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Key species and impact of fishery through food web analysis: A case study from Baja California Sur, Mexico

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ABSTRACT

Ecosystem-Based Management (EBM) aims to support the protection of natural ecosystems and to improve economic activities. It requires considering all of the actors interacting in social-ecological systems (e.g., fish and fishers) in the understanding that their interplay determines the dynamic behavior of the single actors as well as that of the system as a whole. Connections are thus central to EBM. Within the ecological dimension of socio-ecological systems, interactions between species define such connections. Understanding how connections affect ecosystem and species dynamics is often impaired by a lack of data. We propose food web network analysis as a tool to help bridge the gap between EBM theory and practice in data-poor contexts, and illustrate this approach through its application to a coastal marine ecosystem in Baja California Sur, Mexico. First, we calculated centrality indices to identify which key (i.e., most central) species must be considered when designing strategies for sustainable resource management. Second, we analyzed the resilience of the system by measuring changes in food web structure due to the local extinction of vulnerable species (i.e., by mimicking the possible effect of excessive fishing pressure). The consequences of species removals were quantified in terms of impacts on global structural indices and species' centrality indices. Overall, we found that this coastal ecosystem shows high resilience to species loss. We identified species (e.g., *Octopus* sp. and the kelp bass, *Paralabrax clathratus*) whose protection could further decrease the risk of potential negative impacts of fishing activities on the Baja California Sur food web. This work introduces an approach that can be applied to other ecosystems to aid the implementation of EBM in data-poor contexts.

1. Introduction

Marine ecosystems are undergoing major changes through overexploitation, habitat loss, pollution, species introduction, ocean acidification and warming (Halpern et al., 2008a; Hoegh-Guldberg and Bruno, 2010; Burrows et al., 2011; Doney et al., 2012). Fisheries management, once focused primarily on large scale industrial fisheries, is now addressing also on Small-Scale Fisheries (SSFs) and their dependent human communities (Allison and Ellis, 2001; Jacquet and Pauly, 2008; Chuenpagdee, 2011; Kolding et al., 2014). SSFs are ubiquitous and of great importance (Finkbeiner, 2015). Small- and large-scale fisheries each contribute to approximately half of global fisheries capture, but SSFs employ over 96% of the world's fishers (Chuenpagdee et al., 2006).

Given the complexity of the issues and failure of traditional fisheries management efforts (Botsford et al., 1997; Hilborn, 2007), new management strategies have been called for. In particular, there has been a shift in focus from single species or sectors to the whole ecosystem as the unit of management. This view has produced a framework called "Ecosystem-Based Management" (EBM, Long et al., 2015). EBM is increasingly taking hold as demonstrated by the ever greater effort devoted to its application worldwide (Pew, 2003; USCOP, 2004; Lester et al., 2010; Link, 2010). EBM is a cross-sectoral, holistic approach (Link, 2002; Ruckelshaus et al., 2008; Halpern et al., 2008b; Francis et al., 2011; Link et al., 2012) that is expected to prevent the overexploitation of resources, support ecosystem restoration, maintain ecosystem health, and therefore promote human well-being (Long et al., 2015). One of the fifteen principles that constitute the pillars of EBM posits that ecosystem connections are central to understand system behavior and to design effective management strategies (Long et al., 2015). Connections functionally link different parts of a system and allow impacts to spread from one part to the others. Although the attention focuses on connections that link variables of sub-domains of the socio-ecological systems, i.e. how changes in societal priorities or regulative framework may affect the dynamics of species (Long et al., 2015), connections can be central also within the ecological domain of this enlarged ecosystem. Understanding linkages between species, in particular, can improve our

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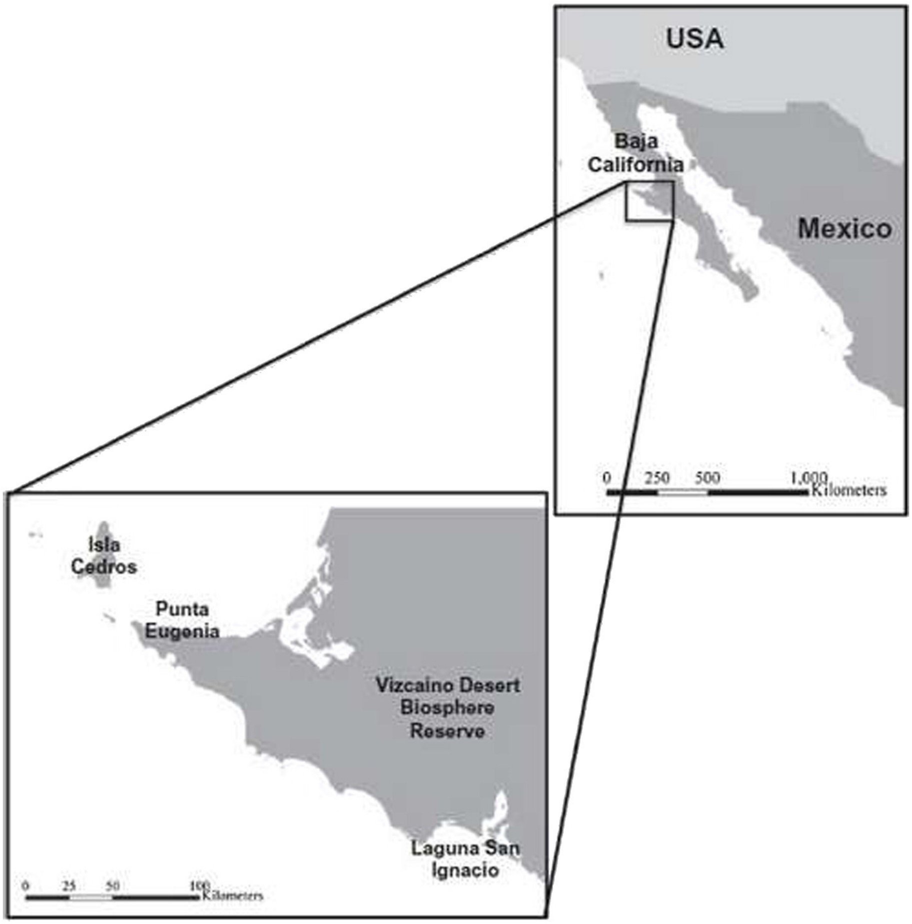

Fig. 1. Map of the study area located along the coast of the Vizcaino Desert Biosphere Reserve in the North Pacific region of Baja California Sur, Mexico (reproduced from Micheli et al., 2014, with permission).

knowledge about how the ecological community may respond to environmental or anthropogenic stress and can thus provide valuable indications of possible impacts on ecosystems of management regulation and policies (Carey et al., 2013).

The interest in structural features of food webs is justified on the grounds of the potential relationship that links food web structure and ecosystem functions (Petchey et al., 1999, 2008). In particular, centrality indices can provide information about the transmission of control (top-down vs. bottom-up) and the flow of energy in ecosystems (Jordán et al., 2006, Jordán, 2009), and overall structural metrics can give indications about the integrity of the food web upon which ecosystem functions depend (Miehls et al., 2009; Bondavalli and Bodini, 2014).

In this study we reconstructed the linkage structure of the coastal marine ecosystem of the North Pacific region of Baja California Sur, Mexico, which is exploited by local SSFs. We produced a qualitative food web that we then used to simulate the disappearance of vulnerable species (Micheli et al., 2014) due to excessive fishing pressure. We studied this food web to reveal: (1) which species are the most central (i.e., functionally important; Jordán and Scheuring, 2002) in the community; (2) whether these central species are also the most vulnerable considering their productivity and the cumulative effects of multiple fisheries (Micheli et al., 2014); (3) how species centrality changes after the removal of one or more species; (4) how the structural features of the community as a whole change when central species disappear or when species are instead removed at random. Results of these analyses have implications for our understanding of food web structure, fishing impacts, and ecosystem-based fisheries management.

2. Methods

2.1. Study area

We performed our investigation on the coastal marine ecosystem located along the coast of the Vizcaino Desert Biosphere Reserve in the North Pacific region of Baja California Sur, Mexico (Fig. 1). This ecosystem supports local fishing communities which are organized in fishing cooperatives (McCay et al., 2014). The North Pacific region can be defined as temperate to subtropical, with sea surface temperatures ranging from 12° to 27 °C throughout the year. This region is characterized by a mosaic of rocky reef and sandy subtidal ecosystems that encompass the southern edge of the range of giant kelp (*Macrocystis pyrifera*) where a zone of persistent upwelling maintains high biological productivity (Martone, 2009).

The fishing cooperatives of the central Baja California region belong to FEDECOOP (Federacion Regional de Sociedades Cooperativas de la Industria Pesquera de Baja California), which acts as a co-management agency with the national and regional fisheries agencies to monitor resources and develop management plans. The fishing cooperatives of the North Pacific date back to the late 1930s, as a manifestation of the Mexican cooperative movement that was mainstreamed into national fisheries development policies (Ponce-Díaz et al., 2009; McCay et al., 2014). SSFs represent 99% of registered fishing vessels on the Baja California and Baja California Sur peninsula (INEGI 2008[1]). Cooperatives have renewable 20-year concessions for different species, including

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[1] http://www.inegi.org.mx/ [last accessed on February 9, 2016].

red spiny lobster (*Panulirus* spp.), abalone (*Haliotis fulgens* and *H. corrugata*), wavy turban snail (*Megastraea undosa*), sea cucumber (*Parastichopus parvimensis*), red sea urchin (*Mesocentrotus franciscanus*), and the red alga *Gelidium robustum*. Fishers also catch many species of finfish but, in contrast with benthic invertebrates and algae, do not hold territorial rights for them (i.e., fishing cooperatives do not have exclusive access to finfish within a geographically defined area; see Afflerbach et al., 2014). Within the food web, species are subjected to different fishing pressure and risks, applied through a variety of fishing methods (Micheli et al., 2014). Therefore, fisheries have different kinds of concessions (i.e., fishing permits), and harvest species which vary greatly in their commercial value. This permits structure imposes disincentives for switching to different fishing targets when one is depleted, in some cases leading to further depletion.

2.2. Food web construction and trophic structure

We constructed an adjacency matrix that reports presence/absence of trophic interactions (i.e., who eats whom) among species or species groups within the food web. Rows represent prey species and columns represent predator species. Each coefficient a_{ij} is 1 if the row species i is a prey of the column species j and 0 elsewhere (Dunne et al., 2002a; Abarca-Arenas et al., 2007; Gaichas and Francis, 2008; Navia et al., 2010, 2012). We constructed an unweighted food web (i.e., all trophic interactions are set to 1) because no information about link strength (i.e., amount of biomass flowing from prey to predators) was available. Community composition and trophic resolution level were based on active collaboration with experts. Starting from species considered in Micheli et al. (2014), we added appropriate nodes for a better representation of a coastal marine food web. All subtidal pelagic and benthic coastal environments and associated species (from rocky reefs, kelp forests, seagrass beds, and sandy bottoms) are well represented. Intertidal habitats, where target species do not occur, and estuaries, which in the study area are not directly adjacent to the fishing grounds, are not included, though some species occasionally use these habitats for foraging or as juveniles. Data on trophic interactions were obtained from the Kelpforest Database (Beas-Luna et al., 2014), literature and general online sources such as FishBase (Froese and Pauly, 2015), Encyclopedia of Life,[2] Discover Life[3] and Animal Diversity Web[4] (see Table S1 in Supplementary material for a detailed description of diet sources for each node). When dietary information was unavailable for some species in the study area, data from similar ecosystems were used to complete the food web. Thus, the food web is mainly literature based due to the lack of local data (e.g., gut content or stable isotopes analysis) that characterized the study area. The prey set of each node, identified from the literature (i.e., diet composition), was checked by expert marine biologists working in Baja California (Table S1). The adjacency matrix that summarizes all trophic interactions is included in Supplementary material (Table S2).The resulting food web of the North Pacific region of Baja California Sur is visualized in Fig. 2. The food web is composed of 121 nodes ($S = 121$) and 979 trophic interactions ($l = 979$). In the graph, each node stands for a species or a trophospecies (i.e., a group of species with equivalent feeding habits and preyed upon by the same set of predators), while directed edges indicate the presence of trophic interactions. Nodes represent 100 species and 21 trophospecies: 3 birds, 3 marine mammals, 75 fish, 34 invertebrates, 4 algae, zooplankton and phytoplankton.

We used network analysis to investigate the food web structure of the Baja California Sur marine system. We identified key (i.e., most central) species through centrality indices and explored the resilience of the system by evaluating the changes in both global structural indices and species' centrality indices due to the local extinction of vulnerable species (as defined by Micheli et al., 2014).

2.3. Global structural indices

There are many structural indices that describe global features of food webs. These global structural indices can be related to various aspects of food web functioning such as energy delivery (Allesina and Bodini, 2004), stability (Rooney et al., 2006), and robustness (Dunne et al., 2002b). Table 1 summarizes the indices we computed to assess the consequences of species' removals on the whole food web structure. We selected the most commonly used indices for which clear ecological interpretation is associated to changes in their values (see the last column in Table 1).

2.4. Trophic levels and centrality indices

To characterize the food web structure we calculated species' trophic level with the cheddar library in the R environment (Hudson et al., 2013). There are different methods for measuring trophic levels of species and trophospecies in food webs (e.g., see Williams and Martinez, 2004, Scotti et al., 2006). We used the prey averaged trophic level that returns for each predator 1 plus the mean trophic level of its prey, using the matrix inversion method of Levine (1980).

Besides the trophic level, we quantified the structural roles of species by computing centrality indices. Such indices were developed in social network analysis and can be used as an approximation of species' functional importance (e.g., see Jordán and Scheuring, 2002, Jordán et al., 2006, Jordán et al. 2007, Abarca-Arenas et al., 2007, Jordán, 2009, Navia et al., 2010). We considered some of the most commonly applied indices: degree centrality, betweenness centrality, and closeness centrality. Table 2 provides a synthetic description of the indices.

Species that show a high value for D_i (degree centrality; Table 2) are hubs (i.e., they locally interact with many other species). When BC_i (betweenness centrality) is high the node i plays an important role in mediating indirect effects. High CL_i (closeness centrality) values identify nodes that, when disturbed (e.g., decline of their population size), spread the impact to other food web nodes more rapidly. Centrality indices were computed with Cytoscape (Shannon et al., 2003) and using the igraph library in the R environment (Csárdi and Nepusz, 2006). See the Supplementary material for the algorithms of centrality indices.

2.5. Removal analysis

Removal analysis was conducted to mimic the effects of a possible collapse of certain species due to overfishing (Hamre, 1994; Dolgov, 2002). Frequently, species may become functionally extinct as a result of excessive fishing pressure (Dayton et al., 1998; Jackson et al., 2001), where their densities are too low to play their ecological role as consumers or resources within the food web. Functional extinctions are relatively common, and would result in a particular node, or species, to no longer be part of a network, functionally. We simulated this scenario here. Species to be removed were selected using the risk-based approach introduced by Micheli et al. (2014). Micheli et al. extended Productivity-Susceptibility Analysis (PSA) to assess the cumulative risk posed by multiple fisheries to the species of the North Pacific marine food web. PSA defines species vulnerability (V) as a function of productivity (P) and aggregated susceptibility (AS): $V = \sqrt{P^2 + AS^2}$. Productivity is calculated by using information on species life history such as age and size at maturity, fecundity, reproductive strategy, and trophic level (Hobday et al., 2007). Two or more fisheries may affect a single species and it is assumed that their cumulative potential impact may be larger (e.g., additive or multiplicative) than that generated by the single

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[2] http://www.eol.org [last accessed on February 9, 2016].

[3] http://www.discoverlife.org/ [last accessed on February 9, 2016].

[4] http://animaldiversity.org/ [last accessed on February 9, 2016].

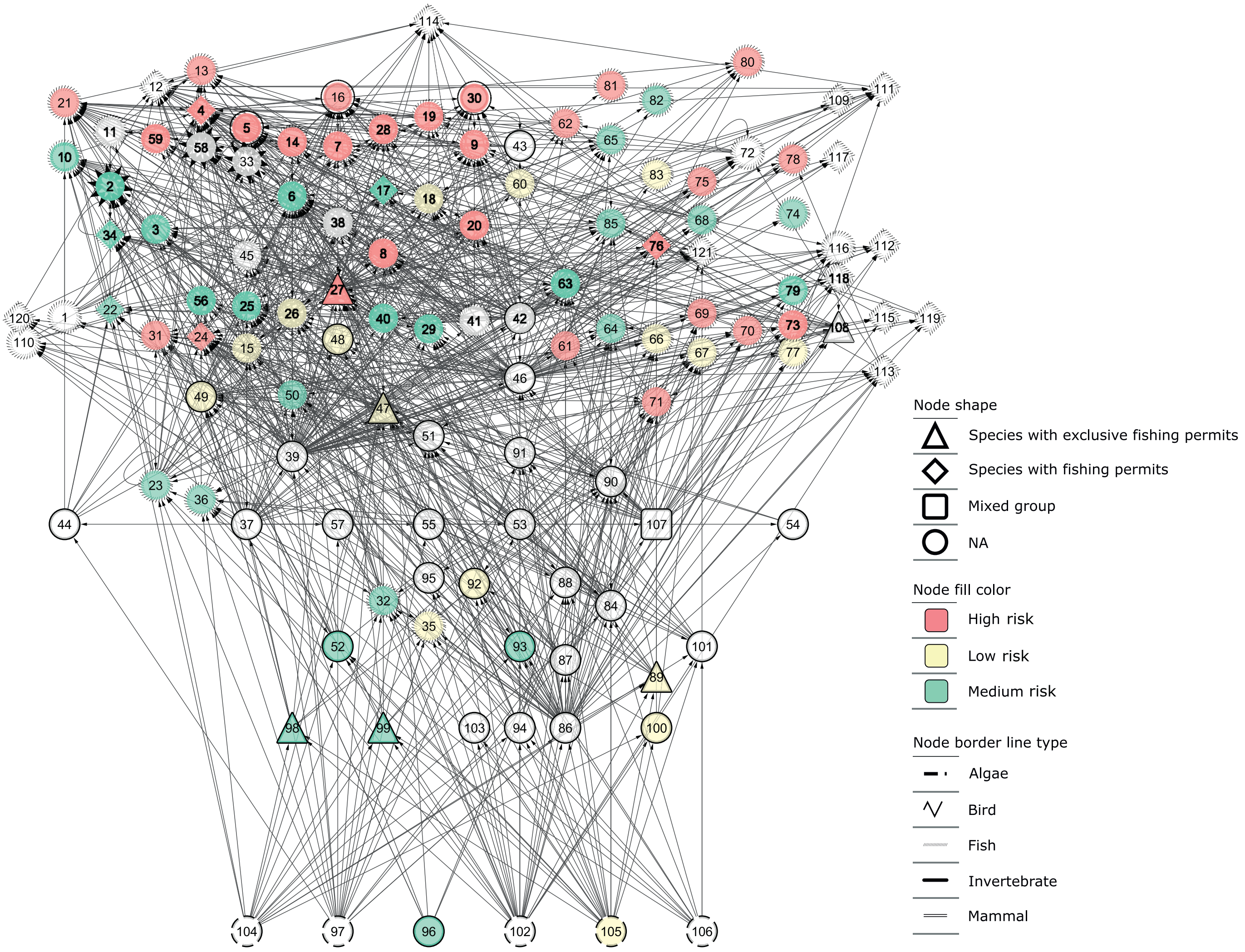

Fig. 2. Food web diagram representing trophic interactions in the area located along the coast of the Vizcaino Desert Biosphere Reserve in the North Pacific region of Baja California Sur, Mexico. Each node represents either a species or a trophospecies. The edges connecting the nodes stand for trophic interactions (each arrowhead edge leaves the prey and enters the predator). Species' vertical position reflects the trophic level. The color of the nodes indicates different levels of vulnerability (V), the border line specifies taxonomic groups and the shape displays fishing permits. The food web diagram was visualized with Cytoscape (Shannon et al., 2003).

fishery with the greatest impact (Halpern et al., 2008b). Aggregated susceptibility accounts for possible cumulative effects of multiple overlapping fishing activities and is assessed on the basis of several attributes (e.g., the selectivity of fishing gears and post-capture mortality of discarded bycatch; see Micheli et al., 2014). To investigate how fishing can modify the structure of the food web we considered the vulnerability of species that takes into account the cumulative risk due to multiple fisheries (Micheli et al., 2014). According to the values of these vulnerability scores we classified species as at high, medium and low risk (Table S3 in Supplementary material). The first group (i.e., high risk) included 28 species: 3 mammals, 24 fish, and 1 invertebrate; medium risk species comprised 28 species: 1 bird, 22 fish, and 5 invertebrates; the latter group (i.e., low risk) was composed of 16 species: 9 fish, 6 invertebrates and 1 algae (Table S3). We explored the impacts of single species removals or different combinations of high/medium/low risk species removals (i.e., by removing combinations of two, three or four nodes at the same time) and considered the effects on the entire food web structure. The impacts on single species were investigated only for the removal of different combinations of high risk species. The number of all possible combinations (N) was determined by: $N = \frac{n!}{r!(n-r)!}$, where n is the number of high/medium/low risk species taken r at a time ($r = 1, 2, 3$, or 4) without repetition. Removal scenarios were targeted first to the 28 high risk species in this food web, which were all removed one at a time. Second, all possible pairs of high risk species were removed. Then we removed all possible combinations of three and four high risk species. We repeated the same procedure by considering the medium and low risk species. In summary, for single species removals we had 28 different scenarios for high and medium risk species, and 16 scenarios for low risk species. Two species removals yielded 378 combinations for both high and medium risk species, and 120 scenarios for low risk species. For three species removals, both high and medium risk species generated 3276 different combinations, whereas 560 scenarios were obtained with the subset of low risk species. Combinations of four species were 20,475 for high and medium risk species, and 1820 for low risk species. We did not consider scenarios in which removals targeted mixed combinations of high, medium and low risk species although we recognize that this is not unrealistic.

The influence of species removals on the whole food web was assessed using global structural indices (Table 1) and visualized through frequency histograms of assortativity coefficient (AC), clustering coefficient (CC), modularity (MD), connectance (C), linkage density (LD), diameter (DM), average path length (APL) and number of nodes with

Table 1
Global structural indices. A brief description for each index is provided (Explanation) together with the meaning as a function of the values computed (Interpretation).

Indices	Explanation	Interpretation
Assortativity coefficient (AC)	Correlation between the degree (i.e., the number of connections) of two neighboring nodes (Newman, 2002; Sokhn et al., 2013).	$AC < 0$, the network is disassortative (i.e., high degree nodes are connected to low degree nodes). $AC > 0$, the network is assortative (i.e., high degree nodes are connected to high degree nodes). $AC = 0$, the connections between nodes do not depend by their degree.
Clustering coefficient (CC)	Measured as the ratio between the number of edges involving the neighbors of a node *i*, and the maximum number of edges that could exist. The clustering coefficient of the food web is the average of the clustering coefficients of all nodes. If the food web is fully connected, the clustering coefficient is then equal to 1.	An increase in the values of this index indicates that species tend to compete with other species in more clustered groups (Sokhn et al., 2013).
Modularity (MD)	Qualitative measure for food web clustering. MD ranges from 0 to 1: if MD approaches 1, this indicates strong modular structure; if the number of intra-modular edges is no more than what could be expected from random networks, then $MD = 0$ (Sokhn et al., 2013).	When this index increases the food web becomes more fragmented and therefore more vulnerable.
Betweenness centrality equal to 0 (BC0)	Betweenness centrality of a node *i* is the fraction of shortest paths in a food web that passes through *i*. The global index derived from this centrality quantifies the number of nodes with betweenness centrality equal to zero.	If the number of species with a betweenness centrality equal to 0 increases, then more species compete with only one particular group of species and hence belong to a unique subnetwork; instead, if there is a decrease this indicates that less species compete (Sokhn et al., 2013).
Connectance (C)	Computed as the ratio between existing and all possible trophic interactions (i.e., $C = l/S^2$, Martinez, 1992).	Lower connectance value can reveal a decrease in food web robustness (Dunne et al., 2002b).
Linkage density (LD)	The average number of feeding links per species.	Lower link density values can reveal a decrease in food web robustness (Dunne et al., 2002b).
Average path length (APL)	The average distance between any two nodes in the undirected network.	A decrease in this index can be an indicator of faster spread of disturbance in the whole food web.
Diameter (DM)	The shortest undirected path (number of trophic interactions) between the two most distant nodes in the network.	This can be an indicator of how fast disturbance can spread in the whole food web.

Table 2
Centrality indices. Degree centralities are divided into: in-degree ($D_{in,i}$), out-degree ($D_{out,i}$) and degree (D_i). Betweenness centralities are separated into the directed (BC_i) and undirected ($undBC_i$) version, while for the closeness centrality we considered the undirected version (CL_i).

Indices	Explanation	Interpretation
In-degree ($D_{in,i}$)	The total number of a node's prey.	High value for $D_{in,i}$ are characteristic of species that show generalist trophic habits.
Out-degree ($D_{out,i}$)	The total number of a node's predators.	Species that exhibit a high value for $D_{out,i}$ are vulnerable species (i.e., species undergoing high predatory pressure).
Degree (D_i)	The degree of node *i* (D_i) is obtained summing together the total number of all its prey (in-degree, $D_{in,i}$) and its predators (out-degree, $D_{out,i}$).	Species that show a high value for D_i are hubs (i.e., they locally interact with many other species).
Betweenness centrality (BC_i)	Counts how many times a target node *i* lies on the shortest paths connecting every other pair of species *j* and *k* in the food web. It considers shortest paths with a strict bottom-up perspective (i.e., tracing biomass flow from primary producers to consumers).	It measures how central a given node is in terms of being included in many shortest paths in the network, thus describing how crucial (i.e., high index values) a species is in mediating the diffusion of indirect effects throughout the whole food web in a bottom-up perspective.
Undirected betweenness centrality ($undBC_i$)	The count is the same as for BC_i but the undirected version accounts for the spread of both bottom-up and top-down effects (i.e., without being constrained by the direction of biomass flow).	The interpretation is the same for BC_i but considering a top-down and bottom-up perspective.
Undirected closeness centrality (CL_i)	Measures the length of the shortest paths from a given species *i* to all other species in the food web.	It measures how close a node is to the others and quantifies how rapidly an effect that generates from species *i* can spread in the food web both from top-down and bottom-up perspective (i.e., it is not constrained by biomass flow direction in the food web and does not implement a strict bottom-up perspective).

betweenness centrality equal to 0 (BC0). The impact of removals on single species was assessed on the basis of changes in their centrality indices. For degree centrality, to quantify the effects of species' removals ($remD_i$) we considered the ratio between the values with (D_i^{rem}) and without removals (i.e., in the original food web; D_i): $remD_i = D_i^{rem}/D_i$. Hence, a value equal to 1 means no change in degree centrality, while values <1 identify those species whose total degree centrality decreased after removals. To assess the changes in betweenness and closeness centralities (indices for which we used the normalized versions that bring all values into the range [0, 1]; see Supplementary material), the values computed for each removal experiment (BC_i^{rem} and CL_i^{rem}) were subtracted from their counterparts computed in the original food web (BC_i and CL_i): $remBC_i = BC_i - BC_i^{rem}$; $remCL_i = CL_i - CL_i^{rem}$. Therefore, a null value means no change, a positive value stands for a decrease and a negative value indicates an increase in the centrality score. The impacts of high risk species removals on centrality indices of all other species in the food web were visualized by heat maps.

To further investigate whether species at risk (according to the definition provided by Micheli et al., 2014) occupy most central structural positions in the food web we compared the consequences of their removal with those produced by random removals of the food web species, independently of their vulnerability score. We considered single species removals as well as combination of up to four species selected at random. Thus, we had respectively 121, 7260, 287,980 and 8,495,410 possible removal scenarios to be compared with the ones based on targeted removals (i.e., these latter scenarios follow the vulnerability index criteria). The presence of a significant difference between the effect of targeted and random deletions indicates that the species that are most vulnerable to fishing pressure are also important from a structural point of view (i.e., this is for testing whether targeted removals have more consistent negative effects on food web topology compared to random deletions). This would imply that the disappearance of vulnerable species can have consequences on the community structure and possibly function. This analysis evaluates whether the vulnerability ranking proposed by Micheli et al. (2014) also reflects species' structural importance.

2.6. Statistical analysis

To investigate a possible aggregation bias (i.e., the presence of significant differences in the centrality indices of species vs. trophospecies) in the original food web (i.e., in absence of any removal) we applied the Kolmogorov-Smirnov test (KS-test). To compare index values obtained after targeted removals (i.e., risk-based) with those obtained from random deletions we performed the Mann-Whitney-Wilcoxon test. All statistical analyses were performed in R.

3. Results

3.1. Topological analysis: global structural indices, trophic levels and centrality indices

The food web is depicted in Fig. 2. The connectance is 0.07 and the network is disassortative ($R = -0.34$, Sokhn et al., 2013): high degree nodes (i.e., nodes with many connections) are connected to low degree nodes (i.e., nodes with few connections). All centrality indices differ significantly between species and trophospecies ($D_{in,species} > D_{in,trophospecies}$, $p < 0.001$; $D_{out,species} < D_{out,trophospecies}$, $p < 0.001$; $D_{species} < D_{trophospecies}$, $p = 0.003$; $undBC_{species} < undBC_{trophospecies}$, $p < 0.001$; $BC_{species} < BC_{trophospecies}$, $p = 0.024$; $CL_{species} < CL_{trophospecies}$, $p = 0.010$, see Table 2 for the description of all indices). This result confirms that the level of aggregation (species vs. trophospecies) can bias the analyses. Trophospecies have a significantly higher number of trophic interactions than single species ($D_{species} < D_{trophospecies}$, $p = 0.003$). This implies that trophospecies may be involved in a higher number of pathways and influence betweenness and closeness values. Thus, we restricted the analysis to individual species (100 nodes) and excluded trophospecies. The values for the indices are reported in Table S3 of Supplementary material. Twelve species occupy the most central positions in the trophic network, based on degree, betweenness, and closeness centralities (Table 3).

3.2. Removal analysis

In general, the food webs generated by the removal experiments (i.e., the food webs constructed using different scenarios of either targeted or random species deletion; see Fig. 3) did not show significantly different values of global structural indices when compared with the values computed in the original food web (i.e., see the red line in Fig. 3). This holds true for the global structural indices AC, CC, MD, C, BC0, APL and DM. Link density shows a progressive increase in the difference between the value in the original web and the ones obtained through species removals (Fig. 3). We found similar patterns of global structural indices for random and selective removals (i.e., when one to four species are removed) across risk levels (i.e., medium and low risk species deletions; see Figs. S1–S5 in Supplementary material).

There is no significant difference between selective and random removals in the case of CC (Mann-Whitney-Wilcoxon test; Table 4). Significant differences emerged, instead, for AC, MD and APL, under removal scenarios from two to four species removed (Table 4). Indices MD and APL were significantly higher when the food web was exposed to targeted removals (Table 4). Different values for C and LD occurred when three and four species were removed (Table 4). Different values for BC0 emerged only when four species were removed (Table 4).

One example of the impact of removals on single species, assessed by computing centrality indices, is given in Fig. 4 (all the others cases are reported in Supplementary material). *Octopus* sp. is the species that, if removed (either individually or in combination with other species), determines the greatest impact (based on centrality index D; see also Figs. S6–S8 in Supplementary material). The most impacted species are all fish species: the pelagic thresher shark *Alopias pelagicus*, the shirtfin weakfish *Cynoscion parvipinnis* and the smooth stargazer *Kathetostoma averruncus*. Two invertebrate species are also affected when some combinations of two to four species are removed: the scallop *Hinnites multirugosus* and the sea cucumber *Parastichopus parvimensis*. Considering index BC, the kelp bass *Paralabrax clathratus*, *Octopus* sp., the halibut *Paralichthys californicus* and the Pacific barracuda *Sphyraena argentea* (three fish and one invertebrate) are the most impacted species in all the removal scenarios (i.e., their value decreases; Figs. S6–S8 in Supplementary material). When *Octopus* sp. is the target of removal, both as single species and in combination with others, >50% of the remaining species shows a decrease in closeness (Figs. 4 and S6–S8 in Supplementary material). The removal of *Paralichthys californicus* and the giant seabass *Stereolepis gigas* also induces a decrease in this index. Phytoplankton, zooplankton, the kelp *Eisenia arborea* and other algae increase their closeness for all combinations of species except for the deletion of *Octopus* sp. (i.e., both as single species or in combination with others), for which their values decrease.

4. Discussion

We identified 12 species as the most central (i.e., topologically and therefore possibly functionally important) in the food web of Baja California (Table 3). Five of these 12 species are the most central for at least three indices and could be thought of as key players in the community. They are: the kelp bass *Paralabrax clathratus*, the California halibut *Paralichthys californicus*, *Octopus* sp., the California sheephead *Semicossyphus pulcher* and the spiny lobster *Panulirus interruptus*. All of them are evaluated as at risk for the cumulative effects of multiple fisheries according to Micheli's vulnerability index (Micheli et al., 2014). Of these five species, three are high risk species, one medium, and one low (see Table 3 and Fig. 2).

Our results show that removing up to four target species (i.e., at risk; see Micheli et al., 2014), does not alter the overall structural attributes of the food web. Thus the network appears to be structurally resilient: it tends to maintain its integrity in the face of several simulated extinction

Table 3
The 12 most central species in the Baja California coastal food web. For each index, we consider the species that occupy the top five positions. For each species and index, we show centrality values and ranking position (1st to 5th).

ID code	Species	Category	D_{in}	D_{out}	D	BC	undBC	CL
6	*Paralabrax clathratus*	Fish	37(1st)		47(2nd)	0.089(2nd)	0.036(2nd)	0.603(2nd)
4	*Paralichthys californicus*	Fish	30(2nd)		40(3rd)	0.071(3rd)	0.021(4th)	0.577(3rd)
27	*Octopus* sp.	Invertebrate		37(1st)	58(1st)	0.111(1st)	0.089(1st)	0.635(1st)
24	*Semicossyphus pulcher*	Fish	24(4th)		32(5th)		0.027(3rd)	0.569(4th)
47	*Panulirus interruptus*	Invertebrate			36(4th)		0.020(5th)	0.569(5th)
21	*Stereolepis gigas*	Fish	28(3rd)			0.030(4th)		
16	*Zalophus californianus*	Mammal	24(5th)					
84	*Pugettia producta*	Invertebrate		25(3rd)				
41	*Clupeids*	Fish		30(2nd)				
105	*Eisenia arborea*	Algae		21(4th)				
49	*Cancer anthonyi*	Invertebrate		19(5th)				
19	*Sphyraena argentea*	Fish				0.016(5th)		

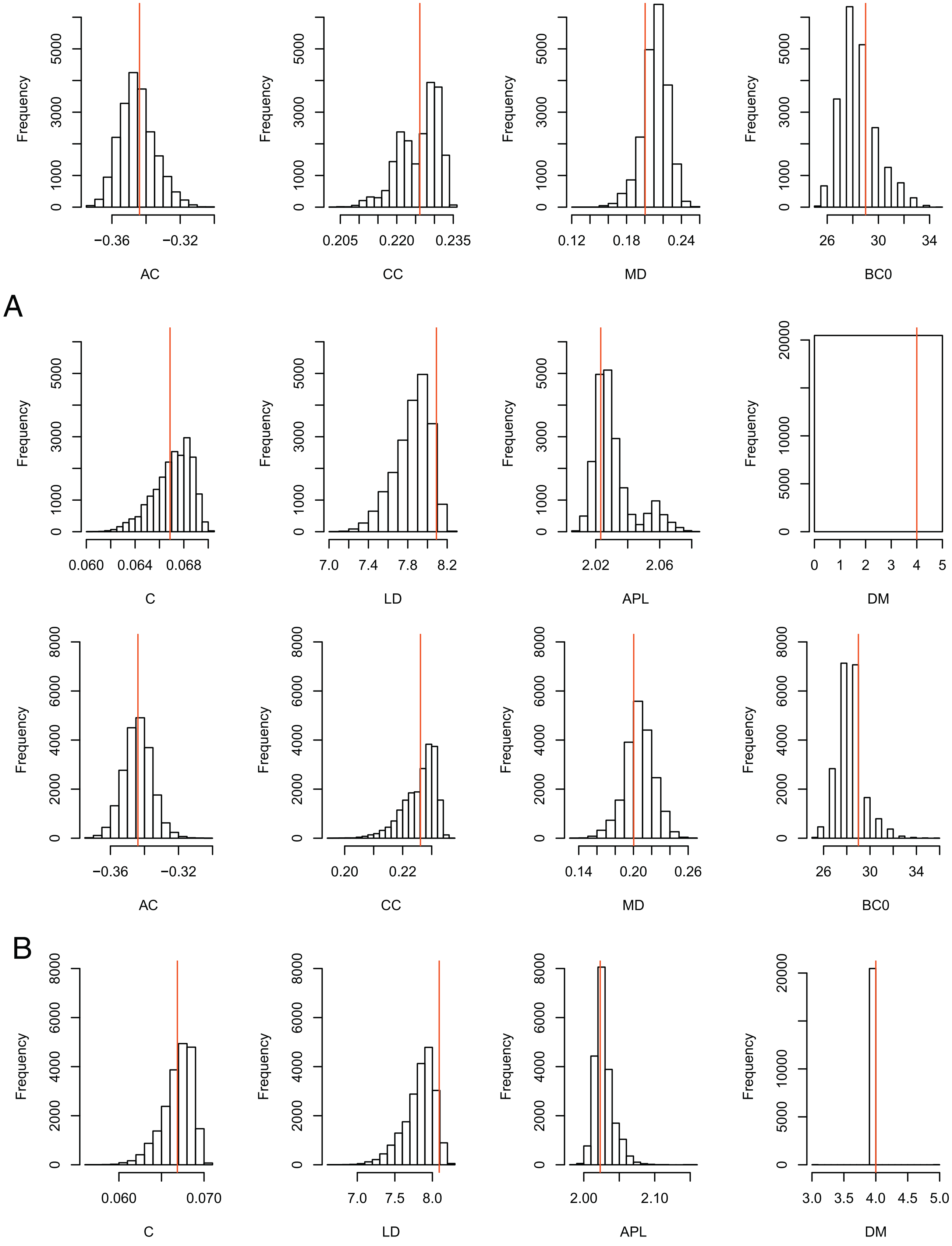

Fig. 3. Frequency histograms for global structural indices following removals of four species (20,475 combinations): high risk species removal (A) and random removals (B). In each chart the red line shows the value of the index for the food web with no removals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4
Mann-Whitney-Wilcoxon test for the comparison of global structural indices computed after either targeted (i.e., high risk) or random removals. The scenarios comprise single removals and multiple removals of all possible combinations up to four species (see the different rows of the table). ASH key labels targeted removals of species at risk; R key identifies random extinctions. Numbers indicate the p-values of the Mann-Whitney-Wilcoxon test. ASH > R indicates that the index is significantly higher for targeted removals than for random removals, while ASH < R stands for significantly lower values in case of targeted removals if compared to random deletions.

Species removed	AC	CC	MD	BC0	C	LD	APL	DM
1	0.980	0.774	0.787	0.656	0.394	0.394	0.712	NA
2	0.010 ASH < R	0.500	<0.001 ASH > R	0.903	0.715	0.715	<0.005 ASH > R	NA
3	≪0.001 ASH < R	0.472	≪0.001 ASH > R	0.145	<0.004 ASH > R	<0.004 ASH > R	≪0.001 ASH > R	NA
4	≪0.001 ASH < R	0.641	≪0.001 ASH > R	≪0.001 ASH > R	≪0.001 ASH > R	≪0.001 ASH > R	≪0.001 ASH > R	0.180

events. Link density is the only structural index that shows a significant difference between the original web and those obtained after removals. This result indicates that, as the number of removed species increases, the average number of feeding links per species decreases. This effect may have consequences on ecological function and food web resilience to additional species loss because it reduces the diet breadth of species and the number of pathways through which materials and energy move through the web, and thus the functional redundancy of the assemblage (e.g., Micheli and Halpern, 2005). The sensitivity of link density to changes in food web structure has been already reported in the literature, with a previous study showing how link density is more sensitive to data aggregation than connectance (Dunne, 2006). Thus, the result of a significant change of link density with species removals is not surprising. In contrast, all other indices were unaffected by removals.

Food web structure is differentially affected in selective (i.e., targeted to high risk species) and random removals depending on the indices considered and the number of species removed (Table 4). The significant differences between target (i.e., risk based) and random removals assume high relevance because the analysis was conducted in a conservative way (i.e., species at risk are also included in random removals).

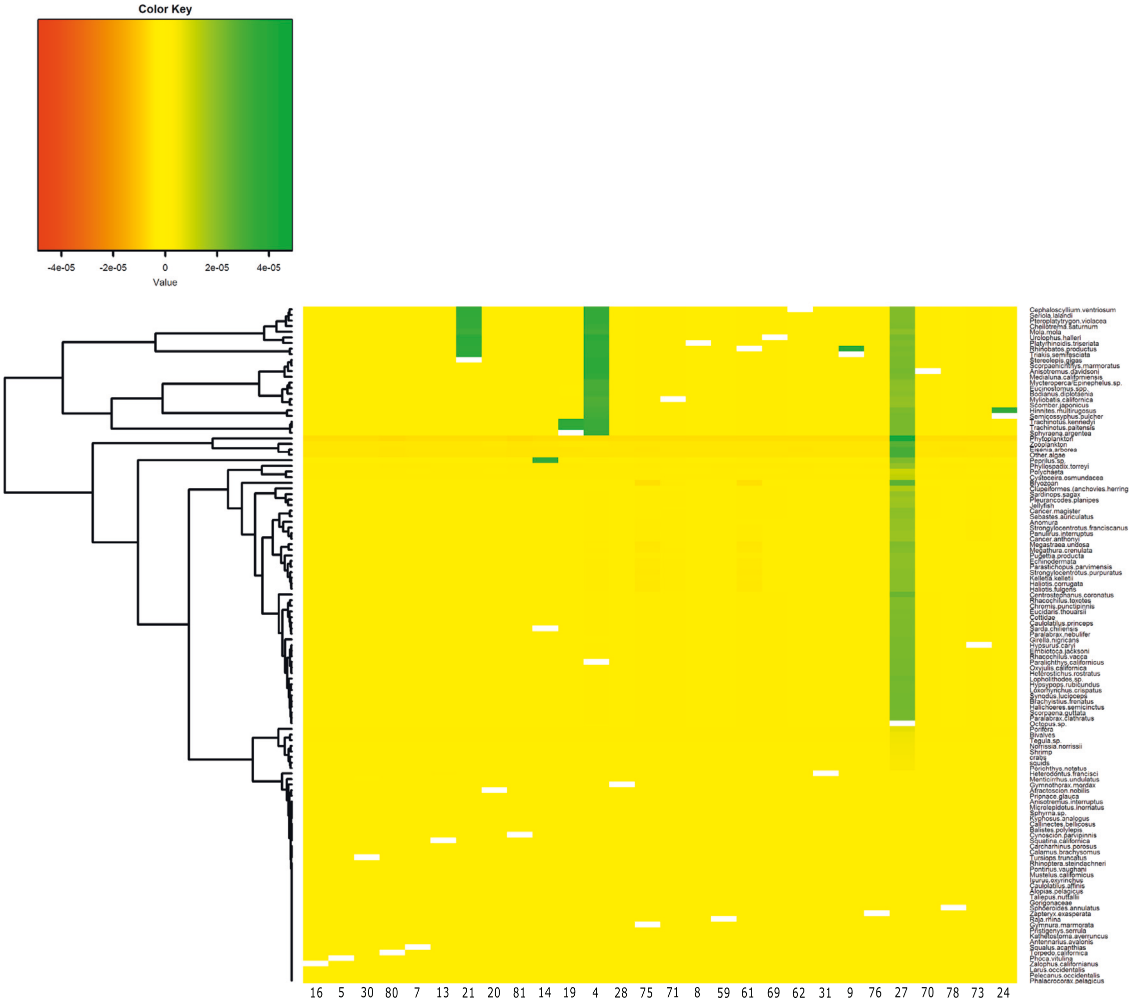

Fig. 4. Changes in closeness centrality due to the targeted removal of one species at high risk (i.e., 28 different scenarios). On the x axis the identification codes (Tables S2, S3) of single species removed (16, *Zalophus californianus*; 5 *Phoca vitulina*; 30 *Tursiops truncatus*; 80 *Torpedo californica*; 7 *Squalus acanthias*; 13 *Squatina californica*; 21 *Stereolepis gigas*; 20 *Atractoscion nobilis*; 81 *Cynoscion parvipinnis*; 14 *Sarda chiliensis*; 19 *Sphyraena argentea*; 4 *Paralichthys californicus*; 28 *Gymnothorax mordax*; 75 *Gymnura marmorata*; 71 *Myliobatis californica*; 8 *Platyrhinoidis triseriata*; 59 *Raja rhina*; 61 *Rhinobatos productus*; 69 *Urolophus halleri*; 62 *Cephaloscyllium ventriosum*; 31 *Heterodontus francisci*; 9 *Triakis semifasciata*; 76 *Zapteryx exasperata*; 27 *Octopus* sp.; 70 *Anisotremus davidsoni*; 78 *Sphoeroides annulatus*; 73 *Hypsurus caryi*; 24 *Semicossyphus pulcher*; we followed the order of species' deletion shown in the heat map). The species removed are indicated by white boxes in each scenario. Along the column are visualized the changes in closeness centrality (i.e., in response to targeted removals) for each species listed on the right side of the heat map. The order along the y axis depends on the clustering method (i.e., complete linkage method with Euclidean distance measure that finds similar clusters). In the upper left corner the color scale used for visualization and the corresponding numerical range for the index. According to this scale, green boxes indicate lowest closeness values after removals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Modularity (MD) was significantly higher when removals targeted to high risk species were compared to random extinctions. Thus, removing species at high risk can create a more fragmented food web. This is due to the central position that some of the high risk species occupy in the network of trophic interactions. Their loss may render the whole network more fragile and thus possibly more vulnerable to further extinction events. Connectance (C) increases significantly when high risk species are removed. It has been shown previously that connectance is related to the relative importance of functional and redundant links in food webs; in particular, when C increases, the number of redundant links becomes greater than that of functional links (Bondavalli and Bodini, 2014). Allesina et al. (2009) showed that functional connections affect food web robustness, whereas redundant links are neutral. Targeted removals, by significantly increasing connectance (and thus the fraction of redundant links) in comparison with random removals, would make the food web less robust than its original counterpart as the number of independent pathways (i.e., those composed by functional connections and that are fundamental for energy delivery) likely decreases (but see Dunne et al., 2002a, 2002b). In summary, the presence of some significant differences (e.g., MD and C) between the effect of targeted and random deletions confirms that species at high risk of depletion from fishing are important from a structural point of view.

The analysis of species centrality expands in a functional perspective the concept of structural connectedness (Jordán et al., 2006; Jordán, 2009). *Octopus* sp. ranked highest for all the centrality indices. Closeness centrality indicates how close a species is to the others; results of this index suggest that *Octopus* sp. plays an important role in the spread of both direct and indirect effects being responsible for their diffusion in the ecosystem via shortest paths. Because the bulk of energy travels through food webs along pathways that tend to be short (Bellingeri and Bodini, 2016), *Octopus* sp. may enter several main routes for energy delivery from primary producers to top species. This hypothesis needs to be tested with empirical measurements and experiments, as the ecological role of *Octopus* sp. in this food web is unknown. Empirical and theoretical studies quantifying the main pathways for energy delivery and the strength of these routes would elucidate the role *Octopus* sp. and other species with high values of closeness centrality play in energy delivery, and whether these species may act as bottlenecks for energy distribution to other species in the food web (Allesina and Bodini, 2004). The high value of closeness for this species (calculated as undirected index) suggests that *Octopus* sp. might be involved in spreading top-down control, e.g., it may be part of a trophic cascade from its predators to its prey. Control by high level consumers upon lower trophic levels can be possible through several paths in a food web. However, fastest spreading is assured by the shortest paths that can become the dominant routes through which control is exerted by top consumers. The highest value of closeness, combined with the highest value of betweenness centrality, suggests that *Octopus* sp. might enter in several of these dominant routes through which cascading trophic interactions may manifest (Hodgson, 2005). Network position in itself, however, does not guarantee a prominent role in top-down regulations. This hypothesis, as highlighted above, remains to be tested.

Octopus sp. is the species that, if removed, determines the greatest change on other species' centrality in our simulation. We found that >50% of the remaining species showed a decrease in their closeness centrality values after the removal of *Octopus* sp. This result suggests that decline or loss of *Octopus* sp. might cause a substantial reorganization of the energy flow in the food web. This is because the reduced closeness for a high proportion of species imposes that pathways for energy delivery would elongate, with potential loss of efficiency. However, this hypothesis arises from a static view and analysis of the food web. In real, dynamic food webs, species would actively respond to species loss through mechanisms such as diet switching (Barnum et al., 2015), which would buffer the effects of species loss. Nevertheless, a reorganization of the energy flows within the ecosystem might still occur, with potential impacts on the amount of energy that reaches the top species and, possibly the fisheries. Gaichas and Francis (2008) have proposed that protecting highly connected species in the network, also called hub species, is crucial for preventing potential impacts of fishing activities on the whole ecosystem structure. The central role that *Octopus* sp. might play, as suggested by the centrality indices, supports the correctness of the present regulative framework, which limits the catch to this species to fishing cooperatives that hold exclusive fishing permits. This regulative framework (i.e., exclusive access to cooperatives) applies also to the spiny lobster *Panulirus interruptus*, another species that plays a major role in the economy of the fishing cooperatives and that is also central in the food web, based on our analysis (Fig. 2). These conclusions that emphasize the role of *Octopus* sp. must be taken with circumspection, however, and further scrutiny on the role this species plays in Baja California is needed. Results obtained in this study strongly depend on the assumptions we made about the position that *Octopus* sp. occupies within the food web and that is defined since the adjacency matrix is compiled. Nevertheless, it has been pointed out that these predators are voracious and adaptable, and they impact many prey species, including commercially valuable fish and invertebrates (Doubleday et al., 2016). Also, several marine predators rely on this species for food. This confirms that the positional importance of *Octopus* sp. as a hub with many incoming and outgoing connections seems a reasonable assumption.

In silico removals conducted in this study provide suggestions about how exploitation of vulnerable species through multiple fisheries could expose the marine community to cascading effects that can lead to modification of structural integrity of the Baja California coastal food web. In general, it seems that the North Pacific Baja California food web shows an intrinsic (i.e., high potential) resilience to species loss. This study highlights the potential of the whole system approach in fisheries management. The local extinction of a central species might cause a restructuring of the energetic backbone of the ecosystem through which energy travels from primary producers to top consumers (Bellingeri and Bodini, 2016). This ultimately may affect the entire fishing sector as fish production is supported by the energetic contribution from lower levels.

By applying a network approach to the coastal food web of Baja California, we have found that many of the species at high risk from multiple fisheries are also the most central in the network. Their reduction or loss may reduce food web robustness, possibly making the community more prone to secondary extinctions. Another consequence that we hypothesize is that patterns of energy transfer may be altered with consequences toward the top of the food chains where, in general, commercially and ecologically important species are found. This study shows the potential of a food web approach for examining possible ecosystem-wide effects of fishing in data-poor contexts, and produces hypotheses to be tested in further research. However, this approach presents some limitations. First, structural food web analyses are based on a static view of network that precludes assessing dynamical aspects. For example, top-down and bottom-up regulative mechanisms are certainly linked to the centrality of species. Most central species are likely to enter the formation of the shortest pathways and are intermediate to many pathways through which top-down (or bottom-up) control is spread; nonetheless, a static food web does not provide any information on how this positional importance affects population dynamics (Scotti and Jordán, 2015). Second, quantitative information about link strength is lacking. This information is essential for relating the positional importance of the species within the energetic budget of the entire community and the pathways for energy delivery that support fisheries (Scotti et al., 2007; Bellingeri and Bodini, 2016). In particular, food webs are sensitive to the lack of information concerning link strength. Considering unweighted and weighted versions of a food web, it has been shown that weighting could affect ranking (i.e., node ordering) of topological indices. Local indices (D_i) are affected by weighting very seriously, instead BC and CL (that consider indirect effects) are less impacted (Scotti et al., 2007). Despite these limitations, a network approach is a promising starting pointfor bridging the gap between EBM theory (i.e., based on the development and improvement of key principles; see Long et al., 2015) and practice (i.e., how can we deal with the complexity associated to whole systems, in particular in the case of data-poor systems?) and strive to manage ecosystems in a more sustainable way.

Supplementary data to this article can be found online at doi:10.1016/j.jmarsys.2016.10.003.

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