PF, Chapuis E, Loeuille N (2017) Impacts of invasive species on food webs: a review of empirical data. Adv Ecol Res 56:1–60

de Rivera CE, Hitchcock NG, Teck SJ, Steves BP, Hines AH, Ruiz GM (2007) Larval development rate predicts range expansion of an introduced crab. Mar Biol 150: 1275–1288

Drenovsky RE, Grewell BJ, D'Antonio CM, Funk JL and others (2012) A functional trait perspective on plant invasion. Ann Bot 110:141–153

Dunne JA (2006) The network structure of food webs. In: Pascual M, Dunne JA (eds) Ecological networks: linking structure to dynamics in food webs. Oxford University Press, New York, NY, p 27–86

Dunne JA, Williams RJ, Martinez ND (2004) Network structure and robustness of marine food webs. Mar Ecol Prog Ser 273:291–302

Ebenman B, Jonsson T (2005) Using community viability analysis to identify fragile systems and keystone species. Trends Ecol Evol 20:568–575

Ebenman BO, Law R, Borrvall C (2004) Community viability analysis: the response of ecological communities to species loss. Ecology 85:2591–2600

Eklöf A, Tang S, Allesina S (2013) Secondary extinctions in food webs: a Bayesian network approach. Methods Ecol Evol 4:760–770

Ens NJ, Harvey B, Davies MM, Thomson HM and others (2022) The green wave: reviewing the environmental impacts of the invasive European green crab (*Carcinus maenas*) and potential management approaches. Environ Rev 30:306–322

Frizzera A, Bojko J, Cremonte F, Vázquez N (2021) Symbionts of invasive and native crabs, in Argentina: the most recently invaded area on the Southwestern Atlantic coastline. J Invertebr Pathol 184:107650

Frost CM, Allen WJ, Courchamp F, Jeschke JM, Saul WC, Wardle DA (2019) Using network theory to understand

and predict biological invasions. Trends Ecol Evol 34: 831–843

Funes M, Saravia LA, Cordone G, Iribarne OO, Galván DE (2022) Network analysis suggests changes in food web stability produced by bottom trawl fishery in Patagonia. Sci Rep 12:10876

Galiana N, Lurgi M, Montoya JM, López BC (2014) Invasions cause biodiversity loss and community simplification in vertebrate food webs. Oikos 123:721–728

Gallardo B, Clavero M, Sánchez MI, Vilà M (2016) Global ecological impacts of invasive species in aquatic ecosystems. Glob Change Biol 22:151–163

Galván DE, Bovcon ND, Cochia PD, González RA and others (2022) Changes in the specific and biogeographic composition of coastal fish assemblages in Patagonia, driven by climate change, fishing, and invasion by alien species. In: Helbling EW, Narvarte MA, González RA, Villafañe VE (eds) Global change in Atlantic coastal Patagonian ecosystems. Springer, Cham, p 205–231

Gellner G, McCann K (2012) Reconciling the omnivory-stability debate. Am Nat 179:22–37

Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. PLOS ONE 7:e32596

Griffen BD, Guy T, Buck JC (2008) Inhibition between invasives: a newly introduced predator moderates the impacts of a previously established invasive predator. J Anim Ecol 77:32–40

Grilli J, Rogers T, Allesina S (2016) Modularity and stability in ecological communities. Nat Commun 7:12031

Grosholz ED, Ruiz GM (1995) Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. Mar Biol 122:239–247

Grosholz ED, Ruiz GM (1996) Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas.* Biol Conserv 78:59–66

Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL, Connors PG (2000) The impacts of a nonindigenous marine predator in a California bay. Ecology 81:1206–1224

Gulka J, Carvalho PC, Jenkins E, Johnson K, Maynard L, Davoren GK (2017) Dietary niche shifts of multiple marine predators under varying prey availability on the northeast Newfoundland coast. Front Mar Sci 4:324

Hidalgo FJ, Barón PJ, Orensanz JML (2005) A prediction come true: the green crab invades the Patagonian coast. Biol Invasions 7:547–552

Hidalgo FJ, Silliman BR, Bazterrica MC, Bertness MD (2007) Predation on the rocky shores of Patagonia, Argentina. Estuaries Coasts 30:886–894

Holt RA, Lawton JH (1994) The ecological consequences of shared natural enemies. Annu Rev Ecol Syst 25:495–520

Hughes AD, Brunner L, Cook EJ, Kelly MS, Wilson B (2012) Echinoderms display morphological and behavioural phenotypic plasticity in response to their trophic environment. PLOS ONE 7:e41243

Hui C, Richardson DM, Landi P, Minoarivelo HO, Garnas J, Roy HE (2016) Defining invasiveness and invasibility in ecological networks. Biol Invasions 18:971–983

Irigoyen AJ, Trobbiani G, Sgarlatta MP, Raffo MP (2011a) Effects of the alien algae *Undaria pinnatifida* (Phaeophyceae, Laminariales) on the diversity and abundance of benthic macrofauna in Golfo Nuevo (Patagonia, Argentina): potential implications for local food webs. Biol Invasions 13:1521–1532

Irigoyen AJ, Eyras C, Parma AM (2011b) Alien algae *Undaria pinnatifida* causes habitat loss for rocky reef fishes in north Patagonia. Biol Invasions 13:17–24

Jensen GC, McDonald PS, Armstrong DA (2002) East meets west: competitive interactions between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsus* spp. Mar Ecol Prog Ser 225:251–262

Kaunzinger CM, Morin PJ (1998) Productivity controls food-chain properties in microbial communities. Nature 395: 495–497

Kennedy TA, Naeem S, Howe KM, Knops JM, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasion. Nature 417:636–638

Koen Alonso MK, Crespo EA, García NA, Pedraza SN, Mariotti PA, Mora NJ (2002) Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. Environ Biol Fishes 63:193–202

Kortsch S, Primicerio R, Aschan M, Lind S, Dolgov AV, Planque B (2019) Food-web structure varies along environmental gradients in a high-latitude marine ecosystem. Ecography 42:295–308

Korzybski A (1933) Science and sanity. An introduction to non-Aristotelian systems and general semantics. Institute of General Semantics, New York, NY, p 747–761

Krause AE, Frank KA, Mason DM, Ulanowicz RE, Taylor WW (2003) Compartments revealed in food-web structure. Nature 426:282–285

Kuijper LD, Kooi BW, Zonneveld C, Kooijman SA (2003) Omnivory and food web dynamics. Ecol Model 163: 19–32

Ladyman J, Lambert J, Wiesner K (2013) What is a complex system? Eur J Philos Sci 3:33–67

Landi P, Minoarivelo HO, Brännström Å, Hui C, Dieckmann U (2018) Complexity and stability of adaptive ecological networks: a survey of the theory in community ecology. In: Mensah P, Katerere D, Hachigonta S, Roodt A (eds) Systems analysis approach for complex global challenges. Springer, Cham, p 209–248

Layman CA, Allgeier JE (2012) Characterizing trophic ecology of generalist consumers: a case study of the invasive lionfish in The Bahamas. Mar Ecol Prog Ser 448:131–141

Layman CA, Giery ST, Buhler S, Rossi R and others (2015) A primer on the history of food web ecology: fundamental contributions of fourteen researchers. Food Webs 4:14–24

Lindeman RL (1942) The trophic-dynamic aspect of ecology. Ecology 23:399–417

Locke A, Hanson JM, Ellis KM, Thompson J, Rochette R (2007) Invasion of the southern Gulf of St. Lawrence by the clubbed tunicate (*Styela clava* Herdman): potential mechanisms for invasions of Prince Edward Island estuaries. J Exp Mar Biol Ecol 342:69–77

Lozada M, Zabala MS, García PE, Diéguez MC and others (2022) Microbial assemblages associated with the invasive kelp *Undaria pinnatifida* in Patagonian coastal waters: structure and alginolytic potential. Sci Total Environ 830:154629

Lundgren JR (1989) Food webs, competition graphs, competition-common enemy graphs, and niche graphs. In: Roberts F (ed) Applications of combinatorics and graph theory to the biological and social sciences. The IMA volumes in mathematics and its applications, Vol 17. Springer, New York, NY, p 221–243

Lurgi M, Galiana N, López BC, Joppa LN, Montoya JM (2014) Network complexity and species traits mediate the effects of biological invasions on dynamic food webs. Front Ecol Evol 2:36

Mair P, Wilcox RR (2020) Robust statistical methods in R using the WRS2 package. Behav Res Methods 52:464–488

Marina TI, Saravia LA, Cordone G, Salinas V, Doyle SR, Momo FR (2018) Architecture of marine food webs: to be or not be a 'small-world'. PLOS ONE 13:e0198217

McCann KS, Hastings A (1997) Re-evaluating the omnivory-stability relationship in food webs. Proc R Soc B 264: 1249–1254

McDonald PS, Jensen GC, Armstrong DA (2001) The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. J Exp Mar Biol Ecol 258: 39–54

McMeans BC, Rooney N, Arts MT, Fisk AT (2013) Food web structure of a coastal Arctic marine ecosystem and implications for stability. Mar Ecol Prog Ser 482:17–28

Medina FM, Bonnaud E, Vidal E, Tershy BR and others (2011) A global review of the impacts of invasive cats on island endangered vertebrates. Glob Change Biol 17:3503–3510

Mendez MM, Livore JP, Márquez F, Bigatti G (2021) Mass mortality of foundation species on rocky shores: testing a methodology for a continental monitoring program. Front Mar Sci 8:620866

Mendonça V, Madeira C, Dias M, Vermandele F and others (2018) What's in a tide pool? Just as much food web network complexity as in large open ecosystems. PLOS ONE 13:e0200066

Miner BG, Sultan SE, Morgan SG, Padilla DK, Relyea RA (2005) Ecological consequences of phenotypic plasticity. Trends Ecol Evol 20:685–692

Monteiro AB, Faria LDB (2016) The interplay between population stability and food-web topology predicts the occurrence of motifs in complex food-webs. J Theor Biol 409:165–171

Montoya JM, Solé RV (2003) Topological properties of food webs: from real data to community assembly models. Oikos 102:614–622

Moran MD, Rooney TP, Hurd LE (1996) Top down cascade from a bitrophic predator in an old-field community. Ecology 77:2219–2227

Müller Baigorria M, Aguilar A, Cabrera Galeano D, Fraire S and others (2022) Caracterización demográfica del cangrejo verde, *Carcinus maenas*, en dos sectores costeros de Las Grutas, Río Negro, Argentina. Informe Técnico No. UNCo-ESCiMAR-01-2022. Escuela Superior de Ciencias Marinas, Universidad Nacional del Comahue. http://rdi.uncoma.edu.ar/bitstream/handle/uncomaid/16872/Informe%20T%C3%A9cnico%20ESCiMar%2001_2022.pdf?sequence=1

Newman ME (2003) The structure and function of complex networks. SIAM Rev 45:167–256

Newman ME, Girvan M (2004) Finding and evaluating community structure in networks. Phys Rev E Stat Nonlin Soft Matter Phys 69:026113

Norin T, Metcalfe NB (2019) Ecological and evolutionary consequences of metabolic rate plasticity in response to environmental change. Phil Trans R Soc B 374:20180180

Odum WE, Heald EJ (1975) The detritus-based food web of an estuarine mangrove community. In: Cronin LE (ed) Estuarine research, Vol 1. Academic Press, New York, NY, p 265–268

Orensanz JM, Schwindt E, Pastorino G, Bortolus A and others (2002) No longer a pristine confine of the world ocean — a survey of exotic marine species in the Southwestern Atlantic. Biol Invasions 4:115–143

Palomo MG, Bagur M, Calla S, Dalton MC, Soria SA, Hawkins SJ (2019) Biodiversity and interactions on the intertidal rocky shores of Argentina (south-west Atlantic). In: Hawkins S, Bohn K, Firth L, Williams G (eds) Interactions in the marine benthos: global patterns and processes. Systematics Association special volume series. Cambridge University Press, Cambridge, p 164–189

Papacostas KJ, Freestone AL (2019) Stronger predation in a subtropical community dampens an invasive species-induced trophic cascade. Biol Invasions 21:203–215

Pascual M, Dunne J (2006) Ecological networks. Linking structure to dynamics in food webs. Oxford University Press, Oxford

Pasti AT, Bovcon ND, Ruibal-Núñez J, Navoa X, Jacobi KJ, Galván DE (2021) The diet of *Mustelus schmitti* in areas with and without commercial bottom trawling (Central Patagonia, Southwestern Atlantic): Is it evidence of trophic interaction with the Patagonian shrimp fishery? Food Webs 29:e00214

Pimm SL (1982) Food webs. Springer, Dordrecht

Poirier LA, Symington LA, Davidson J, St-Hilaire S, Quijón PA (2017) Exploring the decline of oyster beds in Atlantic Canada shorelines: potential effects of crab predation on American oysters (*Crassostrea virginica*). Helgol Mar Res 71:13

Rechimont ME, Galván DE, Sueiro MC, Casas G and others (2013) Benthic diversity and assemblage structure of a north Patagonian rocky shore: a monitoring legacy of the NaGISA project. J Mar Biol Assoc UK 93:2049–2058

Riede JO, Binzer A, Brose U, de Castro F, Curtsdotter A, Rall BC, Eklöf A (2011) Size-based food web characteristics govern the response to species extinctions. Basic Appl Ecol 12:581–589

Ripple WJ, Estes JA, Schmitz OJ, Constant V and others (2016) What is a trophic cascade? Trends Ecol Evol 31: 842–849

Rodríguez LF (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biol Invasions 8:927–939

Rodriguez ID, Marina TI, Schloss IR, Saravia LA (2022) Marine food webs are more complex but less stable in sub-Antarctic (Beagle Channel, Argentina) than in Antarctic (Potter Cove, Antarctic Peninsula) regions. Mar Environ Res 174:105561

Rooney N, McCann KS (2012) Integrating food web diversity, structure and stability. Trends Ecol Evol 27:40–46

Rossong MA, Quijón PA, Snelgrove PV, Barrett TJ, McKenzie CH, Locke A (2012) Regional differences in foraging behaviour of invasive green crab (*Carcinus maenas*) populations in Atlantic Canada. Biol Invasions 14:659–669

Saravia LA (2019) lsaravia/multiweb: R package for multiple interaction ecological networks, version v0.2.9. https://github.com/lsaravia/multiweb

Schaal G, Riera P, Leroux C, Grall J (2010) A seasonal stable isotope survey of the food web associated to a peri-urban rocky shore. Mar Biol 157:283–294

Schwindt E, Carlton JT, Orensanz JM, Scarabino F, Bortolus A (2020) Past and future of the marine bioinvasions along the Southwestern Atlantic. Aquat Invasions 15:11–29

Sentis A, Montoya JM, Lurgi M (2021) Warming indirectly increases invasion success in food webs. Proc R Soc B 288:20202622

Smith-Ramesh LM, Moore AC, Schmitz OJ (2017) Global synthesis suggests that food web connectance correlates to invasion resistance. Glob Change Biol 23:465–473

Stachowicz JJ, Byrnes JE (2006) Species diversity, invasion success, and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. Mar Ecol Prog Ser 311:251–262

Stouffer DB, Bascompte J (2011) Compartmentalization increases food-web persistence. Proc Natl Acad Sci USA 108:3648–3652

Strona G, Nappo D, Boccacci F, Fattorini S, San-Miguel-Ayanz J (2014) A fast and unbiased procedure to randomize ecological binary matrices with fixed row and column totals. Nat Commun 5:4114

Thomsen MS, Wernberg T, Altieri A, Tuya F and others (2010) Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integr Comp Biol 50:158–175

Thomsen MS, Olden JD, Wernberg T, Griffin JN, Silliman BR (2011a) A broad framework to organize and compare ecological invasion impacts. Environ Res 111: 899–908

Thomsen MS, Wernberg T, Olden JD, Griffin JN, Silliman BR (2011b) A framework to study the context-dependent impacts of marine invasions. J Exp Mar Biol Ecol 400: 322–327

Torres PJ, González-Pisani X (2016) Primer registro del cangrejo verde, *Carcinus maenas* (Linnaeus, 1758), en Golfo Nuevo, Argentina: un nuevo límite norte de distribución en costas patagónicas. Ecol Austral 26:134–137

Trussell GC, Ewanchuk PJ, Bertness MD (2002) Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. Ecol Lett 5:241–245

Trussell GC, Ewanchuk PJ, Bertness MD (2003) Trait-mediated effects in rocky intertidal food chains: predator risk cues alter prey feeding rates. Ecology 84:629–640

Trussell GC, Matassa CM, Ewanchuk PJ (2017) Moving beyond linear food chains: trait-mediated indirect interactions in a rocky intertidal food web. Proc R Soc B 284: 20162590

Vermaat JE, Dunne JA, Gilbert AJ (2009) Major dimensions in food-web structure properties. Ecology 90: 278–282

Vinagre C, Mendonça V, Narciso L, Madeira C (2015) Food web of the intertidal rocky shore of the west Portuguese coast — determined by stable isotope analysis. Mar Environ Res 110:53–60

Vinagre C, Mendonça V, Flores AA, Baeta A, Marques JC (2018) Complex food webs of tropical intertidal rocky shores (SE Brazil) — an isotopic perspective. Ecol Indic 95:485–491

White EM, Wilson JC, Clarke AR (2006) Biotic indirect effects: a neglected concept in invasion biology. Divers Distrib 12:443–455

Wilcox R (2018) A robust nonparametric measure of effect size based on an analog of Cohen's *d*, plus inferences about the median of the typical difference. J Mod Appl Stat Methods 17:eP2726

Williams PJ, Floyd TA, Rossong MA (2006) Agonistic interactions between invasive green crabs, *Carcinus maenas* (Linnaeus), and sub-adult American lobsters, *Homarus americanus* (Milne Edwards). J Exp Mar Biol Ecol 329: 66–74

Wootton KL (2017) Omnivory and stability in freshwater habitats: Does theory match reality? Freshw Biol 62: 821–832

Yorio P, Suárez N, Kasinsky T, Pollicelli M, Ibarra C, Gatto A (2020) The introduced green crab (*Carcinus maenas*) as a novel food resource for the opportunistic kelp gull (*Larus dominicanus*) in Argentine Patagonia. Aquat Invasions 15:140–159

Young AM, Elliott JA (2019) Life history and population dynamics of green crabs (*Carcinus maenas*). Fishes 5:4

Appendix. Equations

Trophic level (TL)

$$\mathrm{TL}_i = 1 + \sum\nolimits_{j=1}^{S} \mathrm{NT}_j \mathrm{DC}_{ij} \qquad \text{(A1)}$$

NT_j represents prey trophic level and DC_{ij} is the fraction of prey (j) in the diet of consumer (i). Basal species have a trophic level of 1.

Clustering coefficient (CC)

$$\mathrm{CC}_i = 2\frac{E_i}{k_i(k_i - 1)} \qquad \text{(A2)}$$

The CC reflects the probability that 2 nodes connected to a third node are also connected to each other. The k_i represents the degree of the focal node (i) and E_i is the actual number of neighbors of node (i) (i.e. the number of interactions). In the case of a directed graph, such as a food web, the maximum number of connections in a completely connected neighborhood is the denominator k_i (k_i − 1). When all nodes are neighbors, CC = 1.

Characteristic path length (CPL)

$$\mathrm{CPL} = \frac{2}{S(S-1)} \sum_{i=1}^{S} \sum_{j=1}^{S} \mathrm{CPL}_{\min}(i,j) \qquad \text{(A3)}$$

CPL is a measure of efficiency in transporting information through a network. $\mathrm{CPL}_{\min}$ (i,j) is the shortest path between nodes (i) and (j), and S is the total number of trophic species.

Modularity (Mod)

$$\mathrm{Mod} = \sum_{s} \frac{I_s}{L} - \frac{d_s}{2L} \qquad \text{(A4)}$$

Here, s is the number of modules or compartments, I_s is the number of interactions between species in module s, d_s is the sum of degrees for all species in module s, and L is the total number of interactions.

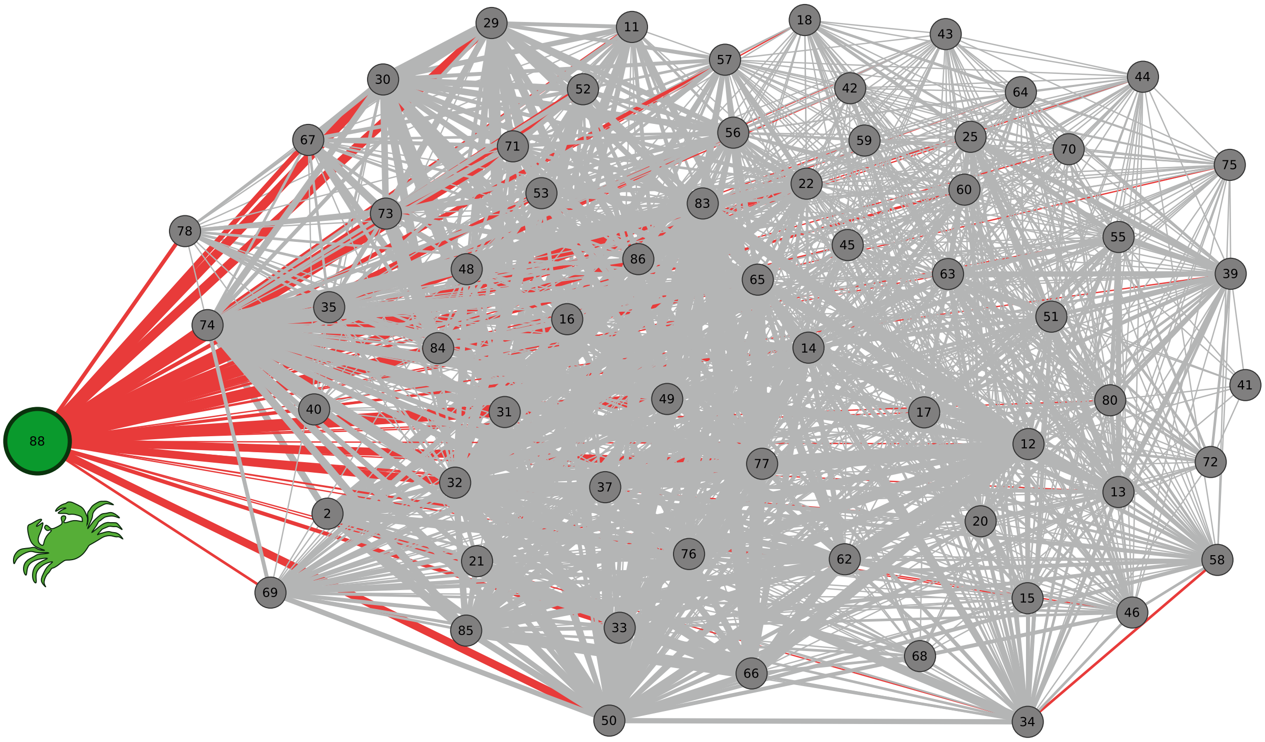

Fig. A1. Representation of the niche overlap graph. Each node represents a trophic species, and each arrow represents an indirect interaction between species. The arrow points out 2 species that share at least one prey. Arrow width is proportional to the number of shared prey; ID is indicated within the nodes (see Table A1). The green crab *Carcinus maenas* is represented as a green node, and its indirect interactions are highlighted in red

Table A1. Trophic species with their associated ID in the rocky intertidal food web of Puerto Madryn (Golfo Nuevo, Argentina)

Trophic species	ID	Trophic species	ID
Biofilm	1	Family Syllidae	45
Ampithoe sp.	2	Nematoda	46
Ceramium sp.	3	*Polysiphonia* sp.	47
Cladophora sp.	4	*Diadumene lineata*	48
Codium sp.	5	*Eleginops maclovinus*	49
Corallina officinalis	6	Family Polynoidae	50
Dictyota sp.	7	Family Terebellidae	51
Porphyra sp.	8	*Patagonotothen cornucola/sima*	52
Ulva prolifera	9	*Parabunodactis imperfecta*	53
Ulva spp.	10	*Epitonium fabrizio*	54
Anthothoe chilensis	11	Family Chaetopteridae	55
Idotea sp.	12	Heteronemertea	56
Mitilidae	13	Family Glyceridae	57
Sphaeroma/Exosphaeroma/Pseudosphaeroma	14	Family Hesionidae	58
Tanais dulongii	15	Family Spionidae	59
Arbacia dufresnii	16	Family Lumbrineridae	60
Balanus glandula	17	Necromass	61
Bryozoa	18	Chironomidae larvae	62
Diatoms	19	Family Sabellidae	63
Monocorophium sp.	20	Family Spirorbinae	64
Orchestia sp.	21	*Fissurella* sp.	65
Serolis sp.	22	*Tegula patagonica*	66
Undaria pinnatifida	23	*Haematopus ater*	67
Detritus	24	*Nacella magellanica*	68
Ascidiacea	25	*Halicarcinus planatus*	69
Phytoplankton	26	Haplotaxida	70
Particulate Organic Matter	27	*Helcogrammoides cunninghami*	71
Zooplankton	28	Hydrozoa	72
Calidris alba	29	*Larus dominicanus*	73
Calidris canutus rufa	30	*Leucippa pentagona*	74
Calidris fuscicollis	31	*Pachycheles chubutensis*	75
Cyrtograpsus spp.	32	*Plaxiphora aurata*	76
Family Eunicidae	33	*Pseudechinus magellanicus*	77
Family Nereididae	34	*Trophon geversianus*	78
Family Phyllodocidae	35	*Gracilaria gracilis*	79
Chaetomorpha sp.	36	*Lasaea adansoni*	80
Chaetopleura isabellei	37	*Ectocarpus* sp.	81
Cyanophyta	38	Sphacelariales	82
Demospongiae	39	Nudibranchia	83
Charadrius falklandicus	40	*Octopus tehuelchus*	84
Copepoda	41	*Siphonaria lessoni*	85
Cumacea	42	*Ribeiroclinus eigenmanni*	86
Family Capitellidae	43	*Ralfsia* sp.	87
Family Cirratulidae	44	*Carcinus maenas*	88

Editorial responsibility: Thomas Wernberg, Crawley, Western Australia, Australia
Reviewed by: 3 anonymous referees

Submitted: August 27, 2022
Accepted: May 23, 2023
Proofs received from author(s): June 22, 2023