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Impacts of species depletion on the food web structure of a marine ecosystem based on topological network analysis

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Abstract

Single-species management ignores the interactions between species, and ecosystem-based fisheries management (EBFM) has become a main method to fisheries management. Understanding food web structures and species interactions is essential for the implementation of EBFM and maintenance of ecosystem functions. Overfishing is one of the main reasons behind the depletion, which could even lead to the depletion of some target species in local areas. So understanding the impacts of species depletion on food web structures is important for the implementation of EBFM. The impacts of species depletion can be transmitted through the food web and cause the local extinction of both target and non-target species. In this study, topological network analysis was applied to examine the impacts of species depletion on the food web structure of Haizhou Bay. Results showed that fine crayfish *Leptochela gracilis*, squid *Loligo* sp., and Japanese snapping shrimp *Alpheus japonicus* have the highest numbers of outgoing links (48, 32 and 31 respectively); thus, these species may be considered key prey species. Whitespotted conger *Conger myriaster*, fat greenling *Hexagrammos otakii*, and bluefin gurnard *Chelidonichthys kumu* were key predators with the highest number of incoming links (37, 36 and 35 respectively). The competition graphs derived from the Haizhou Bay food web were highly connected (more than 40% predators sharing over 10 common prey species), and showed close trophic interaction between high trophic level fishes. Simulation analysis showed that the food web structure has small changes to the depletion of species in a highly complex food web. The most-connected target species did not necessarily indicate high structural importance; however, some species with low connectivity may demonstrate stronger trophic interactions and play important ecological roles in the food web. But most species were more sensitive to the depletion of the most-connected target species than other target species (for instance, for zooplankton, closeness centrality 13.876 in D6, but closeness centrality 82.143 in original food web). Therefore, EBFM should focus on the most-connected target species, but also on those species with few but strong links and feeding relationships in the food web.

Key words: Haizhou Bay, most-connected target species, food web structure, depletion, fishery management, feeding strategy

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1 Introduction

Overfishing is one of the main reasons behind the depletion of some target species (which was defined by economic value) in marine ecosystems (Myers and Worm, 2005; Hernvann and Gascuel, 2020) and could trigger indirect effects on non-target species and fish communities. While fishing activities were generally sustainable during the 1950s, overfishing has caused the depletion of some target species in local areas (Coll et al., 2008). The effects of species depletion can be transmitted to other species through the connections of species in the food web (Duffy and Stachowicz, 2006; Ferretti et al., 2010). Insights from network ecology can advance our knowledge about direct and indirect threats to food web structure posed by species losses. As higher trophic level species are depleted, forage fish show stronger ecosystem effects (Plagányi and Essington, 2014) resulting from the localized extinction of predators in food webs. Increasing depletion of species could also exacerbate the loss of species diversity, accelerate ecosystem instability (Borrvall et al., 2000; McCann, 2000; Houk et al., 2018), and change the food web structure (Shantz et al., 2020). Thus, understanding the impacts of species depletion on the food web structure is necessary for fishery management.

Traditional fisheries management has focused only on individual species and provided advice for sustainable fishing prac-

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tices based on predictive models of single-species dynamics (Trochta et al., 2018). However, this type of management ignores the interactions between species, and neglects the structure and complexity. Ecosystem-based fisheries management (EBFM) has recently become a more useful path to fisheries management, and analysis of the complex dynamics between target and non-target species is an important part of EBFM (Griffith and Fulton, 2014; Hart and Fay, 2020). Understanding of the food web structure and its responses to species extinction in local areas, as the basis for EBFM is essential for explaining the dynamics of the ecosystem. Food web analysis is one of the most direct and effective methods to examine the structure of marine ecosystems (Link, 2002; Brose and Dunne, 2009; Olivier and Planque, 2017).

Many indices and topology model have been proposed to assess the structure and stability of various ecosystems. Marina et al. (2018) described 11 topological network indices to quantify the complexity and structure of food web in the Potter Cove, and they found that the Potter Cove food web may be vulnerable if the most-connected species became locally extinct. A topology model was previously constructed to evaluate how the trophic network could respond to anthropogenic pressures such as the removal of species (Navia et al., 2016). Topology modeling is a useful method with which to analyse the food web structure and trophic interactions. Many topological network indices have been applied to describe the structure of food webs quantitatively (Navia et al., 2016; Olivier and Planque, 2017; Blanchet et al., 2019); these methods can help reveal the food web complexity, connectivity, and degree of species aggregation. Topological graphs can also provide information about the strength of direct and indirect interactions between predators and prey species according to food intake. This network approach could be used to provide a comprehensive understanding of variations in the synthetic properties of the food web structure.

In the present study, the impacts of species depletion on the food web structure and other species in Haizhou Bay were analyzed by topological network analysis. Competition graphs were drawn to reflect the connectivity complexity between these species in the food web, and topological network indices were used to describe the changes of complexity and structure of food webs. The local depletion of most-connected target species was simulated to evaluate the responses of the food web structure and other species to the local extinction compared with the randomly selected target species. This study contributes to a deeper understanding of food web structures and species interactions and will provide essential information for the implementation of EBFM.

2 Materials and methods

2.1 *Study area*

Haizhou Bay is a typical open bay ecosystem in the southern Yellow Sea. This bay has suffered from intensive fishing pressure over the last several decades (Tang et al., 2011). Fishery resources in Haizhou Bay have remarkably changed under the impacts of high fishing pressure, resulting in great variations in the fish community and species diversity (Wu et al., 2019; Li et al., 2021). For instance, Japanese seerfish *Scomberomorus niphonius* was the main target species in the bay in the 1980s, but its abundance has decreased sharply under the effects of increased fishing pressure (Wan et al., 2020). Today, anchovy *Engraulis japonicus* and bluefin gurnard *Chelidonichthys kumu* are the dominant species in Haizhou Bay (Wu et al., 2019). If effective management is not implemented, some species will become extinct locally in the Haizhou Bay. The local depletion of species within the food web may cause instability of the overall food web and trigger indirect effects on other species, especially for the most-connected target species (Quince et al., 2005).

2.2 *Sampling*

The data were collected from five seasonal bottom trawl surveys in Haizhou Bay over the period of March–December 2011. The survey employed a stratified random sampling design with five strata based on the oceanographic, regional, and biological characteristics of the survey area (Fig. 1; Xu et al., 2015a). A total of 24 sampling stations were randomly selected in each survey. The duration of each trawl was approximately 1 h, and the towing speed was 2.5 kn. Details of the survey design, gears, and sampling procedure are available in Xu et al. (2015b).

2.3 *Stomach content analysis*

In this study, a total of 5 052 stomach content samples of 36 main species were analyzed. The biomass of fish analyzed in this study accounted for 99% of the total biomass of all fish species in Haizhou Bay. The feeding habits of other species are from the literature and FishBase database (Froese and Pauly, 2018). Prey species in the stomachs of the sampled species were identified to the lowest classification possible under a double-tube dissection microscope according to their morphological characteristics. The

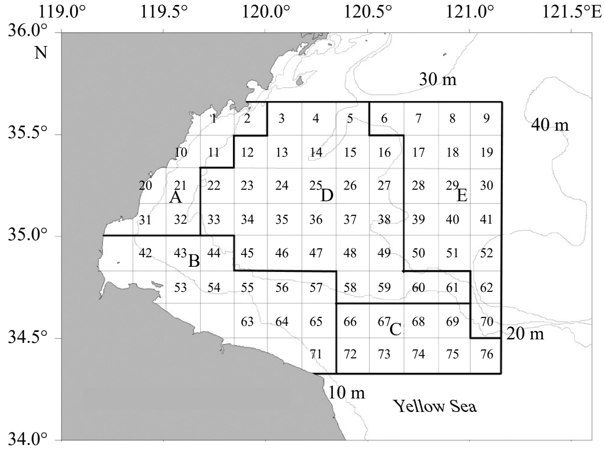

Fig. 1. Sampling areas in Haizhou Bay (A–E: five strata) (Xu et al., 2015a).

prey species were weighed on a precision analytical balance (accuracy, 0.000 1 g) after the moisture on its surface was blotted off (Wang et al., 2018). The proportion of each prey species' weight to the total weight of all prey species in stomachs of predator species was used to represent the feeding ratio between species.

2.4 *Interaction matrix and competition graphs*

A total of 93 species and groups in the Haizhou Bay food web were analyzed. An interaction matrix of pairwise interactions was constructed, with the proportion of food intake being assigned to each element of the matrix. The food web graph was drawn on the basis of the feeding relationships between these species and their links from the binary matrix using Pajek64 5.07 software (http://mrvar.fdv.uni-lj.si/pajek/).

The proportions of incoming and outgoing links of species were also calculated to analyze the interactions between species (Pérez-Matus et al., 2017). Because many species share one or more prey species in a food web, competition graphs were constructed according to the number of common prey species (Pérez-Matus et al., 2017). These graphs can reflect the food competition between predator species and the importance of predator species in the food web on the basis of the similarity of feeding relationships (Marina et al., 2018). A matrix of pairwise interactions was constructed and each element of the matrix depends on the number of common prey species. The graphs were drawn using the Pajek64 5.07 software.

2.5 *Topological network analysis*

Topological network properties were used to describe the complexity and structure of original and simulated food webs. Clustering coefficient (CC), which measures the inter-connection of certain species (Navia et al., 2016), was determined as the average of individual clustering coefficients CC_i of all nodes in the network. The formula for CC_i index is as follows:

$$CC_i = \frac{2E_i}{k_i(k_i-1)}, \tag{1}$$

where CC_i for a given node i is the ratio between the effective number of interactions existing between its k_i nearest-neighbor nodes (E_i) and the maximum possible number of such interactions (Navia et al., 2016). This index describes the average fraction of pairs of species connected to the same species that are also connected to each other.

Betweenness centrality (BC, Móréh et al., 2018) measures how frequently a node appears in the shortest path between each pair of nodes in the food web. This index for a given node i was calculated as follows:

$$BC_i = \frac{2\sum_{j\leqslant k} g_{jk}(i)/g_{jk}}{(N-1)(N-2)}, \tag{2}$$

where N is the number of species, g_{jk} is the number of shorter and equal steps between nodes j and k, and $g_{jk}(i)$ is the number of these steps in which node i is present.

Average shortest path length (PL, Albert and Barabási, 2002) measures the closeness between each pair of species and predicts whether negative effects spread rapidly and widely throughout food webs. The indices of connectance (L/S^2) and number of interactions per species (L/S) reflect the complexity of food webs (Jacob et al., 2011); here, larger values are indicative of greater complexity, L refers to the number of links and S refers to the number of nodes. We also examined the shift in species by using the closeness centrality (CLC) index:

$$CLC = \frac{N-1}{\sum\limits_{j=1}^{N} d_{ij}}, \tag{3}$$

where d_{ij} is the length of the shortest step between nodes i and j in the food web, which is used to quantify the minimal paths from a certain species to all other species (Wasserman and Faust, 1994).

The top 25% of target species (i.e., squid *Loligo* sp., mantis shrimp *Oratosquilla oratoria*, small yellow croaker *Larimichthys polyactis*, Whitespotted conger *Conger myriaster*, fat greenling *Hexagrammos otakii*, and bluefin gurnard *Chelidonichthys kumu*) were selected according to the node degree (links), and they were used in simulation analyses to assess the impacts on food web structure and other species. The removal of the six most-connected target species was then simulated to assess the impacts of species depletion on the structure of the food web and other species (Table 1). We proposed that variations in the food web structure and other species are sensitive to the fluctuations of the most-connected species.

2.6 *Simulations*

For comparison, the simulated depletion of six randomly selected species was also conducted. A total of 100 randomly selected combinations were simulated at each scenario, and the food web indices at each combination were calculated. Finally, we calculated the average values for each index.

3 Results

A total of 93 species and 1 021 links representing feeding relationship between these species were analyzed (Table 2). The total biomass of species analyzed in this study accounted for over 90% of all catches in the survey of Haizhou Bay, including 23 target species.

Table 1. Food web scenarios with simulated depletion of one to six target species

Food web scenarios	Simulated depletion of species
D1	squid (*Loligo* sp.)
D2	squid (*Loligo* sp.), mantis shrimp (*Oratosquilla oratoria*)
D3	squid (*Loligo* sp.), mantis shrimp (*Oratosquilla oratoria*), small yellow croaker (*Larimichthys polyactis*)
D4	squid (*Loligo* sp.), mantis shrimp (*Oratosquilla oratoria*), small yellow croaker (*Larimichthys polyactis*), whitespotted conger (*Conger myriaster*)
D5	squid (*Loligo* sp.), mantis shrimp (*Oratosquilla oratoria*), small yellow croaker (*Larimichthys polyactis*), whitespotted conger (*Conger myriaster*), fat greenling (*Hexagrammos otakii*)
D6	squid (*Loligo* sp.), mantis shrimp (*Oratosquilla oratoria*), small yellow croaker (*Larimichthys polyactis*), whitespotted conger (*Conger myriaster*), fat greenling (*Hexagrammos otakii*), bluefin gurnard (*Chelidonichthys kumu*)

Table 2. Species analyzed in the Haizhou Bay food web

Node	Common name	Species
1	hippolytid shrimp	*Eualus sinensis*
2	silver croaker	*Pennahia argentata*
3	dotted gizzard shad	*Konosirus punctatus* (T)
4	butterfish	*Pampus* sp.
5	kammal thryssa	*Thryssa kammalensis*
6	fat greenling	*Hexagrammos otakii* (T)
7	clearhead icefish	*Protosalanx hyalocranius*
8	zebra sole	*Zebrias zebra*
9	largehead hairtail	*Trichiurus lepturus* (T)
10	kishi velvet shrimp	*Metapenaeopsis dalei*
11	Japanese grenadier anchovy	*Coilia nasus*
12	benthos	–
13	Japanese seabream	*Pagrus major*
14	perch	*Pseudoblennius cottoides*
15	bentooth	*Champsodon snyderi*
16	shortarm octopus	*Octopus ochellatus* (T)
17	pholidae	*Pholis fangi*
18	osbeck’s grenadier anchovy	*Coilia mystus*
19	zooplankton	–
20	phytoplankton	–
21	gastropods	–
22	pointhead flounder	*Cleisthenes herzensteini* (T)
23	greater pipefish	*Syngnathus acus*
24	algae	–
25	jellyfish	*Rhopilema esculenta*
26	jellyfish shrimp	*Latreutes anoplonyx*
27	false kelpfish	*Sebastiscus marmoratus*
28	bastard halibut	*Paralichthys olivaceus*
29	polychaetes	–
30	yellow goosefish	*Lophius litulon* (T)
31	yellow drum	*Nibea albiflora* (T)
32	scaly hairfin anchovy	*Setipinna taty* (T)
33	echinodermata	–
34	Japanese sand shimp	*Crangon affinis*
35	small crustacean	–
36	commerson’s anchovy	*Stolephorus commersonnii*
37	ridged-eye flounder	*Pleuronichthys cornutus*
38	golden cuttlefish	*Sepia esculenta* (T)
39	matsubara	*Sebastes hubbsi*
40	swarthy skate	*Okamejei kenojei*
41	mantis shrimp	*Oratosquilla oratoria* (T)
42	Japanese scad	*Decapterus maruadsi*
43	pinkgray goby	*Amblychaeturichthys hexanema*
44	water Shrimp	*Acetes* sp.
45	branded goby	*Chaeturichthys stigmatias*
46	big head croaker	*Collichthys lucidus*
47	spotted velvetfish	*Erisphex pottii*
48	brown croaker	*Miichthys miiuy*
49	nemertean	–
50	belanger’s croaker	*Johnius belangerii*
51	barcheek goby	*Rhinogobius giurinus*
52	toy shrimp	*Heptacarpus futilirostris*
53	other gobies	–
54	other shrimps	–
55	squid	*Loligo* sp. (T)
56	Japanese sardinella	*Sardinella zunasi*
57	Japanese snapping shrimp	*Alpheus japonicus*
58	Pacific chub mackerel	*Scomber japonicus*
59	Japanese stone crab	*Charybdis japonica*
60	tonguefish	*Soleidae* sp. (T)
61	tanaka’s snailfish	*Liparis tanakae*
62	two-spot swimming crab	*Charybdis bimaculata*
63	lantern cuttlefish	*Sepiola birostrata*
64	bivalves	–
65	mimika bobtail	*Euprymna morsei*
66	azuma emmnion	*Chirolophis japonicus*
67	Japanese common squid	*Todarodes pacificus* (T)
68	Japanese anchovy	*Engraulis japonicus* (T)
69	black scraper	*Thamnaconus septentrionalis* (T)
70	chameleon goby	*Tridentiger trigonocephalus*
71	silver sillago	*Sillago sihama*
72	fine crayfish	*Leptochela gracilis*
73	cardinal fish	*Jaydia lineata*
74	shrimp in drum	*Alpheus disinguendus*
75	leiocarpus	*Callionymus* sp.
76	smallhead hairtail	*Eupleurogrammus muticus*
77	small yellow croaker	*Larimichthys polyactis* (T)
78	bluefin gurnard	*Chelidonichthys kumu* (T)
79	other crabs	–
80	white-spotted conger	*Conger myriaster* (T)
81	korean rockfish	*Sebastes schlegelii* (T)
82	white-hair rough shimp	*Trachysalambria curvirostris* (T)
83	bartail flathead	*Platycephalus indicus*
84	red barracuda	*Sphyraena pinguis*
85	wart-back broad-fronted shrimp	*Latreutes planirostris*
86	Pacific sandlance	*Ammodytes personatus* (T)
87	Chinese ditch prawn	*Palaemon gravieri*
88	eelpout	*Zoarcidae*
89	whiparm octopus	*Octopus variabilis* (T)
90	slender lizardfish	*Saurida elongata* (T)
91	filamentous shrimpgoby	*Myersina filifer*
92	moustached thryssa	*Thryssa mystax*
93	shokihaze goby	*Tridentiger barbatus*

Note: T means target species. T represents the target species, primarily focusing on economically species. – represents no data.

3.1 *Topological network analysis*

The node sizes of white-spotted conger *Conger myriaster* (80) and fat greenling *Hexagrammos otakii* (6) in the topological network of the Haizhou Bay food web were larger than those of the other species (Fig. 2), and their numbers of incoming links were 37 and 36, respectively. For the prey species, the node sizes of zooplankton (19) and small crustaceans (35) were larger than those of other species, and their numbers of outgoing links were 72 and 68, respectively (Fig. 2).

3.2 *Interdependence between species*

Among the species included in the Haizhou Bay food web, whitespotted conger *Conger myriaster* revealed the highest number of incoming links (37 links; Fig. 3), followed by fat greenling *Hexagrammos otakii* (36 links) and bluefin gurnard *Chelidonichthys kumu* (35 links). These species are all important predators in the Haizhou Bay ecosystem. Besides these species, small yellow croaker *Larimichthys polyactis* and largehead hairtail *Trichiurus lepturus* also revealed over 30 incoming links. Fine

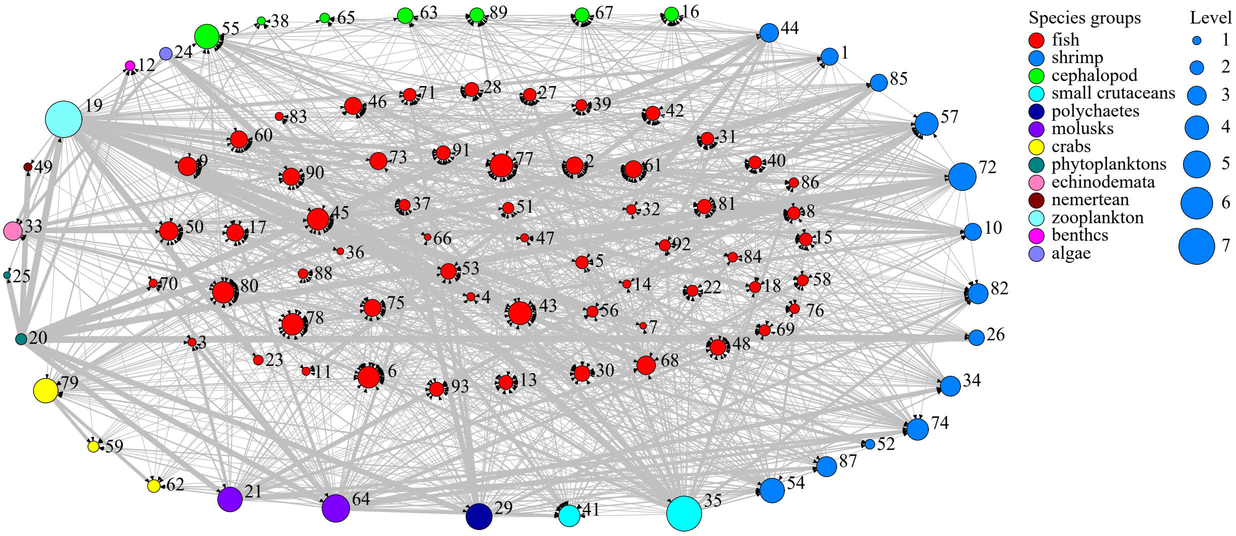

Fig. 2. Topological network structure of the Haizhou Bay food web. Node size indicates the number of links (level, 1–7), and line widths indicate the proportion of food intake. Table 2 details the number of species in the web.

crayfish *Leptochela gracilis* revealed the highest number of outgoing links (48) and, thus, appears to be an important prey species in this food web (Fig. 3). For prey groups, zooplankton and small crustaceans showed more outgoing links than other species (Fig. 3).

3.3 *Competition between species*

The competition graphs showed a high degree of connectivity in the Haizhou Bay food web (Fig. 4). A total of 40 predators sharing over 10 common prey species (Fig. 4a), as well as 25 predators sharing over 15 prey species were noted (Fig. 4b). Among these predators, fat greenling *Hexagrammos otakii*, bluefin gurnard *Chelidonichthys kumu*, small yellow croaker *Larimichthys polyactis*, and whitespotted conger *Conger myriaster* revealed intensive food competition (Fig. 4b).

3.4 *Impacts of species depletion on the food web*

The structural properties of the original and simulated food webs in the Haizhou Bay are shown in Table 3. The values of three topological network indices (i.e., *BC*, L/S^2 , and L/S) were lower in the food webs featuring the simulated depletion of the six most-connected target species (i.e., D1, D3, and D6) than in the original food web; by contrast, most values of these topological network indices were higher in food webs featuring the simulated depletion of six randomly selected species (i.e., R1, R3, and R6) than in the original food web. The values of *CC* (D1, D3 and D6) were lower than that in the original food web, while the values of *PL* increased with the removal of the most-connected target species (Table 3), however, the depletion of most-connected target species did not cause great changes of the five indices.

Table 3 structural properties of the complete food web and food webs with simulated depletion of the six most-connected target species and six randomly selected species in the Haizhou Bay food web.

The simulated depletion of target species could cause variations in the ranks of importance for species in the food web according to three topological network indices (*CC*, *BC*, and *CLC*; Fig. 5). Variations in *CC* suggest that whiparm octopus *Octopus variabilis* and shortarm octopus *Octopus ochellatus* showed larger variations than other species after the simulated depletion of the most-connected target species (Fig. 5a). Small yellow croaker *Larimichthys polyactis* had the highest values of *BC* in the complete food web. According to *BC*, branded goby *Chaeturichthys stigmatias* became the most important species in scenarios D3 and D6 (Fig. 5b). However, in scenarios R1, R3, and R6, all species showed little variations according to the three indices. The *CLC* for all species showed obvious variations, and all species declined greatly when the first most-connected target species was deleted, which means they had less minimal paths from themselves to all other species. Slight variations were observed when randomly selected target species were removed (Fig. 5c). In scenario D6, the *CLC* value for zooplankton was only 13.876, which is much lower than that (82.143) obtained in the original food web (Fig. 5c). The *CLC* values for small crustaceans also decreased remarkably from scenarios D1 to D6 (Fig. 5c).

4 Discussion

4.1 *Connectivity and complexity*

Many studies have focused on the simplification of food webs to reduce the complexity and facilitate research (Bodini et al., 2009; Jordán and Osváth, 2009). However, such simplification could lead to the homogenization of food webs and neglect the detailed information between species interactions (Dunne et al., 2002; Dambacher et al., 2010). Therefore, constructing food webs to the species level whenever possible may help explore multispecies regularities and evaluate the impacts of disturbances on the ecosystems (Boit et al., 2012; Thompson et al., 2012). The Haizhou Bay food web showed high connections at the species level, and this food web contains several strong and weak interactions based on the feeding relationship observed (Fig. 2), which could contribute to the ecosystem stability (Wootton and Stouffer, 2016). Similar trophic interactions were shown between target and non-target species (Fig. 3). Therefore, fishery managements should not only focus on the target species but also consider the cascading effect of non-target species, cascading effect pose an indirect threat to food web structure.

Food webs with high connectivity are resistant to environmental variations and reductions in species diversity (Dunne et al., 2002, 2004). In this study, the Haizhou Bay food web was found to have a high degree of connectivity complexity (L/S = 10.978). In particular, the numbers of incoming links for whites-

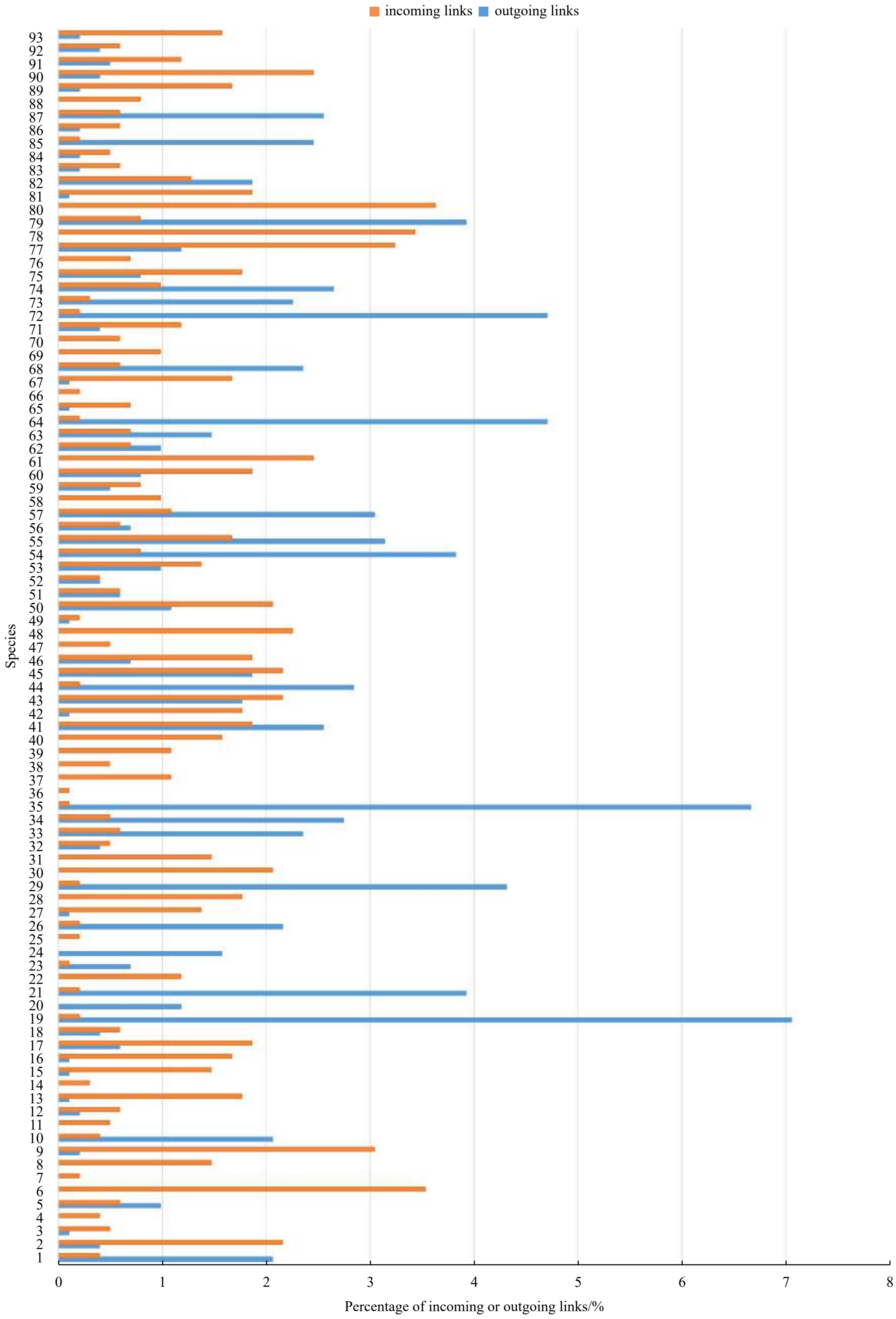

Fig. 3. Percentage of incoming links (orange) and outgoing links (blue) for all species in the Haizhou Bay food web. The species indicated by the number are detailed in Table 2.

potted conger *Chaeturichthys stigmatias*, fat greenling *Hexagrammos otakii* and bluefin gurnard *Chelidonichthys kumu* were very high, which indicates that these species are important predators in the food web. These species feed upon a wide range of

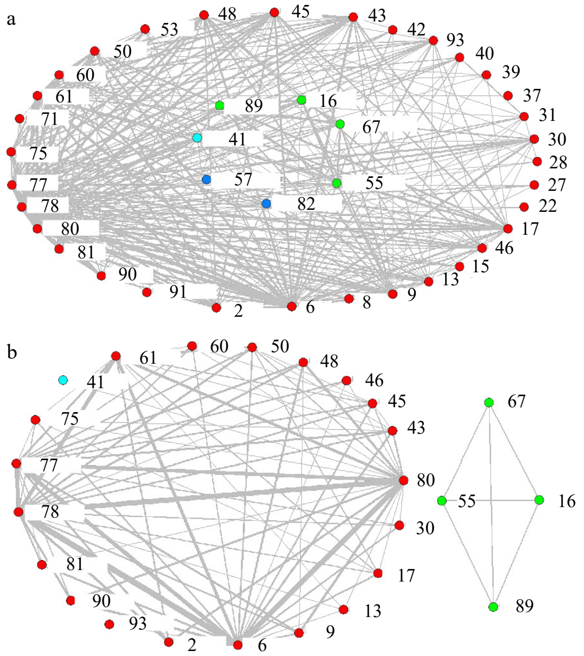

Fig. 4. Competition graphs. a. 40 predators sharing over 10 common prey species in the Haizhou Bay food web; b. 25 predators sharing over 15 common prey species. Link widths indicate the number of prey species. The species indicated by the colored dots are detailed in legend of Fig. 2; the species indicated by the number are detailed in Table 2.

common prey species and their connectivity is high. Thus, these species play key roles in maintaining the structural stability of the food web. These predators are also target species in the Haizhou Bay and compete with other predators for the same prey species (Savenkoff et al., 2007). The species fine crayfish *Leptochela gracilis*, squid *Loligo* sp., and Japanese snapping shrimp *Alpheus japonicus* revealed the largest number of outgoing links, which means they are key prey species in the food web. Analysis of the food web structure and species interactions is essential for the maintenance of ecosystem functions, and will provide essential information for community-wide monitoring and evaluation of the impacts of local extinction through the food web structure.

4.2 *Trophic interaction between species*

Indirect effects are an important mechanism to maintain the ecosystem function and community structure through predation or competition (Wootton, 1994). The competition graphs showed that species in the Haizhou Bay have a high degree of food competition. In the competition graphs, 25 predator species shared over 15 common prey species, which could help maintain the stability of the food web. High connectivity and variations in prey species could alter the energy transfer and material circulation of the food web through direct and indirect connections (Solé and Montoya, 2001). Compared with those in other ecosystems (Marina et al., 2018), species in the Haizhou Bay ecosystem were more closely related in terms of feeding strategy and shared many common prey species. The high feeding complexity of species in the Haizhou Bay food web could help increase the resistance of this food web to environmental variations. Single-species management remains the main approach to protect fishery resources (Sun et al., 2014), but this strategy neglects the feeding complexity between species and exerts minimal effects on the recovery of entire ecosystems. Therefore, fishery management should consider the relationship between feeding and competition among species. Overfishing could cause the local depletion of some target species and decrease the complexity of the feeding–competing relationship. Thus, it is essential to maintain the resistance and stability of food webs and protect the target species for sustainable development of fisheries.

4.3 *Impacts of species depletion through the food web*

Topology model is one of the most useful methods to examine the topology structure of food webs, which can be used to evaluate the impacts of species depletion on food web structure. In this study, target species showed extensive connections with other target and non-target species. The increased depletion of target species would result in the depletion of not only target species but also non-target species (such as branded goby *Chaeturichthys stigmatias* and pinkgray goby *Amblychaeturichthys hexanema*) through food web connections according to the feeding relationship. Predicting the variation of all species under long-term overfishing is extremely challenging because of the complex interaction between these species and other unpredictable factors; however, increased fishing pressure may be expected to lead to the depletion of some target species (Corrales et al., 2015).

The results showed that the depletion of most-connected target species had few impacts on food web structure. For instance, the *CC* index had small changes with the depletion of these species. However, they may have great impacts on the structural importance of other species. These most-connected target species do not necessarily indicate high structural importance in a complex food web, and the depletion of these most-connected target species does not necessarily cause the collapse of food web structure (Navia et al., 2016). The disappearance of these target species did not cause great changes on the values of the food web structure indices calculated in this study. On the contrary, some species with lower connectivity (e.g., redundant species) may show stronger trophic interactions and play important ecological

Table 3. Structural properties of the complete food web and food webs with simulated depletion of the six most-connected target species and six randomly selected species in the Haizhou Bay food web

Indices	Original food web	Simulated food web					
		D1	R1	D3	R3	D6	R6
CC	0.226	0.220	0.226	0.215	0.225	0.214	0.226
BC	0.451	0.416	0.457	0.371	0.475	0.367	0.514
PL	2.115	2.120	2.112	2.236	2.112	2.297	2.127
L/S^2	0.118	0.110	0.119	0.109	0.122	0.103	0.125
L/S	10.978	10.570	10.989	10.833	10.978	8.931	10.839

Note: The D scenarios of the simulated food web are described in Table 1. R1, R3, and R6 respectively indicate the removal of one, three and six randomly selected species, respectively. 1–6: Accumulation of the number of species removed (D, simulated depletion of target species; R, simulated depletion of randomly selected species).

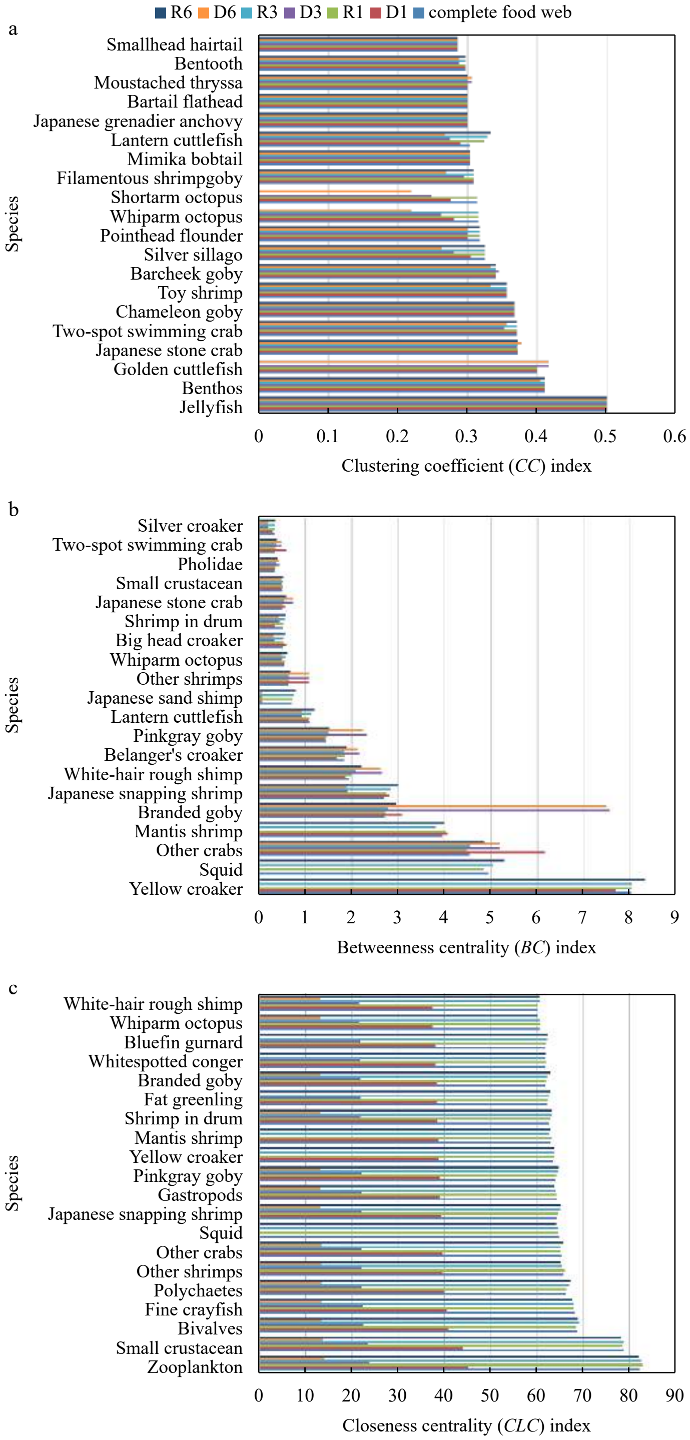

Fig. 5. Ranks of three topological network indices (*CC*, *BC*, and *CLC*) for the top 20 species in the original and simulated food webs (average values of 100 randomly selected combinations for R1, R3 and R6). D1, D3, and D6 are defined in Table 1. R1, R3, and R6 respectively indicate the removal of one, three, and six randomly selected species.

roles (Naeem, 1998; Allesina and Bodini, 2005). The reasons may be contributed to the complexity of feeding relationship between species, and the structure indices respond slowly in a highly complex food web. The more complex the community, the greater its resistance to perturbation (Harding, 1999). Weak interactions (low feeding ratios) in food webs would have a higher buffer capacity when the environment is disturbed or some species disappear (Wootton and Stouffer, 2016).

In the present study, the structural importance of depleted species could be replaced by other species in the web. Empirical evidence suggests that indirect effects exist only in the case of $PL \leqslant 3$ (Williams et al., 2002; Navia et al., 2016). The *PL* values in the Haizhou Bay food web were consistently less than 3, which means the impacts of target species depletion could be transmitted quickly to all other species through the food web. Therefore, EBFM should focus not only on species with high commercial values but also on those species with few but strong links in the marine ecosystem (Quince et al., 2005).

This study found that some species in the Haizhou Bay food web are more sensitive to the fluctuations of the most-connected target species than randomly selected target species. This effect can be transmitted to other species. As target species are depleted, the structure properties of some species may be modified. These results also demonstrate that greater indirect effects were transmitted in the case of $PL \leqslant 3$. For example, the BC of branded goby *Chaeturichthys stigmatias* increased remarkably with the depletion of the most-connected species. However, all species demonstrated only slight variations of the CC because the indices were associated with connections; as only whiparm octopus *Octopus variabilis* and shortarm octopus *Octopus ochellatus* showed many links with the depletion of the most-connected species, so the values of most other species remained stable. Therefore, depletion of most-connected species could lead to slight changes of the structure and properties of the food webs and exert great effects on many non-commercial species in this web. At present, current management policies are often based on simplification for practical purposes and neglect the complexity of the ecosystem.

Although this study has analyzed the changes of food web structure based on topological network analysis from multiple perspectives, there are some limitations in this study. First, topological network only consider the connection between species, ignoring the connection strength between species (such as energy flow). This will lead to the equal feeding weight between the predator and all the prey species, which cannot reflect the feeding preference of the species. Second, the biomass also is not reflected in the model. Therefore, not only the feeding relationship between species should be considered, but also quantitative indicators such as connection weight and biomass should be added to the model in future research, which will play an important role in promoting the analysis of the food web.

5 Conclusions

In conclusion, the Haizhou Bay food web was found to have a high degree of connectivity complexity, and the corresponding competition graphs showed that the species in the web have a high degree of food competition. Most species in the Haizhou Bay food web were more sensitive to the fluctuation of the most-connected target species, and this effect could be transmitted to other species and exert great impacts on many non-commercial species in the food web. As the food web structure is an important part of any ecosystem, future fishery management systems should consider the relationship between feeding and competition among species.

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