



Original Article

Resource partitioning between fisheries and endangered sharks in a tropical marine food web

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Fisheries can act as top predators and affect marine biodiversity and ecosystem functioning via their target species. We studied a coastal food web in the Pacific Ocean that is modular and encompasses 360 species and small- and large-scale fisheries. Small-scale fisheries (SSF), two hammerhead sharks, one stingray, and one flatfish species are network hubs, interacting with multiple species among and within trophic levels (TLs) and modules. SSF and endangered hammerhead sharks act as hyper-hubs, which are network hubs preying on other network hubs and likely imposing widespread top-down effects. Hyper-hubs have two consequences to network structure. First, they show low dietary overlap, connecting the network in complementary ways. Second, they have overlapping indirect interactions, suggesting they can strongly affect each other. Simulations assuming distinct fishery regulations and species extinctions of different TLs and topological roles did not change network structure but redefined hub identity. We hypothesize that competition shapes resource partitioning between fisheries and hammerhead sharks. Our findings suggest that ecosystem-level strategies informed by network approaches can optimize investments to conserve marine ecosystems and ensure food security over coastal areas in the developing world.

Keywords: artisanal fisheries, evidence-based conservation, industrial fisheries, the ghost of competition past

Introduction

Human activities are fundamental processes currently shaping biodiversity patterns and ecosystem functioning over the Earth (Young *et al.*, 2016). Anthropogenic changes threaten ecosystems, urging

us to develop evidence-based approaches to reconcile economic activities, social welfare, and biodiversity conservation (Worm *et al.*, 2009; Lotze *et al.*, 2011). Marine food production is one essential ecosystem service threatened by anthropogenic changes (Costanza *et al.*, 1997). Anthropogenic changes threatening marine ecosys-

tems and food production include pollution (Nixon, 1995), alien species (Bax *et al.*, 2003), climate change (Hillebrand *et al.*, 2018), and overfishing (Pauly and Zeller, 2016). Specifically, overfishing is a severe threat to food provision, jeopardizing human populations that depend on fishing (FAO, 2020).

Overfishing has widespread effects on marine biodiversity, from the fitness of individuals (Pinsky and Palumbi, 2014) to the distribution of abundances and body sizes within populations (Pauly *et al.*, 1998; Baum and Worm, 2009) and patterns of species interaction (Gaichas and Francis, 2008; Navia *et al.*, 2012). Ecological networks describe patterns of species interactions at different spatio-temporal scales (Guimarães, 2020). At the ecosystem level, networks bridge our understanding of community structure and dynamics (Jordano, 2016), for example, by quantifying the species roles in community structure (Guimarães, 2020). In this sense, a recurrent structural pattern shown by ecological networks is modularity, in which groups of species interact more frequently among themselves than with other species within the network (Stouffer and Bascompte, 2011).

Distinct mechanisms, such as adaptive processes shaping ecological traits or interspecific variation in habitat specialization, can lead to modular food webs (Krause *et al.*, 2003; Rezende *et al.*, 2009). Theory predicts that modularity enhances food web stability (May, 1973; Stouffer and Bascompte, 2011) by minimizing perturbation spreading (Krause *et al.*, 2003). Empirical data show that modularity can sustain the long-term persistence of food webs even under intense environmental and fishing pressures (D'Alelio *et al.*, 2019). Understanding how modularity enhances biodiversity persistence depends on quantifying species roles in the network structure. For example, lower incidences of highly connected species (network hubs) and other species whose interactions connect modules reduce the number of pathways that otherwise would allow cascading effects across the food web (Myers *et al.*, 2007).

Networks allow in-depth assessments of the ecological consequences of fishing via direct and indirect effects (Bieg *et al.*, 2018). Thus, network approaches complement other approaches that address fishing impacts on community properties (Worm *et al.*, 2009; Lotze *et al.*, 2011). For instance, the incorporation of fisheries as nodes within food webs provides insights into their impacts on marine communities (Dunne *et al.*, 2016; Pérez-Matus *et al.*, 2017; Glaum *et al.*, 2020; Ávila-Thieme *et al.*, 2021). Such studies address, for example, how the decline of top predators triggers trophic cascades (Estes *et al.*, 1998; Bascompte *et al.*, 2005); the spread of fishing effects via short interaction chains and small sets of target species (Gaichas and Francis, 2008; Navia *et al.*, 2016); and the impacts of fisheries as super-generalist consumers (Dunne *et al.*, 2016; Pérez-Matus *et al.*, 2017), which can be positive for some non-target species (Ávila-Thieme *et al.*, 2021) but often impose adverse outcomes for biodiversity persistence and fisheries (Glaum *et al.*, 2020).

One next step to improve evidence-based conservation strategies is to use the socio-ecological perspective on food web dynamics to study the interplay between marine species and fisheries in shaping ecological networks (Márquez-Velásquez *et al.*, 2020). For example, it is relevant to assess whether interaction patterns of fisheries and top and mesopredators are redundant or complementary (Yodzis, 2001; Pichegru *et al.*, 2009). Large sharks play central roles within marine food webs (Navia *et al.*, 2010; Bornatowski *et al.*, 2014). Describing shark dietary overlap with fishing targets can unravel mechanisms shaping their contemporary patterns of resource use and inform conservation strategies for these endangered species (Dulvy *et al.*, 2014).

Ecological theory posits interspecific competition is a fundamental mechanism underlying patterns of ecological interactions (MacArthur and Levins, 1967; Connell, 1980). Prey abundance can often be a limiting factor leading to intense competition among marine predators (Ward *et al.*, 2006; Hayata *et al.*, 2021). Consequently, contemporary patterns of resource partitioning among predators can result from evolutionary divergence among competing species (MacArthur and Levins, 1967; Connell, 1980). Given the widespread effects of anthropogenic activities on food webs, the human-induced rewiring of trophic interactions can reshape interspecific competition patterns and lead to novel forms of resource partitioning (Baum and Worm, 2009).

We combined data on fishing patterns and trophic interactions to assemble a coastal marine food web subject to intensive fishing in the tropical Pacific Ocean. Our goals were to (i) describe the food web structure and the topological roles species and fisheries play; (ii) assessing whether fisheries and keystone predators have redundant or complementary interaction patterns; (iii) determine how anthropogenic threats vary according to species roles; and (iv) assess potential effects of species extinctions and restrictions on fisheries, on food web structure, and species roles.

Material and methods

Species-interaction data

We obtained species-interaction data from stomach contents of species caught by shrimp fisheries in the coast of Colombia [2° 45'N, 78° 10'W–3° 50'N, 77° 20'W; see Navia *et al.* (2016) and Supplementary Figure S3]. We assembled data from 11 203 stomachs of 59 predator species and found 301 prey species (Supplementary Table S1).

Artisanal and industrial fleets and their catches

We added small-scale fisheries (SSF) and large-scale fisheries (LSF) as additional nodes, and their catches as additional links in the network. SSF encompass various fishing gears, including bottom trawls used by shallow-water shrimp fisheries, hand lines, longlines, gill-nets, and beach seines. LSF include exclusively deep-water shrimp fisheries (Gallardo *et al.*, 2018). Both SSF and LSF primarily target shrimps, and their bycatches encompass many fish and invertebrate species. We used only presence/absence interaction data because information on species abundance, biomass, and catch rates are currently unavailable for the study area.

Network structure

We summarized species-interaction data in an adjacency matrix, **A**, depicting all trophic interactions and fishing targets. The element a_{ij} of **A** is 1 if species i and j interact and 0 otherwise. We computed the trophic level (TL) for each species using data from the literature and the databases *Fish Base* (Froese and Pauly, 2018) and *Sea Around Us* (www.seaaroundus.org). We categorized TLs as TL 1: <2, TL 2: 2.00–2.50, TL 3: 2.51–3.00 (lower TLs), TL 4: 3.01–4.00 (intermediate TLs), and TL 5: >4.01 (higher TLs). We used Gephi 0.9.2 (Bastian *et al.*, 2009) and Network Splitter 3D by A. Barão (<https://gephi.org/plugins/#/plugin/network-splitter-3d>) to draw food webs. We computed connectance as $C = L/S^2$ (Martinez, 1992), where L is the number of observed interactions and S is the number of nodes. We computed modularity metric M (New-

man and Girvan, 2004) combined with the simulated annealing optimization algorithm (Guimerà and Amaral, 2005; see the Supplementary material for details).

Species roles

We used two approaches to characterize the role of species and fisheries in the network structure. First, we combined the standardized within-module degree (z) and among-module connectivity (c) to define the role of a node i (Guimerà and Amaral, 2005, see the Supplementary material for thresholds). Second, we used two centrality metrics (Freeman, 1978) as a proxy for each species influence on the network. Specifically, we used (i) closeness centrality (CC), which describes the shortest paths from a given node to all other nodes to describe the influence of a given node in terms of short indirect pathways to other species in the network; and (ii) betweenness centrality (BC), which depicts how often a node i belongs to the shortest path between nodes j and k (Freeman, 1978) and describes the influence of a node as their participation in the pathways connecting nodes in the network. We used UCINET IV (Borgatti *et al.*, 2002) to compute CC and BC .

Threat statuses and species contribution to network structure

To investigate the relationship between a species' threat status and its contribution to network structure, we used threat statuses from the IUCN red list (IUCN, 2020) and the Colombian national conservation status (Ardila *et al.*, 2002; Chasqui *et al.*, 2017), when available. The Colombian threat categories are relevant because species may be threatened only at the national level (Supplementary Table S1). We merged the "vulnerable" and "near-threatened" statuses into a single "higher risk" category. We included species under the status "least concern" in the "lower risk" category as these widespread and abundant taxa are unlikely to die out in the near future (IUCN, 2020).

We performed a principal component analysis on the correlation matrix among node degree (D_i), within-module degree (z_i), and among-module connectivity (c_i). Subsequently, we used the resulting first principal component as a proxy for species contributions to network structure, U (Estrada, 2007; Sazima *et al.*, 2010; Vidal *et al.*, 2014). This approach provides a metric that synthetically describes several aspects of species contributions to network structure (see Costa *et al.*, 2007). We investigated the relationship between threat statuses and species contributions to network structure using a two-sample randomization test (Manly, 1997; see the Supplementary material).

Interaction similarity and indirect effects

We computed Jaccard's similarity index (Jaccard, 1912) to describe pairwise similarities in dietary items between fisheries and all the species within the food web (See Supplementary material). Complementarily, we computed the topological overlap index, TO^3 (Jordán, 2009), to describe the trophic overlap between species based on their indirect pathways (see Supplementary material for details). We computed TO^3 using CoSbiLab Graph (Valentini and Jordán, 2010).

Simulations of species extinctions and fishery regulations

We used simulations to assess the potential impacts of (i) species extinctions and (ii) fishery regulations on food web structure. We removed only one focal node (SSF, LSF, or a given species) and its interactions from the food web in each simulation scenario. Following the removal of the focal species and its links, we re-computed modularity (M), within-module degree (z_i), and among-module connectivity (c_i). Thus, our extinction scenarios encompassed species belonging to all possible combinations of species roles and TLs (Supplementary Tables S2 and S3). Whenever possible, we simulated the extinction of fishing target and non-target species for each TL and topological role, one species at a time (Gallardo *et al.*, 2018, Supplementary material). To simulate restrictive regulations on fisheries, we performed additional simulations removing small- and large-scale shrimp fisheries independently. Finally, we simulated a catastrophic extinction event simultaneously involving all 11 species previously removed (independently) belonging to all TLs and topological roles (Supplementary Tables S2 and S3).

Results

Food web structure

The food web without fisheries encompasses 360 species and 985 interactions. When we incorporated SSF and LSF and their catches, the number of links in the food web increased to 1090. The food web with fisheries had a higher average number of interactions per node (3.01 vs. 2.74) and connectance (0.0083 vs. 0.0076) than its counterpart without fisheries. The incorporation of fisheries as nodes led to a slight reduction in modularity, but both networks are significantly modular ($M = 0.51$ without fisheries and $M = 0.47$ with fisheries $p < 0.001$, $n = 500$ randomizations). The food web without fisheries has 7 modules whose sizes range between 25 and 95 taxonomic units, whereas the food web with fisheries has 9 modules ranging from 14 to 68 entities each (Table 1; Figure 1a and d).

Species roles

Networks hubs include a few predator species (less than 2% of the food web) and SSF (Figure 1c and f). In the food web without fisheries, network hubs encompass two *Sphyrna* hammerhead sharks, the smooth-hound shark *Mustelus lunulatus* and the brown sole *Achirus klunzingeri*. By including SSF, the smooth-hound shark *M. lunulatus* lost its status as a network hub, whereas the round stingray *Urotrygon rogersi* become one network hub, joining the brown sole and the two hammerheads. Network hubs connect the food web in distinct ways, as indicated by the fact that, in both cases, most network hubs belong to different modules (Figure 1c and f) and by the variation in centrality across network hubs. SSF and two hammerhead sharks show markedly higher betweenness and closeness centralities (Supplementary Table S1).

Module hubs are highly connected to species within a given module but have few connections with the rest of the network. They represent less than 4% of the species in both types of food webs. The similarity between food webs with and without fisheries extends to the taxonomic composition and TLs of module hubs, encompassing species of shrimps, bony fishes, and sharks (Figure 1c and f; Supplementary Table S1).

About 10% of the species are connectors that link modules. Connectors include the crab *Callinectes arcuatus*, the shrimp

Table 1. Structure of a tropical marine food web in the Colombian coast.

Descriptors	Food web with fisheries	Food web without fisheries
Number of nodes (S)	362	360
Number of links (L)	1090	985
Average links per species (L/S)	3.01	2.74
Connectance	0.0083	0.0076
Number of modules	9	7
Modularity (M)	0.47*	0.51*
% Network hubs	1.38	1.11
% Module hubs	3.87	3.33
% Connectors	11.33	10.28
% Peripherals	83.43	85.28

Network metrics depict two alternative network constructions, one with and another without SSF and LSF and their catches as additional nodes and links. * $p < 0.001$.

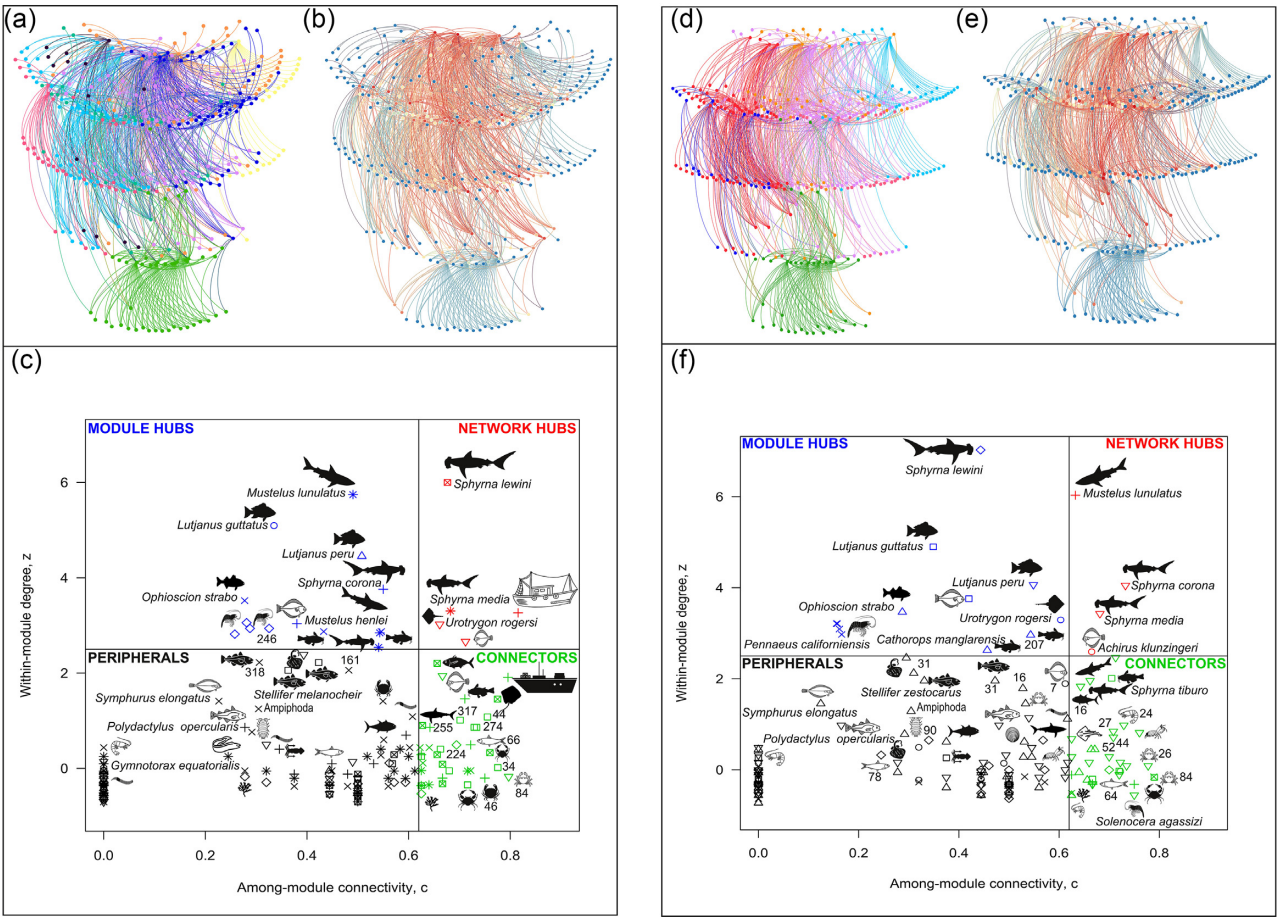


Figure 1. The modular structure of the coastal food web in the tropical Pacific region organized according to species' TL and interaction patterns. Food webs with (a and b) and without (d and e) fisheries and their catches as additional nodes and links. The colors of the nodes and links correspond to the modules to which each species belongs (a and d) and their among-module connectivity (b and e). In the temperature scale used for b and e, cold and hot colors indicate, respectively, low and high intermodular connectivity. The plots shown in c and f describe the topological roles of species within the network as defined by the coordinates (c, z) that depict the balance between intermodular connectivity (c) and intramodular connectivity (z). The point for each species is colored according to its topological role, which can be: networks hub (red, high values of both intra- and intermodular connectivity), module hubs (blue, high intramodular connectivity but low intermodular connectivity), connectors (green, low intramodular connectivity but high intermodular connectivity), or peripheral (black, low values of both intra and intermodular connectivity). The symbols in C and F identify the module to which species belong. The complete list of species names is provided in Supplementary Table S1.

Solenocera agassizi, the sharks *Sphyrna tiburo* and *Mustelus henlei*, many pelagic species, and LSF (Figure 1; Supplementary Table S1). Connectors show contrasting dietary preferences that define complementary paths connecting the food web. Peripheral species with few connections comprise most of the network (85% of the species, Figure 1b and e, Supplementary Table S1 and Figure S1a and b).

Several fishery targets change their roles when the network encompasses fisheries. As SSF increase among-module connectivity, many peripheral bony fish species of commercial interest become connectors in the network with fisheries (Supplementary Table S1). In contrast, fisheries also change the roles of many invertebrate species from connectors to peripherals. Accordingly, generalist predators, such as *M. lunulatus* and *Sphyrna corona*, change their roles from network to module hubs. Conversely, *Sphyrna lewini* and *U. rogersi* change from module hubs to network hubs, likely due to fisheries adding network pathways that do not occur naturally.

Both networks have the most primary producers (TL1) within one single module. Primary and secondary consumers (TL2–TL4) are often module hubs. Top predators and fisheries (TL5) interact with most of the modules as network hubs or connectors (Supplementary Figure S2a and b). Mesopredators (TL3 and TL4) are mostly connectors and peripherals (Supplementary Figure S2c and d).

Threat statuses and species contribution to the food web structure

The species with higher contributions to network structure (*U.*, Supplementary Table S1) are also those facing the most severe threats (test statistic = 3.012; $p < 0.05$; Figure 2b). For example, the network hub *S. lewini* and the module hub *M. lunulatus*, both nationally threatened in Colombia, with the former also being critically endangered globally, show markedly high contributions to network structure. The same occurs with many module hubs (Figures 1c and 2a). Conversely, in our study system, many species under low threat levels play peripheral topological roles (Figure 2a and b).

The similarity in interaction patterns between fisheries and top predators

SSF and large sharks have similar topological roles (Figure 1c). However, they show low dietary similarity, suggesting that network hubs are functionally complementary and connect the food web via different direct interactions (Figure 3a and b). SSF exploit 66 taxa, whereas the hammerhead sharks *S. lewini* and *Sphyrna media* prey on 65 and 48 taxa, respectively. LSF (a connector) exploit 39 taxa. These complementary interaction patterns do not imply isolated network hubs. In fact, indirect pathways connect the fisheries and shark in the system, as indicated by the high trophic overlap index (TO^3) among SSF and LSF (SSF = 0.31 and LSF = 0.24) and the shark *S. lewini* (0.08). In contrast, peripheral species have lower degrees of overlap in their indirect effects (Supplementary Table S1).

Simulations of species extinctions and fishery regulations

In our simulations, species extinctions did not change modularity. The relative frequencies of topological roles remained similar regardless of the biological and economic roles of the species dying out (Supplementary Table S2). For example, SSF remain a net-

work hub in most scenarios (Supplementary Table S4). However, the identities of species playing each structural role change following extinctions. For instance, distinct species of *Sphyrna* sharks emerged as network hubs after simulated extinctions (Supplementary Table S2). The complementary simulation considering the joint extinction of 11 species resulted in only 1 fish species—the stingray *U. rogersi*—and SSF remaining as the network hubs (Supplementary Table S4). Removing shallow-water shrimp fisheries did not change food web modularity and the frequencies of topological roles.

Discussion

Anthropogenic competition as a candidate mechanism underlying resource partitioning

Competition avoidance likely underlies the structure of other marine food webs in which keystone sharks belong to distinct modules (Rezende *et al.*, 2009). Empirical evidence supports that fisheries compete with top predators in coastal ecosystems (e.g. Yodzis, 2001; Pichegru *et al.*, 2009). We show evidence of resource partitioning between fisheries and hammerhead sharks in a tropical marine food web, reinforcing the notion that competition avoidance influences the organization of this community (Galindo *et al.*, 2021).

One may expect that both sharks and fisheries should behave adaptively. Fisheries can behave as adaptive foragers to optimize catch rates (Bertrand *et al.*, 2007). Adaptive fishing strategies include shifts in target species to maximize benefits (Sethi *et al.*, 2010), analogous to the adaptive rewiring of ecological networks (Raimundo *et al.*, 2018). However, SSF do not rewire their interactions via adaptive target shifts in the study region. These fleets are non-selective and use multiple species, responding to variation in resource availability via changes in fleets size and fishing efforts (Rueda *et al.*, 2012). Hammerhead sharks, therefore, may be forced into suboptimal dietary choices imposed by competition with SSF, which act as dominant supergeneralist predator overcoming the other highly connected species.

We acknowledge that inferring interspecific competition from resource use patterns alone can be misleading (Pichegru *et al.*, 2009). Alternatively, opportunistic foraging of sharks in distinct habitats could explain the same pattern (Navia *et al.*, 2017). On the other hand, fishing has been intensive in the region for decades, and hammerhead sharks are becoming increasingly rare (Navia and Mejía-Falla, 2016). Studies in nearby no-take zones can test our hypothesis that anthropogenic competition shapes resource partitioning. For sites where fishing is banned, we predict hammerhead sharks prey on redundant prey species, including dozens of species monopolized by fisheries outside no-take areas. Testing this hypothesis is relevant because it can advance our understanding of contemporary dynamics of anthropogenic food webs based on general theories that explain how competitive divergence acts as a fundamental mechanism shaping community structure (MacArthur and Levins, 1967; Connell, 1980).

Hyper-hubs and their effects

We propose the concept of “hyper-hub”, referring to nodes—SSF and hammerhead sharks—feeding on all topological roles, including other network hubs. Hyper-hubs represent hyperconnected species particularly likely to impose pervasive top-down effects (Navia and Mejía-Falla, 2016). The concept of hyper-hub connects the network approach and the idea that humans act as *hyperkeystone* species whose impacts on other keystone taxa trigger cascading effects that spread rapidly at the ecosystem level (Worm and Paine, 2016).

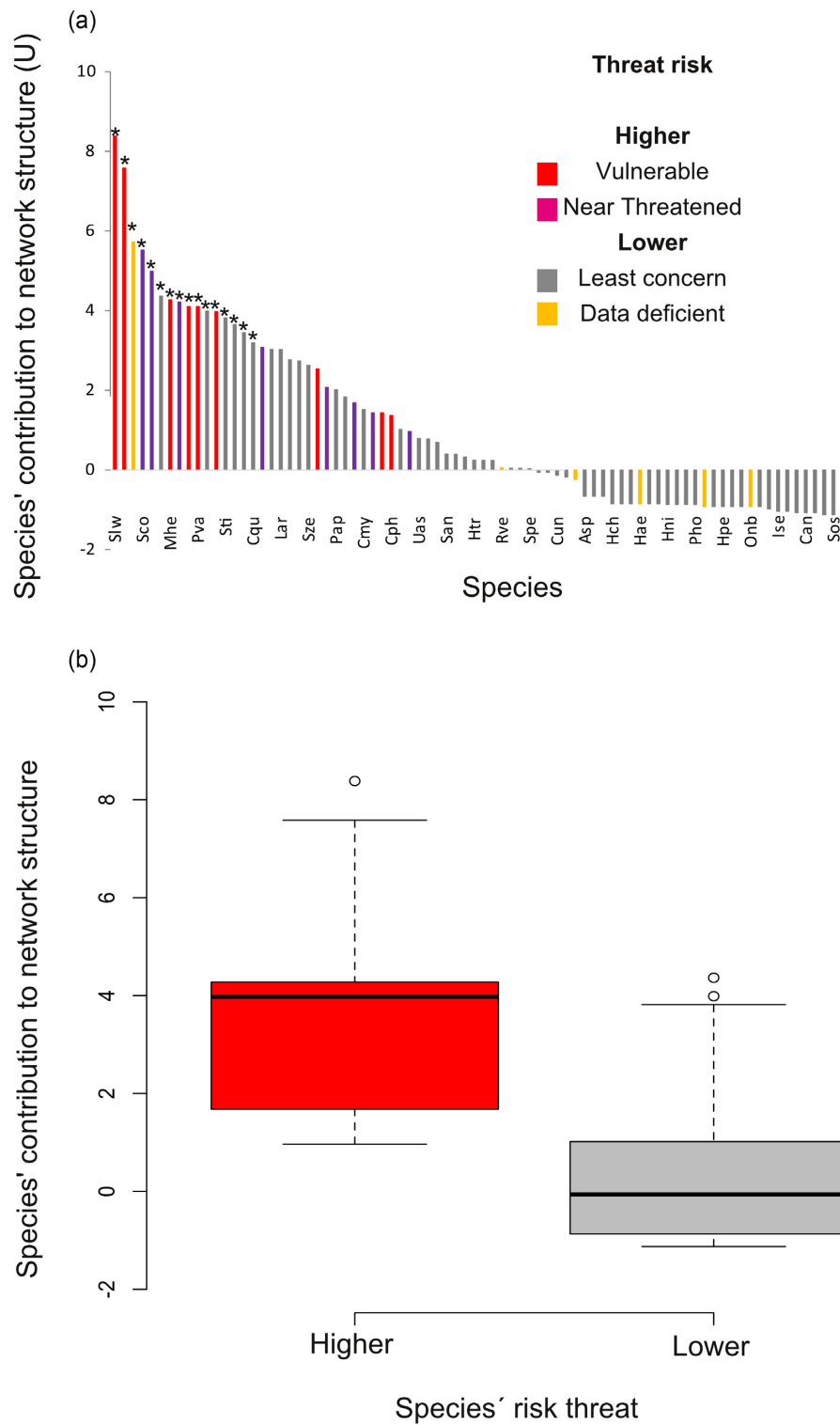


Figure 2. (a) Species' contribution to network structure and threat statuses according to IUCN's Red List criteria. (b) Species' contribution to network structure (mean \pm s.e.), comparing species sets with contrasting threat statuses (higher vs. lower). Asterisks denote network and module hubs.

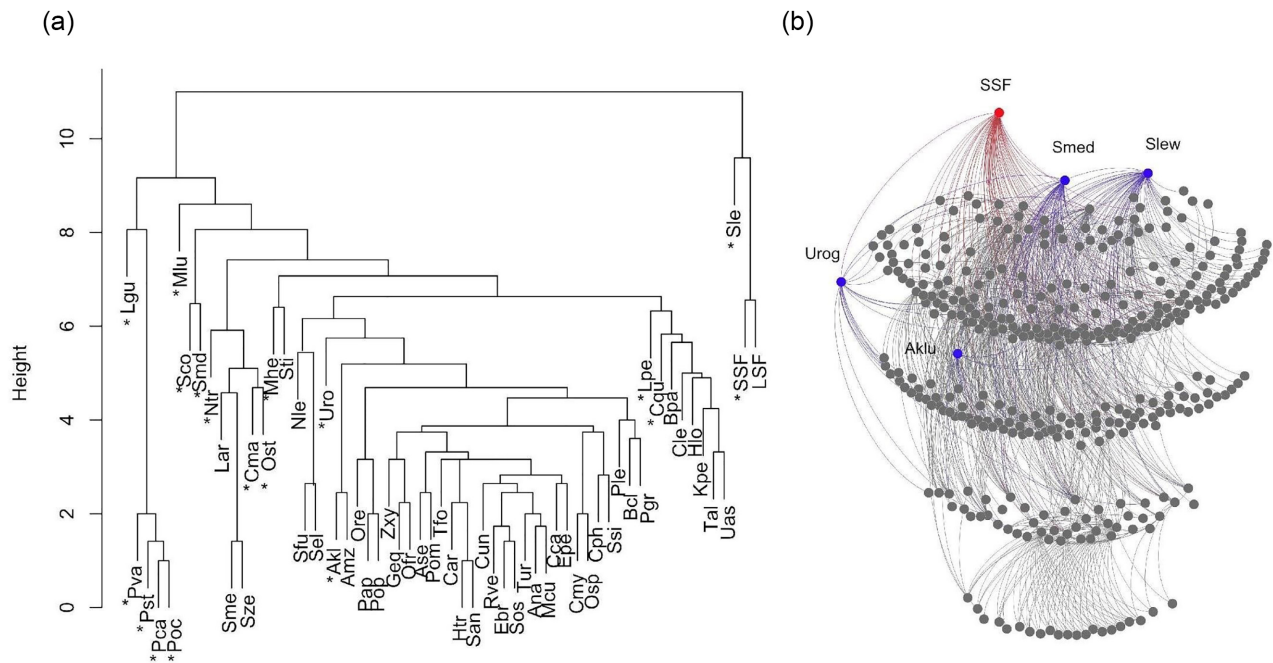


Figure 3. (a) Pairwise dietary similarity between predators as informed by the Jaccard index. Asterisks denote network and module hubs. (b) Food web with fisheries, highlighting the interactions of SSF (red) and of predator species that also act as network hubs (blue). Grey nodes depict all other topological roles. SSF: small-scale fisheries; Smed: *Sphyrna media*; Slew: *Sphyrna lewini*; Urog: *Urotrygon rogersi*; Aklu: *Achirus klunzingeri*.

Hyper-hubs have highly overlapping indirect effects, as described by the trophic overlap index, despite their dissimilar direct interactions. Overlapping indirect interactions arise from high centrality values of a few nodes combined with short average path length within the network. Consequently, the extinction of a *Sphyrna* hyper-hubs will rapidly affect not only its resources but other hyper-hubs and their prey through indirect effects. It remains unclear if such indirect effects will positively or negatively affect species abundances across TLs. There is, however, empirical evidence that the demographic decline of *Sphyrna* sharks is likely affecting a wide variety of taxa, including bony fishes, squids, and shrimps (Galindo *et al.*, 2021).

By now, our study reinforces the notion that the conservation of *Sphyrna* sharks can promote the long-term persistence of marine biodiversity in the Colombian Pacific (Dulvy *et al.*, 2014; Chasqui *et al.*, 2017). The higher vulnerability of central species raises concerns regarding the imminent functional disruption of food webs due to anthropogenic extinctions. Non-selective fisheries may be imposing strongly asymmetrical competitive pressures on the progressively rare hammerhead sharks (Puentes *et al.*, 2014; Navia and Mejía-Falla, 2016). In this context, our study reinforces a pattern described for some terrestrial ecosystems (Vidal *et al.*, 2014) that the positive correlation between species vulnerability to extinction and their contribution to network structure (Figure 2).

Simulations of extinctions and fishery regulations

Our simulations contribute to the assessment of how extinctions and fishery regulations can affect this food web. The simulations show SSF remain as a network hub regardless of which species die out. Network structure did not change after removing species belonging to all TLs and topological roles, including hyper-hubs. Also,

the removal of shallow-water shrimp fisheries did not affect modularity. We should take these results, suggesting a high structural resilience of the food web to extinctions and fishery regulations, cautiously. Our simulations did not incorporate the dynamics of species abundances and interaction rewiring arising from competitive release (Raimundo *et al.*, 2018), which may propagate the impact of extinctions and regulations via cascading effects. In this context, the identity of species acting as network hubs often changes after simulated extinctions.

When we removed top predators showing high topological centrality from the network, species from intermediate TLs, such as *M. lunulatus* and *S. tiburo*, emerge as network hubs. Previous studies (Myers *et al.*, 2007; Baum and Worm, 2009; Navia *et al.*, 2010) support this finding and corroborate the notion that generalist mesopredators can play critical roles in food web dynamics under anthropogenic disturbances (Amariles *et al.*, 2017; Galindo *et al.*, 2021). Consequently, functional redundancy among generalist mesopredators can buffer the effects of extinctions of top predators (Navia *et al.*, 2010). Understanding the mechanisms shaping changes in species' topological roles is critical to predicting how anthropogenic processes affect food webs (D'Alelio *et al.*, 2019). Species' traits, such as body size and mobility, often underly modularity (Olmo Gilabert *et al.*, 2019). Understanding how such traits mediate species' roles is a problem that deserves further investigation.

Implications for conservation and fishery management strategies

Our results suggest that conservation efforts should extend beyond commercial species, which are primarily peripheral network nodes. Considering the complementarity of direct interactions and the in-

tertwined indirect effects of hyper-hubs, the demographic rescue (Carlson *et al.*, 2014) of the hammerhead sharks *S. lewini* and *S. media* are likely to rapidly propagate across the food web and reshape patterns of interactions and species abundances. However, the direction and magnitude of such changes remain to be understood.

Beyond describing how hyper-hubs can impose top-down control via direct or indirect effects, our study corroborates the notion that bottom-up processes also influence biodiversity patterns in marine food webs (Lynam *et al.*, 2017). Notably, the brown sole *A. klunzingeri*, a network hub, appears among the prey consumed by hyper-hubs, suggesting that this mesopredator may play a key role in community dynamics by connecting top-down and bottom-up effects.

Concluding remarks

The impact of non-selective fishing is reshaping the structure and dynamics of tropical marine food webs. Developing countries urgently need to implement innovative scientific programmes that combine network modelling and biomonitoring as a two-way road informing ecosystem-based approaches to conservation that extend beyond commercial and flagship species. Citizen science projects involving artisanal fishers can be particularly useful to implement such an approach. For example, participatory projects can use the predictions of ecological models to design experimental measures to reduce bycatches and promote the demographic rescue of endangered populations of hyper-hub species. Field data arising from citizen science projects could assess the predictions and assumptions of networks model underlying conservation strategies.

Our study contributes to the emerging socio-ecological approach to food web modelling. In temperate regions, socio-ecological studies considering the roles of SSF within food webs have shown, for example, that their direct adverse effects on top predators are counterbalanced by indirect positive impacts on the biomass of non-harvested species, albeit leading to a drastic decrease in plankton (Ávila-Thieme *et al.*, 2021). Another recent model suggests that the overexploitation of species with higher population biomasses can trigger extinction cascades affecting non-target species and threaten biodiversity, ecosystem functions and fisheries (Glaum *et al.*, 2020). Such approaches can disentangle the positive and negative effects of fisheries across TLs and on non-target species. A fundamental question that remains open is the extent to which trophic cascades induced by fisheries are common in tropical systems, where top and mesopredator species can show complementary direct interactions but highly overlapping indirect effects.

Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

Author contribution

VMV, AFN, RSR, PRG, and RLGR conceived and designed the work. VMV compiled datasets from the literature and performed laboratory work, for which AFN provided materials and guidance. VMV, RLGR, and AFN analysed the data. VMV, RLGR, AFN, PRG, and RSR interpreted the results. VMV and RLGR wrote the paper and led the revisions, and AFN, RSR, and PRG contributed to several drafts of the manuscript.

Data availability statement

The data that support the findings of this study are available in the Supplementary Material of this article.

Conflict of interest

The authors have no conflict of interest to declare.

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