



Original Article

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

Viviana Márquez-Velásquez^{1,2,3}, Andrés F. Navia^{2,4}, Ricardo S. Rosa⁵, Paulo R. Guimarães, Jr.^{3,6}, and Rafael L. G. Raimundo^{3,7,8,*}

¹Programa de Pós-Graduação em Ciências Biológicas (Zoologia), Universidade Federal da Paraíba, João Pessoa, 58051-900 PB, Brazil

²Fundación Colombiana para la Investigación y Conservación de Tiburones y Rayas, SQUALUS, Calle 10ª No. 72-35, Apto. 310E, Cali, Colombia

³IRIS Research Group, Innovation for Resilience, Inclusion and Sustainability, Laboratory of Animal Ecology, Universidade Federal da Paraíba, Campus IV, Rio Tinto, 58297-000 PB, Brazil

⁴Grupo de investigación en Ecología Animal, Departamento de Biología, Universidad del Valle, 25360 Cali, Colombia

⁵Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, João Pessoa, 58051-900 PB, Brazil

⁶Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, 05508-090 SP, Brasil

⁷Departamento de Engenharia e Meio Ambiente e Programa de Pós-Graduação em Ecologia e Monitoramento Ambiental (PPGEMA), Rio Tinto, 58297-000 PB, Brazil

⁸Programa de Pós-Graduação em Ecologia e Monitoramento Ambiental (PPGEMA), Universidade Federal da Paraíba, Campus IV, Rio Tinto, 58297-000 PB, Brazil

*Corresponding author: tel: +55 83 9917-6970; e-mail: rafael.raimundo@academico.ufpb.br

Viviana Márquez-Velásquez, Andrés F. Navia, Ricardo S. Rosa, Paulo R. Guimarães, Jr. and Rafael L. G. Raimundo Resource partitioning between fisheries and endangered sharks in a tropical marine food web. – ICES Journal of Marine Science, 0: 1–10.

Received 21 January 2021; revised 24 May 2021; accepted 21 June 2021.

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. * $p < 0.001$.

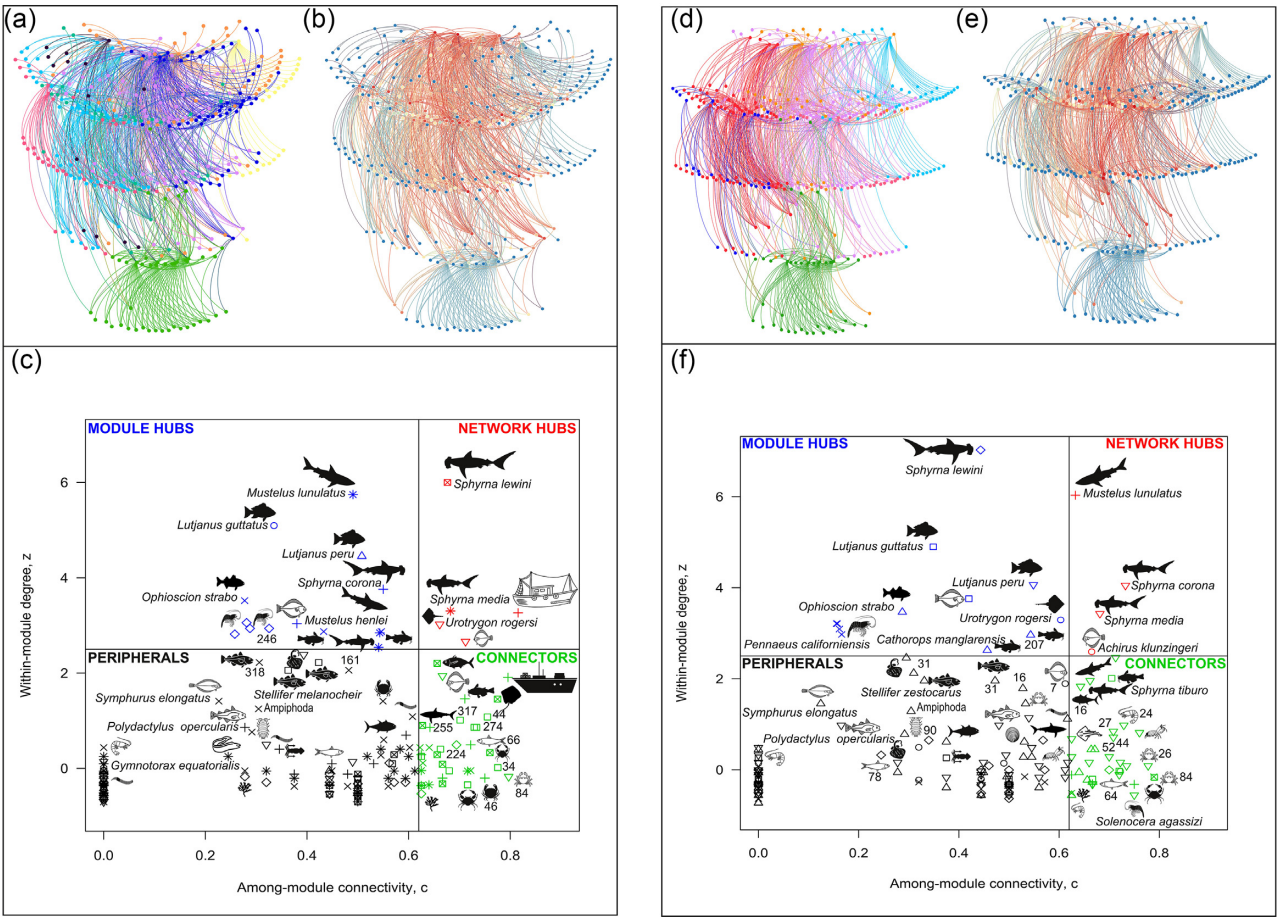


Figure 1. The modular structure of the coastal food web in the tropical Pacific region organized according to species' TL and interaction patterns. Food webs with (a and b) and without (d and e) fisheries and their catches as additional nodes and links. The colors of the nodes and links correspond to 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).

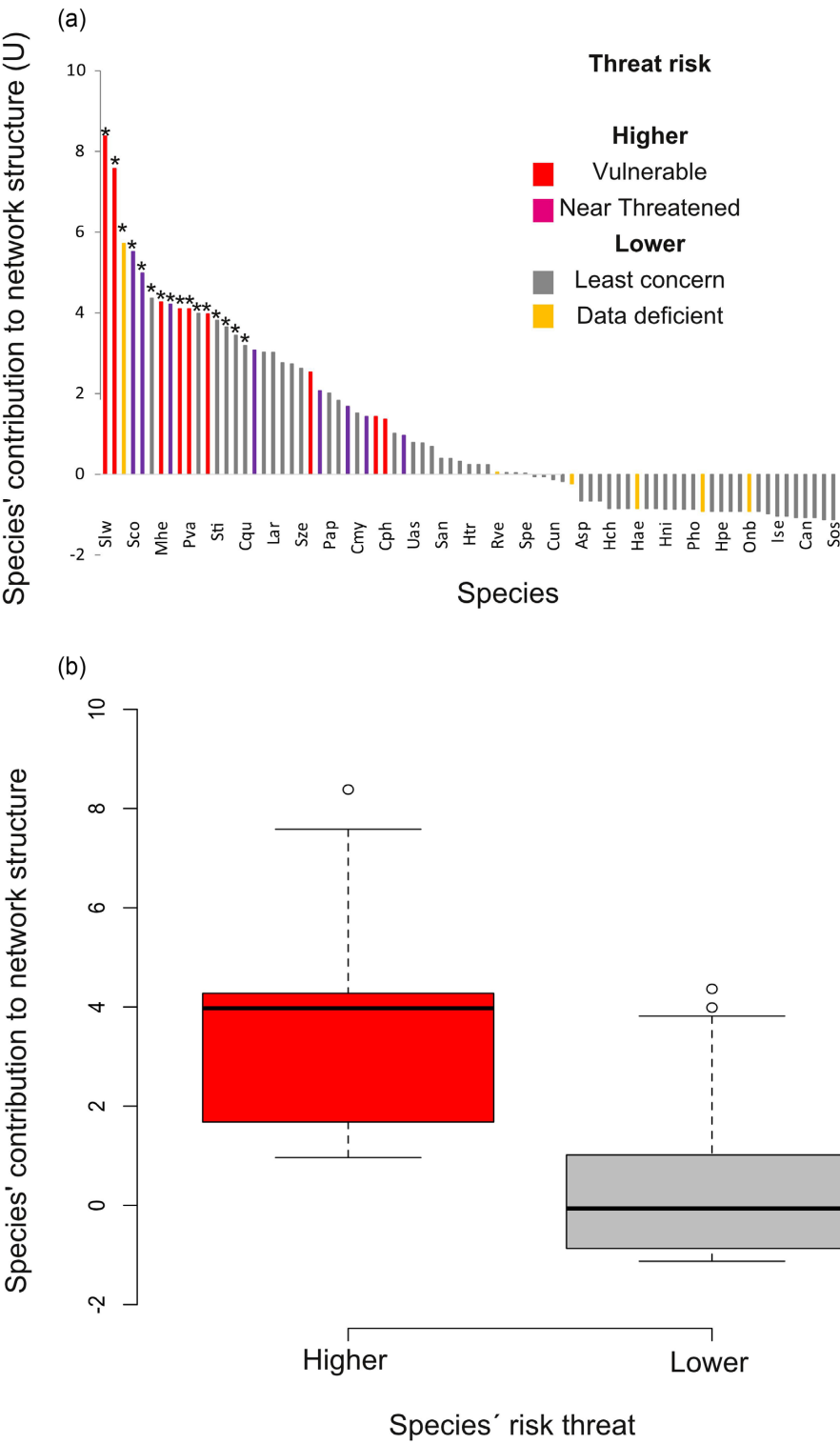


Figure 2. (a) Species' contribution to network structure and threat statuses according to IUCN's Red List criteria. (b) Species' contribution to network structure (mean \pm s.e.), comparing species sets with contrasting threat statuses (higher vs. lower). Asterisks denote network and module hubs.

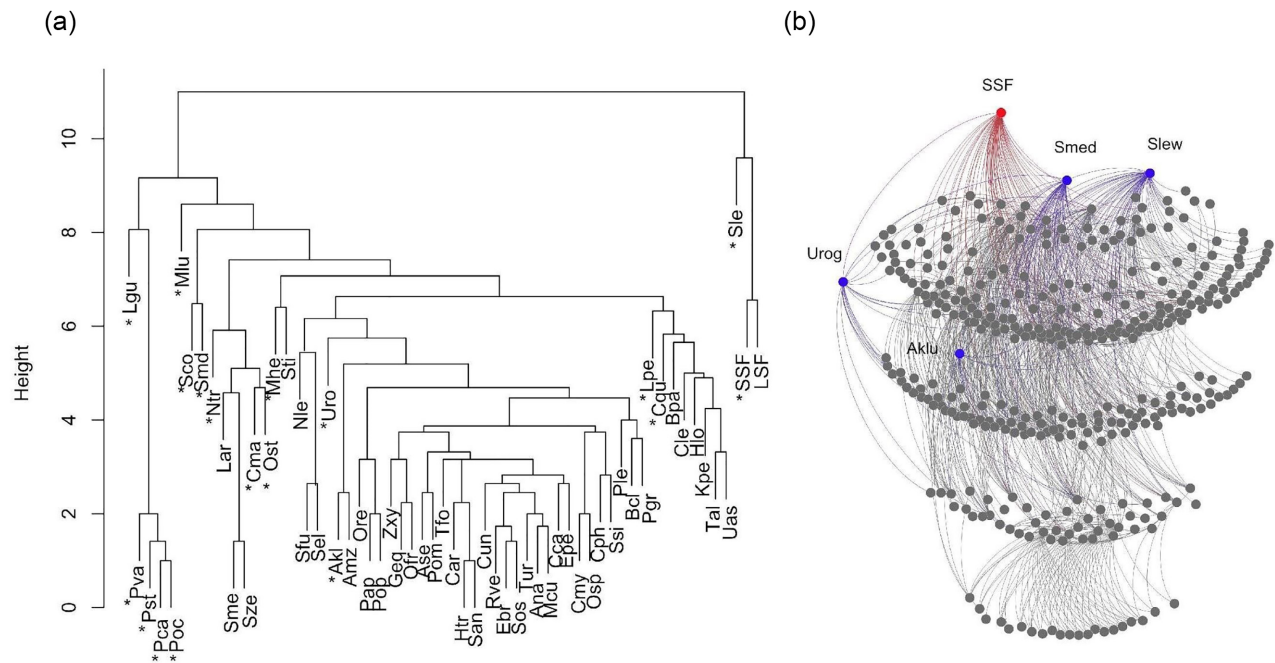


Figure 3. (a) Pairwise dietary similarity between predators as informed by the Jaccard index. Asterisks denote network and module hubs. (b) Food web with fisheries, highlighting the interactions of SSF (red) and of predator species that also act as network hubs (blue). Grey nodes depict all other topological 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.

Acknowledgements

The Paraíba State Research Foundation (FAPESQ) and CAPES (Brazilian Ministry of Education) funded VMV. PRG was funded by CNPq (307134/2017–2), FAPESP (2018/14809–0), and the Royal Society, London (CHL/R1/180156). We thank all colleagues of the SQUALUS Foundation, especially Daniela Gómez, Diego Amariles, and Jose Gabriel Pérez, for their assistance and help during the laboratory work. VMV thanks the Gómez Martinez family for their hospitality during her stay at SQUALUS Foundation. This is IRIS contribution #2.

References

- Amariles, D. F., Navia, A. F., and Giraldo, A. 2017. Food resource partitioning of the *Mustelus lunulatus* and *Mustelus henlei* (Elasmobranchii: carcharhiniformes). *Environmental Biology of Fishes*, 100: 717–732.
- Ardila, N., Navas, G., and Reyes, J. 2002. Libro rojo de los invertebrados marinos de Colombia. INVEMAR, Santa Marta, 180p.
- Ávila-Thieme, M. I., Corcoran, D., Pérez-Matus, A., Wieters, E. A., Navarrete, S. A., Marquet, P. A., and Valdovinos, F. S. 2021. Alteration of coastal productivity and artisanal fisheries interact to affect a marine food web. *Scientific Reports*, 11: 1–14.
- Bascompte, J., Melián, C. J., and Sala, E. 2005. Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 5443–5447.
- Bastian, M., Heymann, S., and Jacomy, M. 2009. Gephi: an open-source software for exploring and manipulating networks. In *Proceedings of the Third International AAAI Conference on Weblogs and Social Media*.
- Baum, J. K., and Worm, B. 2009. Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, 78: 699–714.
- Bax, N., Williamson, A., Aguero, M., Gonzalez, E., and Geeves, W. 2003. Marine invasive alien species: a threat to global biodiversity. *Marine Policy*, 27: 313–323.
- Bertrand, S., Bertrand, A., Guevara-Carrasco, R., and Gerlotto, F. 2007. Scale-invariant movements of fishermen: the same foraging strategy as natural predators. *Ecological Applications*, 17, 331–337.
- Bieg, C., McCann, K. S., McMeans, B. C., Rooney, N., Holtgrieve, G. W., Lek, S., Peng Bun, N. *et al.* 2018. Linking humans to food webs: a framework for the classification of global fisheries. *Frontiers in Ecology and the Environment*, 16: 412–420.
- Borgatti, S. P., Everett, M. G., and Freeman, L. C. 2002. UCINET IV: Software for Social Network Analysis. Analytic Technologies, Harvard, MA.
- Bornatowski, H., Navia, A. F., Braga, R. R., Abilhoa, V., and Maia-Corrêa, M. F. 2014. Ecological importance of sharks and rays in a structural food web analysis in southern Brazil. *ICES Journal of Marine Science*, 71: 1586–1592.
- Carlson, S. M., Cunningham, C. J., and Westley, P. A. 2014. Evolutionary rescue in a changing world. *Trends in Ecology and Evolution*, 29: 521–530.
- Chasqui, V., Polanco, L. A., Acero, F. A., Mejía-Falla, P. A., Navia, A., Zapata, L. A., and Caldas, J. P. 2017. Libro rojo de peces marinos

- de Colombia. In Instituto de Investigaciones Marinas y Costeras Inveimar, Ministerio de Ambiente y Desarrollo Sostenible. Serie de Publicaciones Generales de INVEIMAR, N 93, Santa Marta, Colombia.
- Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, 35: 131–138.
- Costa, L. F., Rodrigues, F. A., Travies, G., and Boas, F. 2007. Characterization of complex networks: a survey of measurements. *Advances in Physics* 56: 167–242.
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K. *et al.* 1997. The value of the world's ecosystem services and natural capital. *Nature*, 387: 253–260.
- D'Alelio, D., Hay Mele, B., Libralato, S., Ribera d'Alcalà, M., and Jordán, F. 2019. Rewiring and indirect effects underpin modularity reshuffling in a marine food web under environmental shifts. *Ecology and Evolution*, 9: 11631–11646.
- Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., Carlson, J. K. *et al.* 2014. Extinction risk and conservation of the world's sharks and rays. *eLife*, 3: e00590.
- Dunne, J. A., Maschner, H., Betts, M. W., Huntly, N., Russell, R., Williams, R. J., and Wood, S. A. 2016. The roles and impacts of human hunter-gatherers in North Pacific marine food webs. *Scientific Reports*, 6, 21179.
- Estes, J. A., Tinker, M. T., Williams, T. M., and Doak, D. F. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science*, 282, 473–476.
- Estrada, E. 2007. Characterization of topological keystone species local, global and “meso-scale” centralities in food webs. *Ecological Complexity*, 4, 48–57.
- FAO. 2020. The State of World Fisheries and Aquaculture 2020. Sustainability in Action. Food and Agriculture Organization of the United Nations, Rome.
- Freeman, L. C. 1978. Centrality in social networks, conceptual clarification. *Soc. Networks*, 1, 215–239.
- Froese, R., and Pauly, D. 2018. FishBase. www.fishbase.org (last accessed 10 December 2018).
- Gaichas, S. K., and Francis, R. C. 2008. Network models for ecosystem-based fishery analysis: a review of concepts and application to the Gulf of Alaska marine food web. *The Canadian Journal of Fisheries and Aquatic Sciences*, 65: 1965–1982.
- Galindo, E., Giraldo, A., and Navia, A. F. 2021. Feeding habits and trophic interactions of four sympatric hammerhead shark species reveals trophic niche partitioning. *Marine Ecology Progress Series*, 665: 159–175.
- Gallardo, N., Hernández, S., Mojica, H., and Puentes, V. 2018. Avances de Acuicultura y Pesca. Volumen IV. Especial: Caracterización de pesquerías en Colombia. Autoridad Nacional de Acuicultura y Pesca - AUNAP© and Fundación Fauna Caribe Colombiana - FFCC©. Barranquilla, en Colombia. 216 p.
- Glaum, P., Cocco, V., and Valdivinos, F. S. 2020. Integrating economic dynamics into ecological networks: the case of fishery sustainability. *Science Advances*, 6: eaaz4891.
- Guimarães, P. R. Jr 2020. The structure of ecological networks across levels of organization. *Annual Review of Ecology, Evolution, and Systematics*, 51: 433–460.
- Guimerà, R., and Amaral, L. A. N. 2005. Cartography of complex networks: modules and universal roles. *Journal of Statistical Mechanics: Theory and Experiment*, 2005: nihpa35573.
- Hayata, M. A., Bornatowski, H., and Freitas, R. H. 2021. Patterns and partitioning of food resources by elasmobranchs in southern Brazil. *Environmental Biology of Fishes*, 104: 437–450.
- Hillebrand, H., Brey, T., Gutt, J., Hagen, W., Metfies, K., Meyer, B., and Lewandowska, A. 2018. Climate Change: warming Impacts on Marine Biodiversity. In *Handbook on Marine Environment Protection*. Springer, Cham. 353–373.
- IUCN. 2020. The IUCN Red List of Threatened Species. Version 2019-3. <http://www.iucnredlist.org> (last accessed 14 February 2020).
- Jaccard, P. 1912. The distribution of flora in the alpine zone. *New Phytologist*, 11, 37–50.
- Jordán, F. 2009. Keystone species and food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364: 1733–1741.
- Jordano, P. 2016. Chasing ecological interactions. *PLoS Biology*, 14: e1002559.
- Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E., and Taylor, W. W. 2003. Compartments revealed in food-web structure. *Nature*, 426, 282–285.
- Lotze, H. K., Coll, M., and Dunne, J. A. 2011. Historical changes in marine resources, food web structure and ecosystem functioning in the Adriatic Sea, Mediterranean. *Ecosystems*, 14: 198–222.
- Lynam, C. P., Llope, M., Möllmann, C., Helaouët, P., Bayliss-Brown, G. A., and Stenseth, N. C. 2017. Interaction between top-down and bottom-up control in marine food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 114: 1952–1957.
- MacArthur, R., and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist*, 101, 377–385.
- Manly, B. F. J. 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology. Second edition. Chapman and Hall, London, UK.
- Márquez-Velázquez, V., Raimundo, R. L. G., Rosa, R. S., and Navia, A. F. 2020. The use of ecological networks as tools for understanding and conserving marine biodiversity. In *Marine Coastal Ecosystems Modelling and Conservation*. Ed by F. Jordán and M. Ortiz. Springer Nature. Cham, Switzerland.
- Martinez, N. D. 1992. Constant connectance in community food webs. *The American Naturalist*, 139, 1208–1218.
- May, R. M. 1973. Qualitative stability in model ecosystems. *Ecology*, 54: 638–641.
- Myers, R., Baum, J. K., Sheperd, T. D., Powers, S., and Peterson, C. H. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, 315: 1846–1850.
- Navia, A. F., and Mejía-Falla, P. A. 2016. Fishing effects on elasmobranchs from the Pacific Coast of Colombia. *Universitas Scientiarum*, 21: 9–22.
- Navia, A. F., Cortés, E., and Mejía-Falla, P. A. 2010. Topological analysis of the ecological importance of elasmobranch fishes: a food web study on the Gulf of Tortugas, Colombia. *Ecological Modelling*, 221: 2918–2926.
- Navia, A. F., Cortés, E., Jordán, F., Cruz-Escalona, V. H., and Mejía-Falla, P. A. 2012. Changes to marine trophic networks caused by fishing. In *Diversity of Ecosystems*. IntechOpen, Rijeka, Croatia. 417–452.
- Navia, A. F., Cruz-Escalona, V. H., Giraldo, A., and Barausse, A. 2016. The structure of a marine tropical food web, and its implications for ecosystem-based fisheries management. *Ecological Modelling*, 328, 23–33.
- Navia, A. F., Mejía-Falla, P. A., López-García, J., Giraldo, A., and Cruz-Escalona, V. H. 2017. How many trophic roles can elasmobranchs play in a marine tropical network? *Marine and Freshwater Research*, 68: 1342–1353.
- Newman, M. E. J., and Girvan, M. 2004. Finding and evaluating community structure in networks. *Physical Review E*, 69: 026113–15.
- Nixon, S. W. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia*, 41, 199–219.
- Olmo Gilabert, R., Navia, A. F., De La Cruz-Agüero, G., Molinero, J. C., Sommer, U., and Scotti, M. 2019. Body size and mobility explain species centralities in the Gulf of California food web. *Community Ecology*, 20: 149–160.
- Pauly, D., and Zeller, D. 2016. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nature Communications*, 7, 10244.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. 1998. Fishing down marine food webs. *Science*, 279, 197–212.
- Pérez-Matus, A., Ospina-Alvarez, A., Camus, P. A., Carrasco, S. A., Fernandez, M., Gelcich, S., and Subida, M. D. 2017. Temperate rocky subtidal reef community reveals human impacts across the entire food web. *Marine Ecology Progress Series*, 567, 1–16.
- Pichegru, L., Ryan, P. G., Le Bohec, C., van der Lingen, C. D., Navarro, R., Petersen, S., Lewis, S. *et al.* 2009. Overlap between vulnerable top

- predators and fisheries in the Benguela upwelling system: implications for marine protected areas. *Marine Ecology Progress Series*, 391, 199–208.
- Pinsky, M. L., and Palumbi, S. R. 2014. Meta-analysis reveals lower genetic diversity in overfished populations. *Molecular Ecology*, 23: 29–39.
- Puentes, V., Escobar, F. D. Polo, C. J. and Alonso, J. C. 2014. Estado de los Principales Recursos Pesqueros de Colombia – (2014). Serie Recursos Pesqueros de Colombia – AUNAP. Oficina de Generación del Conocimiento y la Información, Autoridad Nacional de Acuicultura y Pesca – AUNAP, Bogotá, Colombia. 244 pp.
- Raimundo, R. L., Guimarães, P. R., and Evans, D. M. Jr. 2018. Adaptive networks for restoration ecology. *Trends in Ecology and Evolution*, 33: 664–675.
- Rezende, E. L., Albert, E. M., Fortuna, M., and Bascompte, J. 2009. Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. *Ecology Letters*, 12: 779–788.
- Rueda, M., Doncel, O., Vilorio, E. A., Mármol, D., García, C., Girón, A., García, L. *et al.* 2012. Atlas de la pesca marino-costera de Colombia: 2010–2011. In Tomo Pacífico. Serie de publicaciones del Invemar. Invemar y ANH, Santa Marta. 100p.
- Sazima, C., Guimarães, P. R. Jr, Dos Reis, S. F., and Sazima, I. 2010. What makes a species central in a cleaning mutualism network?. *Oikos*, 119: 1319–1325.
- Sethi, S. A., Branch, T. A., and Watson, R. 2010. Global fishery development patterns are driven by profit but not trophic level. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 12163–12167.
- Stouffer, D. B., and Bascompte, J. 2011. Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences of the United States of America*, 108: 3648–3652.
- Valentini, R., and Jordán, F. 2010. COSBILab Graph: the network analysis module of COSBILab. *Environmental Modelling & Software*, 25, 886–888.
- Vidal, M. M., Hasui, E., Pizo, M. A., Tamashiro, J. Y., Silva, W. R., and Guimarães, P. R. Jr. 2014. Frugivores at higher risk of extinction are the key elements of a mutualistic network. *Ecology*, 95: 3440–3447.
- Ward, A. J., Webster, M. M., and Hart, P. J. 2006. Intraspecific food competition in fishes. *Fish and Fisheries*, 7: 231–261.
- Worm, B., and Paine, R. T. 2016. Humans as a hyperkeystone species. *Trends in Ecology and Evolution*, 31: 600–607.
- Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., and Jensen, O. P. 2009. Rebuilding global fisheries. *Science*, 325: 578–585.
- Yodzis, P. 2001. Must top predators be culled for the sake of fisheries?. *Trends in Ecology and Evolution*, 16: 78–84.
- Young, H. S., McCauley, D. J., Galetti, M., and Dirzo, R. 2016. Patterns, causes, and consequences of Anthropocene defaunation. *Annual Review of Ecology, Evolution, and Systematics*, 47: 333–358.

Handling Editor: Marta Coll