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

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1   **Key species and impact of fishery through food web analysis: a case from Baja California Sur, Mexico**

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12

13   **Abstract**

14   Ecosystem Based Management (EBM) aims to support the protection of natural ecosystems and to improve

15   economic activities. It requires considering all of the actors interacting in social-ecological systems (e.g., fish

16   and fishers) in the understanding that their interplay determines the dynamic behavior of the single actors

17   as well as that of the system as a whole. Connections are thus central for EBM and in the ecological domain

18   of the enlarged socio-ecological system interactions between species define such connections. In their

19   trophic form they shape ecosystem food webs. Understanding how connections affect ecosystem and

20   species dynamics is often impaired by a lack of data. We propose food web network analysis as a tool to

21   help to bridge the gap between EBM theory and practice in case of data-poor contexts showing an

22   application to a coastal marine ecosystem in Baja California Sur, Mexico. First, we calculated centrality

23   indices to identify which key (i.e., most central) species must be considered when designing strategies for

24   sustainable resource management. Second, we analyzed the resilience of the system by measuring the

25   changes in food web structure due to the local extinction of vulnerable species (i.e., by mimicking the

26   possible effect of an excessive fishing pressure). The consequences of species removals were quantified in

27   terms of impacts on global structural indices and species' centrality indices. Overall, we found that this

28   ecosystem shows high resilience to species loss. We identified species (e.g., Octopus sp. and the kelp bass,

29   Paralabrax clathratus) whose protection could further decrease the risk of potential negative impacts of

30   fishing activities on the Baja California Sur food web. This work introduces an approach that can be applied

31   to other ecosystems to aid the implementation of EBM in data-poor contexts.

32

33   *Keywords:* Ecosystem-Based Management; Food webs; Network analysis; Overfishing; Centrality indices;

34   Small-Scale Fisheries

Introduction

Marine ecosystems are undergoing huge pressures 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 interested primarily on large scale industrial fisheries, is now focusing also on Small-Scale Fisheries (SSFs) and their dependent human communities (Allison et al. 2001, Jacquet et al. 2008, Chuenpagdee 2011, Kolding et al. 2014). SSFs are pervasive 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 et al. 2007), new management strategies have been called for. These have essentially introduced 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 ground as demonstrated by the ever greater effort devoted to its applications worldwide (Pew 2003, USCOP 2004, Lester et al. 2010, Link 2010). EBM EBM is a cross-sectoral, holistic approach (Link 2002a, Ruckelshaus et al. 2008, Halpern et al. 2008b, Francis et al. 2011, Link et al. 2012) as it 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 its pillars (Long et al. 2015) highlights that connections are central to understand ecosystem behavior and to design effective management strategies. 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 system, 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 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).

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 presently exploited by local SSFs. We produced a qualitative food web that we then used to simulate species deletions mimicking the disappearance of vulnerable species (Micheli et al. 2014) due to excessive fishing pressure. We studied this food web to unveil: (1) which species are the most central in the community; (2) whether these central species are also the most vulnerable ones 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 and when species are instead

70 removed at random. The interest in structural features of food webs is justified on the grounds of the

71 potential relationship that links food web structure and ecosystem functions (Petchey et al. 1999, 2007). In

72 particular, centrality indices can provide information about the transmission of control (top-down vs.

73 bottom-up) and the flow of energy in ecosystems (Jordán et al. 2006, 2009), and overall structural metrics

74 provide indications about the integrity of the food web upon which ecosystem functions depend (Miehls et

75 al. 2009, Bondavalli and Bodini 2014). Results of this investigation are then discussed as for their

76 implications on food web structure, fishing impacts, and management.

77

78

79 **Methods**

80 *Study Area*

81 We performed our investigation on the coastal marine ecosystem that supports local fishing communities,

82 which are organized in fishing cooperatives (McCay et al. 2014), located along the coast of the Vizcaino

83 Desert Biosphere Reserve in the North Pacific region of Baja California Sur, Mexico (Figure 1). The North

84 Pacific region can be defined as temperate to subtropical, with sea surface temperatures ranging from 12°

85 to 27° C throughout the year. This region is characterized by a mosaic of rocky reef and sandy subtidal

86 ecosystems that encompass the southern edge of the range of giant kelp (*Macrocystis pyrifera*) where a

87 zone of persistent upwelling maintains high biological productivity (Martone 2009).

88

89   [Figure 1 goes here]

90

91 The fishing cooperatives of the central Baja California region belong to FEDECOOP (Federacion Regional de

92 Sociedades Cooperativas de la Industria Pesquera de Baja California), which acts as a co-management

93 agency with the national and regional fisheries agencies to monitor resources and develop management

94 plans. The fishing cooperatives of the North Pacific date back to the late 1930s, as a manifestation of the

95 Mexican cooperative movement that was mainstreamed into national fisheries development policies

96 (Ponce-Diaz et al. 2009, McCay et al. 2014). SSFs represent 99% of registered fishing vessels on the Baja

97 California and Baja California Sur peninsula (INEGI 2008[1]). Cooperatives have renewable 20-year

98 concessions for different species, including red spiny lobster (*Panulirus spp.*), abalone (*Haliotis fulgens* and

99 *H. corrugata*), wavy turban snail (*Megastraea undosa*), sea cucumber (*Parastichopus parvimensis*), red sea

100 urchin (*Mesocentrotus franciscanus*), and red algae *Gelidium robustum*. Fishers also catch many species of

101 finfish but, in contrast with benthic invertebrates and algae, do not hold territorial rights for them (i.e.,

102 fishing cooperatives do not have exclusive access to finfish within a geographically defined area; see

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

103   Afflerbach et al. 2014). Within the food web, species are subjected to different fishing pressure, applied

104   through a variety of fishing methods, and risk (Micheli et al. 2014).

105

106   *Food web construction and trophic structure*

107   We constructed an adjacency matrix that reports presence/absence of trophic interactions (i.e., who eats

108   whom) among species or species groups within the food web. Rows represent prey species and columns

109   represent predator species. Each coefficient a_{ij} is 1 if the row species i is a prey of the column species j and

110   0 elsewhere (Dunne et al. 2002a, Abarca-Arenas et al. 2007, Gaichas and Francis 2008, Navia et al. 2010,

111   2012). We constructed an unweighted food web (i.e., all trophic interactions are set to 1) because no

112   information about link strength (i.e., amount of biomass flowing from prey to predators) was available.

113   Community composition and trophic resolution level were based on active collaboration with experts:

114   starting from species considered in Micheli et al. 2014, we expanded the nodes dataset on the base of a

115   coastal marine food web contest. Data on trophic interactions were obtained from the Kelp forest Database

116   (Beas-Luna et al. 2014), literature and general online descriptor such as FishBase (Froese and Pauly 2015),

117   Encyclopedia of Life[2], Discover Life[3] and Animal Diversity Web[4] (see Table S1 in Supplementary Material for

118   a detailed description of diet sources for each nodes). When dietary information was unavailable for some

119   species in the study area, data from similar ecosystems were used to complete the food web, thus it is

120   more literature based due to lack of data (e.g., gut content or stable isotopes analyses) that characterized

121   our study area. Every nodes diet was checked by expert marine biologists working in Baja California (Table

122   S1). The adjacency matrix that summarizes all trophic interactions is included in the Supplementary

123   Materials. The resulting food web of the North Pacific region of Baja California Sur is visualized in Figure 2.

124   The food web is composed of 121 nodes (S = 121) and 979 trophic interactions (l = 979). In the graph, each

125   node stands for a species or a trophospecies (i.e., a group of species with equivalent feeding habits and

126   preyed upon by the same set of predators), while directed edges indicate the presence of trophic

127   interactions. Nodes represent 100 species and 21 trophospecies: three birds, three marine mammals, 75

128   fish, 34 invertebrates, four algae, zooplankton and phytoplankton.

129

130   [Figure 2 goes here]

131

132   We used network analysis to investigate the food web structure of the Baja California Sur marine system.

133   We wanted to identify key (i.e., most central) species through centrality indices and explore the resilience

134   of the system by evaluating the changes in both global structural indices and species' centrality indices due

135   to the local extinction of vulnerable species (as defined by Micheli et al. 2014).

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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].

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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).

[Table 1 goes here]

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 Sheuring 2002, Jordán et al. 2006, 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.

[Table 2 goes here]

In summary, species that show a high value for D_i are hubs (i.e., they locally interact with many other species). When BC_i is high the node i plays an important role in mediating indirect effects. High CL_i values identify nodes that, when disturbed (e.g., decline of their population size), more rapidly spread the impact to other food web nodes. 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.

169 *Removal analysis*

170 Removal analysis was conducted to mimic the effects of possible collapse of certain species due to

171 overfishing (Hamre 1994, Dolgov 2002). Species to be removed were selected using the risk-based

172 approach introduced by Micheli et al. (2014). Micheli et al. extended Productivity Susceptibility Analysis

173 (PSA) to assess the cumulative risk posed by multiple fisheries to the species of the North Pacific marine

174 food web. PSA defines species vulnerability (V) as a function of productivity (P) and aggregated

175 susceptibility (AS): $V = \sqrt{P + AS}$. Productivity is calculated by using information on species life history

176 such as age and size at maturity, fecundity, reproductive strategy, and trophic level (Hobday et al. 2007).

177 Two or more fisheries may affect a single species and it is assumed that their cumulative potential impact

178 may be larger (e.g., additive or multiplicative) than that generated by the single fishery with the greatest

179 impact (Halpern et al. 2008b). Aggregated susceptibility accounts for possible cumulative effects of multiple

180 overlapping fishing activities and is assessed on the basis of several attributes (e.g., the selectivity of fishing

181 gears and post-capture mortality of discarded bycatch; see Micheli et al. 2014). To investigate how fishing

182 can modify the structure of the food web we considered the vulnerability of species that takes into account

183 the cumulative risk due to multiple fisheries (Micheli et al. 2014). According to the values of these

184 vulnerability scores we classified species as at high, medium and low risk (Table S2 in Supplementary

185 Material). The first group (i.e., high risk) included 28 species: three mammals, 24 fish, and one invertebrate;

186 medium risk species comprised 28 species: one bird, 22 fish, and five invertebrates; the latter group (i.e.,

187 low risk) was composed of 16 species: nine fish, six invertebrates and one algae (Table S2). We explored the

188 impacts of different combinations of high/medium/low risk species removal (i.e., by removing

189 combinations of one, two, three or four nodes at the same time) and considered both the effects on single

190 species and on the entire food web structure. The number of all possible combination (*C*) was determined

191 by: $C(n, r) = \frac{n!}{r!\,(n-r)!}$, where *n* is the number of high/medium/low risk species taken *r* at a time (i.e., one,

192 two, three or four). Removal scenarios were targeted first to the 28 high risk species, which were all

193 removed one at a time. Second, all possible pairs of high risk species were removed. Then we removed all

194 possible combinations of three and four high risk species. We repeated the same procedure by considering

195 the medium and low risk species. In summary, for single species removals we had 28 different scenarios for

196 high and medium risk species, and 16 scenarios for low risk species. Two species removals yielded 378

197 combinations for both high and medium risk species, and 120 scenarios for low risk species. For three

198 species removals, both high and medium risk species generated 3,276 different combinations, whereas 560

199 scenarios were obtained with the subset of low risk species. Combinations of four species were 20,475 for

200 high and medium risk species, and 1,820 for low risk species. We did not consider scenarios in which

201 removals targeted mixed combinations of high, medium and low risk species although we recognize that

202 this is not unrealistic.

203   The influence of single species removals on the whole food web was assessed using global structural indices

204   (Table 1) and visualized through frequency histograms of assortativity coefficient (AC), clustering coefficient

205   (CC), modularity (MD), connectance (C), linkage density (LD), diameter (DM), average path length (APL) and

206   number of nodes with betweenness centrality equal to 0 (BC0). The impact of removals on single species

207   was assessed on the basis of changes in their centrality indices. For degree centrality, to quantify the

208   effects of species' removals ($remD_i$) we considered the ratio between the values with (D_i^{rem}) and without

209   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

210   degree centrality, while values < 1 identify those species whose total degree centrality decreased after

211   removals. To assess the changes in betweenness and closeness centralities (indices for which we used the

212   normalized versions that bring all values into the range [0, 1]; see Supplementary Material), the values

213   computed for each removal experiment (BC_i^{rem} and CL_i^{rem}) were subtracted from their counterparts

214   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

215   value means no change, a positive value stands for a decrease and a negative value indicates an increase in

216   the centrality score. The impacts of single species removals on centrality indices of all other species in the

217   food web were visualized by heat maps.

218   To further investigate whether species at risk (according to the definition provided by Micheli et al. 2014)

219   occupy most central structural positions in the food web we compared the consequences of their removal

220   with those produced by random removals (i.e., obtained by taking into account all of the food web species,

221   independently of their V score). We considered single species removals as well as combination of up to four

222   species selected at random. Thus, we had respectively 121, 7,260, 287,980 and 8,495,410 possible removal

223   scenarios to be compared with the ones based on targeted removals (i.e., these latter scenarios follow the

224   V index criteria). The presence of a significant difference between the effect of targeted and random

225   deletions indicates that the species that are most vulnerable to fishing pressure are also important from a

226   structural point of view (i.e., this is for testing whether targeted removals have more consistent negative

227   effects on food web topology compared to random deletions). This would imply that the disappearance of

228   vulnerable species can have consequences on the community structure and possibly function. This analysis

229   evaluates whether the vulnerability ranking proposed by Micheli et al. (2014) also reflects species'

230   structural importance.

231

232   *Statistical analysis*

233   To investigate a possible aggregation bias (i.e., the presence of significant differences in the centrality

234   indices of species vs. trophospecies) in the original food web (i.e., in absence of any removal) we applied

235   the Kolmogorov-Smirnov test (KS-test). To compare index values obtained after targeted removals (i.e.,

236   risk-based) with those obtained from random deletions we performed the Mann-Whitney-Wilcoxon test.

237   All statistical analyses were implemented in R.

238

239 **Results**

240 *Topological analysis: global structural indices, trophic levels and centrality indices*

241 The food web is depicted in Figure 2 The connectance is 0.07 and the network is disassortative (R = -0.34,

242 Sokhn et al. 2013): high degree nodes (i.e., nodes with many connections)are connected to low degree

243 nodes (i.e., nodes with few connections). All centrality indices differ significantly between species and

244 trophospecies ($D_{in,species} > D_{in,trophospecies}$, p < 0.001; $D_{out,species} < D_{out,trophospecies}$, p << 0.001; $D_{species} < D_{trophospecies}$, p

245 < 0.003; $undBC_{species} < undBC_{trophospecies}$, p << 0.001; $BC_{species} < BC_{trophospecies}$, p < 0.024; $CL_{species} < CL_{trophospecies}$, p <

246 0.010, see Table 2 for indices description). This result confirms that the level of aggregation (species vs.

247 trophospecies) bias the analyses: trophospecies might have a significantly high number of trophic

248 interaction and because of this they may take part in a higher number of pathways with consequences on

249 betweenness and closeness values. Thus, we restricted the analysis to species (100 nodes). The values for

250 the indices are given in the Table S2 of Supplementary Material. Twelve species occupy the most central

251 positions in the trophic network, based on degree, betweenness, and closeness centralities (Table 3).

252

253   [Table 3 goes here]

254

255 *Removal analysis*

256 In general, the food webs generated by the removal experiments (i.e., the food webs constructed using

257 different scenarios of either targeted or random species deletion; see Figure 3) did not show significantly

258 different values of global structural indices when compared with the values computed in the original food

259 web (i.e., see the red line in Figure 3). This holds true for the global structuring indices AC, CC, MD, C, BC0,

260 APL and DM values. Link density shows a progressive increase in the difference between the value in the

261 original web and the ones obtained through species removals (Figure 3). We found similar patterns on

262 global structural indices for random and selective removals (i.e., when one to four species are removed)

263 across risk levels (i.e., medium and low risk species deletions; see Figures S1-S5 in Supplementary Material).

264

265   [Figure 3 goes here]

266

267 There is no significant difference between selected removals and random removals in case of CC (Mann-

268 Whitney-Wilcoxon test; Table 4). Significant differences emerged, instead, for AC, MD and APL, under

269 removal scenarios from two to four species removed. Indices MD and APL were significantly higher when

270 the food web was exposed to targeted removals (Table 4). Different values for C and LD occurred when

271 three and four species were removed (Table 4). Different values for BC0 emerged only when four species

272 were removed (Table 4).

273

274   [Table 4 goes here]

275

276   One example of the impact of removals on single species by computing centrality indices is given in Figure 4

277   (all the other cases are reported in the Supplementary Material). *Octopus sp.* seems to be the species that,

278   if removed (either individually or in combination with other species), determines the greatest impact

279   (based on centrality index D; see also Figures S6-S8 in Supplementary Material). The most impacted species

280   are all fish species: *Alopias pelagicus*, *Cynoscion parvipinnis* and *Kathetostoma averruncus*. Two

281   invertebrate species are also affected when some combinations of two to four species are removed: the

282   scallop *Hinnites multirugosus* and the sea cucumber *Parastichopus parvimensis*. Considering index BC,

283   *Paralabrax clathratus*, *Octopus sp.*, *Paralichthys californicus* and *Sphyraena argentea* (three fish and one

284   invertebrate) are the most impacted species in all the removal scenarios (i.e., their value decreases; Figures

285   S6-S8 in Supplementary Material). When *Octopus sp.* is the target of removal, both as single species and in

286   combination with others, more than 50% of the remaining species shows a decrease in closeness (Figures 4

287   and S6-S8 in Supplementary Material. The removal of *Paralichthys californicus* and *Stereolepis gigas* also

288   induces a decrease in this index. Phytoplankton, zooplankton, the kelp *Eisenia arborea* and other algae

289   increase their closeness for all combinations of species except for the deletion of *Octopus sp.* (i.e., both as

290   single species or in combination with others), for which their values decrease.

291

292   [Figure 4 goes here]

293

294

295   **Discussion**

296   We identified 12 species as the most central (i.e., topologically important) in the food web of Baja California

297   (Table 3). Five of these 12 species are the most central for at least three indices and could be thought of as

298   key players in the community. They are: the kelp bass *Paralabrax clathratus*, the California halibut

299   *Paralichthys californicus*, *Octopus sp.*, the California sheephead *Semicossyphus pulcher* and the spiny

300   lobster *Panulirus interruptus*. All of them are evaluated as at risk for the cumulative effects of multiple

301   fisheries according to Micheli's vulnerability index (Micheli et al. 2014). Of these five species, three are high

302   risk species, one medium, and one low (see Table 3 and Figure 2).

303   Our results show that removing up to four target species (i.e., at risk; see Micheli et al. 2014), does not alter

304   the structural attributes of the food web. Thusthe network results as structurally resilient: its structure

305   tends to maintain its integrity in the face of several simulated extinction events. The only structural index

306   that shows a significant difference between the value of the original web and that obtained after removals

307   is link density. This indicates that as the number of removed species increases the average number of

308 feeding links per species decreases. This effect may have consequences on ecological function and food

309 web resilience to additional species loss because it reduces the diet breadth of species and the number of

310 pathways through which materials and energy move through the web, and the functional redundancy of

311 the assemblage (e.g. Micheli and Halpern 2005). The sensitivity of link density to changes in food web

312 structure has been already reported in the literature, with a previous study showing how link density is

313 more sensitive to data aggregation than connectance (Dunne et al. 2006). Thus, the result of a significant

314 change of link density with species removals is not surprising. In contrast, all other indices were unaffected

315 by removals.

316 Comparing selected (i.e., targeted to high risk species) to random removals we found that the community

317 structure is differently affected depending on the indices considered and the number of species removed

318 (Table 4). The significant differences between target (i.e., risk based) and random removals are even more

319 important because the analysis was conducted in a conservative context (i.e., even risk species are used for

320 random removal scenarios). Modularity (MD) was significantly higher when removals targeted to high risk

321 species were compared to random extinctions. Thus, removing species at high risk can create a more

322 fragmented food web. This is due to the central position that some of the high risk species occupy in the

323 network of trophic interactions. Their loss seems not be immediately critical for the community but it may

324 render the whole network more fragile and thus possibly more vulnerable to further extinction events.

325 Connectance (C) increases significantly when high risk species are removed. According to Bondavalli and

326 Bodini (2014), as this parameter augments the number of redundant links becomes higher in comparison

327 with that of functional links. Allesina et al. (2009) showed that functional connections affect food web

328 robustness, whereas redundant links are neutral in its respect. Targeted removals thus, by significantly

329 increasing connectance (and the fraction of redundant links) in comparison with random removals, would

330 make the food web less robust than its original counterpart as the number of independent pathways (i.e.,

331 those composed by functional connections and that are fundamental for energy delivery) likely decreases

332 (but see Dunne et al. 2002). In summary, the presence of some significant difference (e.g., MD, C in Table 4)

333 between the effect of targeted and random deletions it is a confirmation that species undergoing strong

334 fishing pressure are also important from a structural point of view.

335 The analysis of species centrality expands in a functional perspective the concept of structural

336 connectedness (Jordán et al. 2006, Jordán 2009). *Octopus sp*. ranked highest for all the centrality indices.

337 Closeness centrality indicates how close a species is to the others; according to this, it can be inferred that

338 *Octopus sp*. plays an important role in the spread of both direct and indirect effects being responsible for

339 their diffusion in the ecosystem via shortest paths. Since it has been ascertained that in food webs the bulk

340 of energy travels along pathways that tend to be short (Bellingeri and Bodini 2015), *Octopus sp*. may enter

341 several main routes for energy delivery from primary producers to top species. This hypothesis needs to be

342 tested with empirical measurements and experiments, as the ecological role of *Octopus sp*. in these food

343 webs is unknown. Empirical and theoretical studies quantifying the main pathways for energy delivery and

344 the strength of these links would elucidate the role *Octopus sp.* and other species with high values of

345 closeness centrality play in energy delivery, and whether these species may act as bottlenecks for energy

346 distribution to otherspecies in the food web (Allesina and Bodini 2004). The high value of closeness for this

347 species, being calculated as undirected index, suggests that *Octopus sp.* might be involved in spreading of

348 top-down control, e.g., it may be part of trophic cascade leading from its predators to its prey. Control by

349 higher level consumers upon lower levels can be possible through several paths in a food web. However,

350 fastest spreading is assured by the shortest paths that can become the dominant routes through which

351 control is exerted by top consumers. The highest value of closeness, combined with the highest value of

352 betweenness centrality, suggests that *Octopus sp.* might enter in several of these dominant routes through

353 which cascading trophic interactions may manifest (Hodgson 2005). Network position in itself, however,

354 does not guarantee a prominent role in top-down regulations. This hypothesis, as highlighted above,

355 remains to be tested.

356 Considering the simulated impact of fishing, *Octopus sp.* is the species that, if removed, determines the

357 greatest change on other species' centrality. We found that more than 50% of the remaining species after

358 the removal of *Octopus sp.* showed a decrease in their closeness centrality values. This result suggests that

359 decline or loss of*Octopus sp.* might cause a substantial reorganization of the energy flow in the food web.

360 This is because the reduced closeness for a high proportion of species imposes that pathways for energy

361 delivery would elongate, with loss of efficiency. However, this hypothesis arises from a static view of the

362 food web. In real, dynamic food webs, species would actively respond to species loss through mechanisms

363 such as diet switching (Barnum et al. 2015). Nevertheless, a reorganization of the energy flow within the

364 ecosystem might still occur, with potential impacts on the amount of energy that reaches the top species

365 and, possibly the fisheries. Gaichas et al. (2008) have proposed that protecting highly connected species in

366 the network (also called hub species) is crucial to prevent potential structural impacts of fishing activities

367 on the whole ecosystem. The central role that *Octopus sp.* might play, as it is suggested by the centrality

368 indices, supports the correctness of the present regulative framework, which limits the catch to this species

369 to fishing cooperatives that hold exclusive fishing permits. This regulative framework (i.e., exclusive access

370 to cooperatives) applies also to *Panulirus interruptus,* another species that plays a relevant role in the

371 economy of fishery cooperatives and that is also central in the food web, based on this analysis (Figure 2).

372 These conclusions that emphasize the role of Octopus must be taken with circumspection, however, and

373 further scrutiny on the role this species plays in Baja California is needed. Results obtained in this study

374 strongly depend on the assumptions we made about the position that Octopus occupies within the food

375 web and that is defined since the adjacency matrix is compiled. Nevertheless it has been pointed out

376 (Doubleday et al. 2016) that these predators are voracious and adaptable and they impact many prey

377 species, including commercially valuable fish and invertebrates. Also several marine predators rely on this

378   species for food. This confirms that the positional importance of Octopus as a hub with many incoming and

379   outgoing connections seem a reasonable assumption.

380   *In silico* removals conducted in this study provide suggestions about how exploitation of vulnerable species

381   through multiple fisheries could expose the marine community to cascading effects that can lead to

382   modification of structural integrityof the Baja California coastal food web. In general, it seems that the

383   North Pacific Baja California food web shows an intrinsic (i.e., high potential) resilience to species loss. This

384   study highlights the potential of the whole system approach in fishery related questions. For example, the

385   potential ecological importance of individual species emerges not only in a single fishery perspective, but

386   also from the view point of the whole community structure: a species collapse may have community-wide

387   effects beyond the immediate consequences for its fishery. A central species local extinction might impose

388   a restructuring of the energetic backbone of the ecosystem (Bellingeri and Bodini 2016) through which

389   energy travels from primary producers to top consumers. This ultimately may affect the entire fishing

390   sector as fish production is supported by the energetic contribution from lower levels.

391   This study shows the potential of a food-web approach for examining possible ecosystem-wide effects of

392   fishing in data-poor contexts, and produces hypotheses to be tested in further research. However, this

393   approach presents some limitations. First, , structural food web analyses are based on a static view of

394   network that precludes grasping dynamical aspects. For example, the top-down regulative mechanisms are

395   certainly linked to the centrality of the species. Most central species are likely to enter the formation of the

396   shortest pathways and are intermediate to many pathways through which control is spread; nonetheless, a

397   static food web does not inform about how this positional importance affects population dynamics.

398   Second, quantitative information about link strength is lacking: this information would be essential to relate

399   the positional importance of the species within the energetic budget of the entire community and the

400   pathways for energy delivery that support fisheries (Scotti et al. 2007, Bellingeri and Bodini 2016). In

401   particular food web are sensitive to lack of link-strength: considering unweighted and weighted version it is

402   proven that weighting could affects ranking (i.e., the node ordering) of topological indices: local indices (D_i)

403   are affected by weighting very seriously, instead BC and CL (that consider indirect effects) are less disturbed

404   (Scotti et al. 2007). Despite these limitations, the network approach can be a starting promising way to

405   bridge the gap between EBM theory (i.e., based on the development and improvement of key principles;

406   see Long et al. 2015) and practice (i.e., how can we deal with the complexity associated to whole systems,

407   in particular in the case of data-poor systems?) and strive to manage in a more conscious way most

408   ecosystems as possible. By this study, in particular, we have shown that many of the species at high risk

409   from multiple fisheries are also the most central in the network. Their reduction or loss may reduce food

410   web robustness, possibly making the community more prone to secondary extinctions. Another

411   consequence that we hypothesize is that patterns of energy transfer may be altered with consequences

412   toward the top of the food chains where, in general, commercially and ecologically important species are

413   found.

414

415

416   **Acknowledgments**

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Tables

Indices	Explanation	Interpretation
Assortativity coefficient (AC)	It is a 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)	It is 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)	It is a 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 graph 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 subgraph; instead, if there is a decrease this indicates that less species compete (Sokhn et al. 2013).
Connectance (C)	It is 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)	It is 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)	It is 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)	It is 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 1 – Global structural indices. A brief description for each index is provided (Explanation) together

with the meaning as a function of their values (Interpretation).

Indices	Explanation	Interpretation
Degree centralities **($D_{in,i}$, $D_{out,i}$, D_i)**	The degree of node i (D_i) is obtained summing together the total number of all of its prey (in-degree, $D_{in,i}$) and of its predators (out-degree, $D_{out,i}$).	They measure the local importance of species. Species that show a high value for D_i are hubs (i.e., they locally interact with many other species).
Betweenness centrality **(BC_i)**	It 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 **($undBC_i$)**	It 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 accounts for the spread of both bottom-up and top-down effects (i.e., without being constrained by the direction of biomass flow).	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 top-down and bottom-up perspective.
Undirected closeness centrality **(CL_i)**	It measures the length of the shortest paths from a given species i to all other species that can be reached 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).

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606 **Table 2 –** Centrality indices. A brief description for each index is provided (Explanation) together with the

607 meaning as a function of their values (Interpretation).

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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)		

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627 **Table 3 –** The 12 most central species in the Baja California coastal food web. For each index, we consider

628 the species that occupy the top five positions. For each species and index, we show centrality values and

629 ranking position (1st to 5th).

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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

631

632 **Table 4 –** Mann-Whitney-Wilcoxon test for the comparison of global structural indices computed after

633 either targeted (i.e., high risk) or random removals. The scenarios comprise single removals and multiple

634 removals of all possible combinations up to four species (see the different rows of the table). ASH key labels

635 targeted removals of species at risk; R key identifies random extinctions. Numbers indicate the p-values of

636 the Mann-Whitney-Wilcoxon test. ASH > R indicates that the index is significantly higher for targeted

637 removals than for random removals, while ASH < R stands for significantly lower values in case of targeted

638 removals if compared to random deletions.

639

640   **Figure captions**

641

642   **Figure 1 –** Map of the study area located along the coast of the Vizcaino Desert Biosphere Reserve in the

643   North Pacific region of Baja California Sur, Mexico (reproduced from Micheli et al. 2014, with permission).

644

645   **Figure 2 –** Food web diagram representing trophic interactions in the area located along the coast of the

646   Vizcaino Desert Biosphere Reserve in the North Pacific region of Baja California Sur, Mexico. Each node

647   represents either a species or a trophospecies. The edges connecting the nodes stand for trophic

648   interactions (each arrowhead edge leaves the prey and enters the predator). Species' vertical position

649   reflects the trophic level. The color of the nodes indicates different levels of vulnerability (V), the border

650   line specifies taxonomic groups and the shape displays fishing permits. The food web diagram was

651   visualized with Cytoscape (Shannon et al. 2003).

652

653   **Figure 3 –** Frequency histograms for global structural indices following removals of four species (20,475

654   combinations): high risk species removal (A) and random removals (B). In each chart the red line shows the

655   value of the index for the food web with no removals.

656

657   **Figure 4 –** Changes in closeness centrality due to the targeted removal of species at high risk. On the x axis

658   there are the combination of species removed, they are indicated by white boxes. Species for which

659   consequences are visualized are listed on the right side of the heat map. The order is changing on the basis

660   of clustering method (i.e., complete linkage method with Euclidean distance measure that finds similar

661   clusters). In the upper left corner the color scale used for visualization and the corresponding numerical

662   range for the index. According to this scale, green boxes indicate lowest closeness values after removals.