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Topology-based analysis of pelagic food web structure in the central and eastern tropical Pacific Ocean based on longline observer data

Qinqin Lin[1], Jiangfeng Zhu[1, 2*]

[1] College of Marine Sciences, Shanghai Ocean University, Shanghai 201306, China

[2] Key Laboratory of Sustainable Exploitation of Oceanic Fisheries Resources of Ministry of Education, Shanghai Ocean University, Shanghai 201306, China

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Abstract

The tropical Pacific Ocean supports many productive commercial fisheries. However, few studies of ecosystem structure in the tropical Pacific Ocean have been carried out. In this study, we analyzed the food web structure in the central and eastern tropical Pacific Ocean based on trophic relationships of 35 pelagic species collected by Chinese tuna longline observers from June to November in 2017. Topology indices (node degree, D; centrality indices, BC and CC; topological importance indices, TI^1, TI^3; keystone indices, K, K_t and K_b) and Key-Player algorithms (KPP-1, KPP-2) were used to select key species and construct a simplified food web combined with body size data. The Kendall rank correlation and hierarchical clustering analysis indicated that different topology indices resulted in consistent rankings of key species. Most key species were the same as those selected in other studies in the Pacific Ocean, such as Shortbill spearfish (*Tetrapturus angustirostris*), Swordfish (*Xiphias gladius*), Albacore tuna (*Thunnus alalunga*), cephalopods and scomber. The food web would be separated into many unconnected parts (F=0.632, F^D=0.795, R^D=0.957) after the removal of the five key species, indicating the key roles of these species in the food web structure and stability. Body size was considered an influential indicator in constructing the simplified food web. This study can improve our understanding of the food web structure in the tropical Pacific Ocean and provide scientific basis for further ecosystem dynamics studies.

Key words: topology, food web structure, tropical Pacific, key species, size structure

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1 Introduction

The tropical Pacific Ocean is rich with fish resources and supports many productive pelagic fisheries. Research on food web of the Pacific Ocean has attracted greater attention in recent years (Allen and Robertson, 1994; Sibert et al., 2006; Dambacher et al., 2010). The feeding behavior of fish and other organisms is the basis for the construction of marine trophic relations (Tang and Su, 2001; Frank et al., 2005; Zhang, 2005). The evaluation of ecosystem dynamics requires quantitative description of the food web structure (Allesina et al., 2008). With direct and indirect links among species, the structure of food web is often complex. Simplifying food web structure based on key species playing decisive roles in the community has become common in food web studies (Everett and Borgatti, 2002; Luczkovich, et al., 2003; Schmitz, 2009). The identification of key species depends not only on its feeding relationships, but also on its position in the community structure, especially the topological position (Power et al., 1996). Therefore, topology-based network analysis provides a useful method to improve our understanding of food web structure (Jordán et al., 2006; Zhu et al., 2016).

Olson and Watter (2003) explored the interactions among species or group and ecological implications in the eastern tropical Pacific Ocean using Ecopath with Ecosim (EwE) model. However, individual species or a group being regarded as a single "node" in the network often obscures important ecological process of species (Woodward et al., 2005). The simulation experiments (Emmerson and Raffaelli, 2004) and the size-based model (Polovina and Woodworth-Jefcoats, 2013) developed for the subtropical Pacific indicated that a species' trait can be characterized with body size in the ecological network. Previous studies have shown substantial declines in the abundances of top predator species following the large-scale fisheries in the Pacific Ocean, which may lead to great changes in the trophic relationship of large predators and even the whole ecosystem (Pauly et al., 1998; Cox et al., 2002; Polovina et al., 2009).

Previous food web studies of oceanic Pacific Ocean were largely based on data from adjacent areas, due to the difficulty of obtaining samples by scientific survey in open-ocean, which was often time and cost-consuming in practice (Bigelow et al., 2002; Worm et al., 2005; Gerrodette et al., 2012; Zhu et al., 2012). In this study, we analyzed the food web structure in the tropical waters of the central and eastern Pacific Ocean. Topology indices (node degree, D; centrality indices, BC and CC; topological importance indices, TI^1, TI^3; keystone indices, K, K_t and K_b) and the Key-Player algorithms (KPP-1, KPP-2) were used to select key species and then simplify the food web combined with body size data. We

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*Corresponding author, E-mail: jfzhu@shou.edu.cn

also carried out Kendall rank correlations and hierarchical clustering to test relationships among the topology indices. This study can provide important information for improving our knowledge about food web structure and its ecological implications in the central and eastern tropical Pacific, which has not been investigated yet.

2 Materials and methods

2.1 *Study area*

The stomach content and size data in this study were derived from samples collected by China's tuna longline observers in the central and eastern Pacific Ocean from June to November 2017. The sampling sites were shown in Fig. 1 (13°09′N–34°27′S, 100°03′–176°17′W). On-board observers stored the stomach content in 10% formalin labeled with the sample information. The samples were sent to the laboratory of Shanghai Ocean University for further analysis. If measurable, the size, sex and other biological information of fish were also recorded by observers.

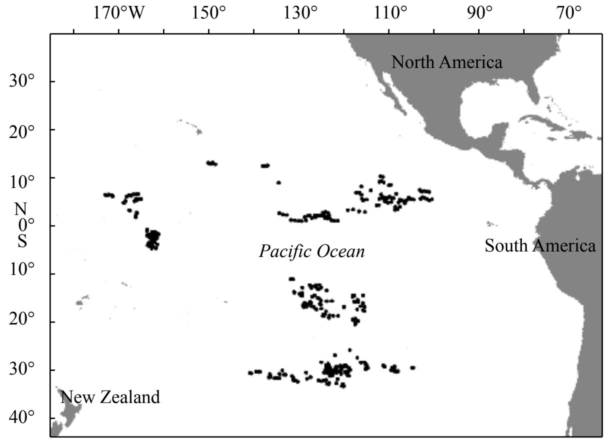

Fig. 1. Location of the stomach sampling by longline observer in the central and eastern tropical Pacific from June to November in 2017. Each dot represents a position where a longline set was deployed.

2.2 *Diet analysis*

The raw diet data in this study was the same as those used in the ecosystem modeling by Feng et al. (2019). Information of stomach content samples including length (mm), mass (g) and quantity of prey item were measured. Prey species were identified based on marine taxonomy publications (e.g., Cheng and Zheng, 1987; Dai and Xu, 2007). For species that could not be identified visually and via the stereo microscope, we subsampled the muscle and sent to a professional institution for DNA sequence analysis for species identification based on published DNA database. This process was conducted independently by the institution. Sagittal otoliths of prey species were also used for species identification according to previous otoliths collections in the laboratory. Detailed diet composition data can be referred to Feng et al. (2019) and not repeated here.

We determined the main prey by calculating relative density (*RD*),

$$RD = \frac{n_i}{N} \times 100\%, \tag{1}$$

where n_i is the number of prey i, and N is the total number of prey in the sample (Hyslop, 1980). If RD>10%, the prey is regarded as the main prey of predator species (Li et al., 2004). Meanwhile, the food composition of predators, i.e., the frequency and weight percentages of each prey, can be measured. According to these data of each prey, we divided the predator's preference for prey into five levels (1.0–5.0). The preference level of species combined with size data were used to analyze the change of food web structure in this study.

2.3 *Topological analysis*

The basic idea of food web topology is to quantitatively describe the degree of closeness between the species and the impact of each species on the overall food web with a series of topological indices (Pascual and Dunne, 2006; Robinson et al., 2007). We used various topological indices to quantify the positional importance of each individual species, including the most widely used node degree, centrality indices, keystone indices, topological importance indices (Jordán and Scheuring, 2002) and the Key-Player algorithms (Borgatti, 2003). These indices are described as follows:

(1) Node degree (D)

$$D_i = D_{\mathrm{in},i} + D_{\mathrm{out},i}, \tag{2}$$

where D represents the number of feeding relationships of species i with other species, D_{in} represents the number of prey, and D_{out} represents the number of predators. D is one of the most local measures in the topological network. If we know the value of node degree of all species, then the distribution of links of the food web can be obtained.

(2) Centrality indices

$$BC_i = \frac{2 \times \sum\limits_{j<k} \frac{g_{jk}(i)}{g_{jk}}}{(N-1) \times (N-2)}, \tag{3}$$

where the betweenness centrality (BC) measures the frequency of species i on the shortest path between species j and k, which represents the ability to control the exchange of information in the food web. In Eq. (3), N is the number of species in the study, g_{jk} represents the number of isometric minimum paths between species j and k, and $g_{jk}(i)$ is the number of species i on the minimum path between j and k ($i \neq j$, $i \neq k$). The larger the value of BC_i, the more influence the species has on the food web.

$$CC_i = \frac{N-1}{\sum\limits_{j=1}^{N} d_{ij}}, \tag{4}$$

where the closeness centrality (CC) represents the sum of the minimum distances from a species to all other species, which indicates the speed of transmitting information. In Eq. (4), d_{ij} represents the shortest path length between species i and j. The smaller the value of CC_i, the faster the species transmits information in the food web.

(3) Topological importance indices (TI)

$$TI_i^n = \frac{\sum\limits_{m=1}^{n} \sum\limits_{j=1}^{N} a_{m,ji}}{n}, \tag{5}$$

where TI measures the total effects on the food web originated from species i to other species in n steps, which can express both direct and indirect effects. In Eq. (5), $a_{m,ji}$ represents the effect of species i on j when i reached j in m steps, n is the maximum step length, and m ranges from 1 to n. For example, when m=1, i and j are two species with direct predator-prey relationship, and the effect of i on j can be represented as: $a_{1,ji}=1/D_i$, where D_i is the degree of species i. TI quantitatively describes the ability of species to spread information, and the effects in the food web are multiplicative and additive. When m=2, we should consider two paths from i to j. We assume that one path to reach j from i is through x and another path is through y. Then the effect of i on j through x can be demonstrated with $a_{1,xj} \times a_{1,ix}$ and the effect through y is $a_{1,yj} \times a_{1,iy}$ accordingly. Therefore, the two-step can be defined as: $a_{2,ji} = a_{1,xj} \times a_{1,ix} + a_{1,yj} \times a_{1,iy}$. And the n-step effects originated from species i can be obtained by the TI index.

(4) Keystone indices (K)

$$K_{\mathrm{b}}^{(i)}=\sum_{c=1}^{n}\left(\frac{1}{d_c}+\frac{1}{d_c}K_{\mathrm{b},c}\right), \tag{6}$$

$$K_{\mathrm{t}}^{(i)}=\sum_{e=1}^{m}\left(\frac{1}{f_e}+\frac{1}{f_e}K_{\mathrm{t},e}\right), \tag{7}$$

$$K_i=K_{\mathrm{b}}^{(i)}+K_{\mathrm{t}}^{(i)}, \tag{8}$$

where K quantifies species' positions at an intermediate scale to express the importance of species i in the whole food web structure. K considers not only direct predators or prey of a species but also their neighbors indirectly connected to the species. $K(i)$ contains two indices, the bottom-up keystone index (K_{b}) and the top-down keystone index (K_{t}). In Eq. (6), n is the number of predators of species i, d_c is the number of prey of its cth predator and $K_{\mathrm{b},c}$ is the bottom-up keystone index of the cth predator. Similarly, in Eq. (7), m is the number of prey eaten by species i, f_e is the number of predators of its eth prey and $K_{\mathrm{t},e}$ is the top-down keystone index of the eth prey. K is a continuous calculation process and K_{b} should be calculated first for higher species.

Key-Player algorithm is composed of two approaches. One is fragmentation approach (KPP-1) which examines the extent to which a single species or a group of species maintains the cohesiveness of the food web. The other is reach approach (KPP-2) which defines the strength of a single species or a group of species in connecting others within the food web. The species that can transmit information to others at the fastest speed are regarded as key species (Breiger et al., 2003; Dambacher et al., 2010). An optimal choice of k nodes is a KP-set and we increased k up to 5 in this study. KPP-1 contains two indices, the Fragmentation (F) and the distance-weighted fragmentation (F^{D}). The F may not increase after the removal of a species, but only the F^{D} changes.

$$F=1-\frac{\sum_i s_i\left(s_i-1\right)}{N\left(N-1\right)}, \tag{9}$$

$$F^{\mathrm{D}}=1-\frac{2\sum_{i>j}\frac{1}{d_{ij}}}{N\left(N-1\right)}, \tag{10}$$

where s_i is the number of species in its ith component (subgraphs), and d_{ij} represents the distance between species j and i. The F and F^{D} range from 0 to 1, and the closer F and F^{D} are to 1, the greater the impact the species has on the food web structure.

KPP-2 is used to find the species that spreads information in the food web the most, and KPP-2 can be expressed as the Distance-weighted Reach (R^{D}).

$$R^{\mathrm{D}}=\frac{\sum_j\frac{1}{d_{Mj}}}{N}, \tag{11}$$

where d_{Mj} represents the minimum distance of any species j from a set of M species. The R^{D} ranges from 0 to 1. The closer R^{D} is to 1, the faster the delivery speed of information is.

We also calculated the Kendall rank correlations between different indices to check whether these indices provided similar information and analyzed the significance among the eight indices. Kendall rank correlations are used to measure the degree of correspondence between rankings and the value lies between −1 and 1. If the indices are completely independent, the coefficient value will be 0. The increasing values imply increasing association between the indices. We then applied hierarchical clustering on these ranking results to show the relationships between indices. The requirement of clustering analysis for data is that the intra-group variance of clustering groups is smaller, while the inter-group variance is larger. Euclidean distance is the most commonly used measurement method in clustering analysis. First, the values of each index were standardized by SPSS, and then we defined the similarity degree of indices based on Euclidean distance. The combination of these indices can accurately describe the importance of species in the food web.

2.4 *The construction of the simplified food web*

Predator-prey relationship within a food web is more strongly determined by size structures rather than species' taxonomic and eco-chemical identities. Size-based predation plays an important role in constructing the food web structure (Polovina and Woodworth-Jefcoats, 2013). We hypothesized that the selection of prey depends on the size of the interacting species, thus, a static continuous food web can be established by combining predation relationships and size data after the key species were identified. The predators' size data recorded by the observer was grouped and the most representative size distribution was used in our study. The size distribution of the prey was found to be relatively larger based on the records in diet analysis; the common lengths of prey were obtained from published databases (i.e., http://fishdb.sinica.edu.tw/ and http://www.fishbase.org/). The size ranges of predators and prey species used in this study are listed in Table 1.

The software used for qualitative analysis in the study includes MS Excel, SPSS, R, Ucinet6 (http://www.analytictech.com/ucinet/), CoSBiLab Graph 1.0 (http://www.cosbi.eu/research/) and Key-Player 1.44 (http://www.analytictech.com/products.htm). Specifically, D, BC and CC were calculated by Ucinet 6; TI^1, TI^3, K, K_{b} and K_{t} were calculated by CoSBiLab Graph 1.0; F, F^{D} and R^{D} were calculated by Key-Player 1.44; and SPSS was used for clustering analysis.

3 Results

3.1 *Feeding relationships*

We analyzed the predation relationships among 35 species

Table 1. The size range of key predators and prey for use in constructing food web

Predators	Fork length/cm	Prey	Common length/cm
Bigeye tuna	105–155	Cephalopods	15–25
Opah	85–105	Scomber	15–30
Swordfish	125–190	Longnose lancetfish	30–60
Blue marlin	165–210	Barracuda	20–50
Shortbill spearfish	130–165	Silver spinyfin	5–10
Albacore tuna	80–95	Puffer	15–20
Striped marlin	165–210		
Snake mackerel	100–120		
Pelagic thresher	135–165		

Note: The common lengths of billfishes were measured as lower jaw fork length, and that of sharks as pre-caudal length.

(Fig. 2), focusing on the trophic interactions. For the 21 predator species, Shortbill spearfish (*Tetrapturus angustirostris*) ate the highest number of prey, followed by Swordfish (*Xiphias gladius*), Albacore tuna (*Thunnus alalunga*), and Bigeye tuna (*Thunnus obesus*). For the 16 prey species, cephalopods in the middle of the network, had the most feeding relationships with predators, followed by scomber and Longnose lancetfish (*Alepisaurus ferox*). Longnose lancetfish and Swordfish are both predators and prey in the diet analysis. The bait species used for the longline fishing in this study are sardines, Spotted chub mackerel (*Scomber australasicus*) and Bullet tuna (*Auxis rochei*); thus cephalopods are the most common natural prey in the food web.

Feeding relationships in the central and eastern tropical Pacific network. Red nodes represent predators and blue nodes represent prey.

3.2 *Topological indices*

The food web was analyzed by topological indices based on the diet data among species, and the results of each index are shown in Table 2. For different topological indices, the species with the highest rank are considered key species (or species group).

Node degree (*D*) is the most widely used index for representing the specific position of a species. The *D* of cephalopods was the largest among all species (*D*=17), which suggests that there were 17 predators eating cephalopods and they can easily affect the abundance of other species in the food web, followed by scomber (*D*=12). For predators, Shortbill spearfish and Swordfish preyed on 7 species (*D*=7), followed by Albacore tuna (*D*=5), which indicates that they were top predators in the food web and they have multiple feeding relationships with other species.

For prey species, the species with the two highest *BC* values were cephalopods (*BC*=288.35) and scomber (*BC*=132.97). For predator species, the highest *BC* was recorded by Shortbill spearfish (*BC*=89.12), followed by Swordfish (*BC*=47.76). This indicated that cephalopods and Shortbill spearfish can play a key role in controlling the exchange of information in the food web. *CC* measures the shortest path among species. The three species with the highest *CC* were cephalopods (*CC*=71), Swordfish (*CC*=88) and scomber (*CC*=89), which indicated that they could

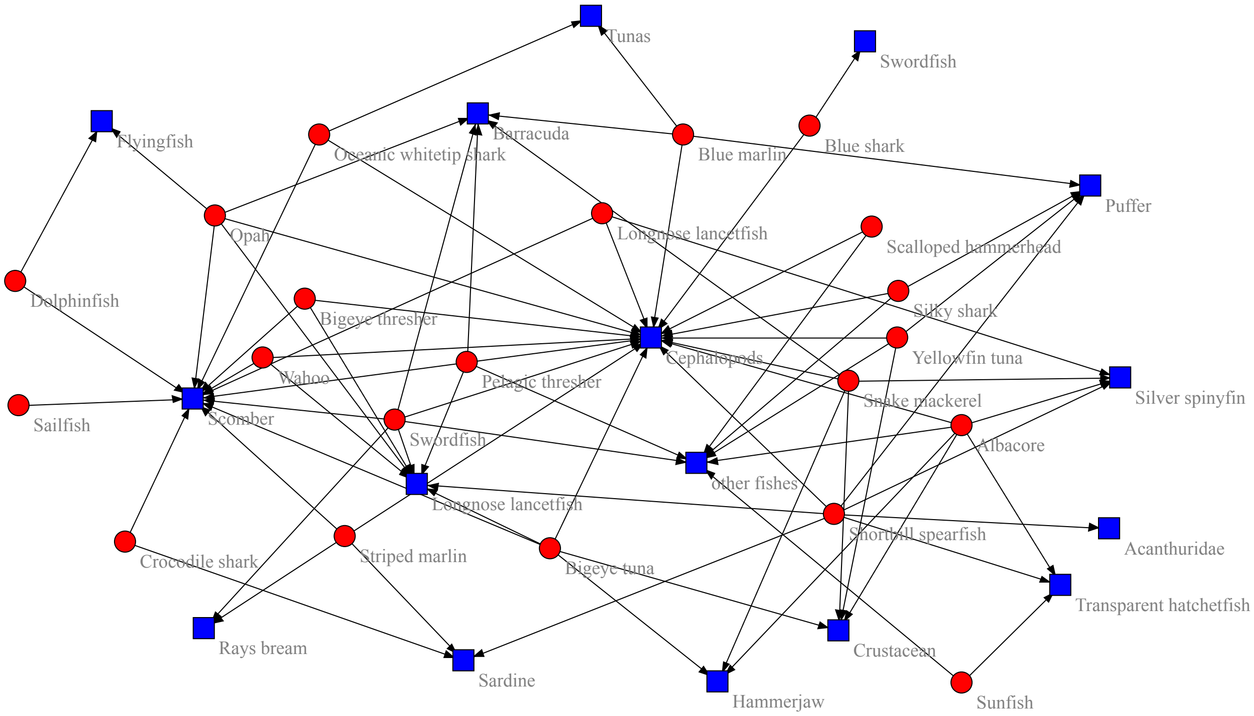

Fig. 2. Feeding relationships in the central and eastern tropical Pacific network. Red nodes represent predators and blue nodes represent prey.

Table 2. The ranking results of eight topological indices in the central and eastern tropical Pacific food web

Number	Species/group	Scientific name	D		BC		CC		TI^1		TI^3		K		K_t		K_b	
1	Yellowfin tuna	*Thunnus albacares*	**21**	17	**21**	288.35	**21**	71	**6**	2.37	**6**	0.79	**21**	4.69	**6**	2.37	**21**	4.69
2	Bigeye tuna	*Thunnus obesus*	**24**	12	**24**	132.97	**4**	88	**8**	1.37	**8**	0.46	**24**	4.35	**8**	1.37	**24**	4.35
3	Opah	*Lampris guttatus*	**25**	10	**6**	89.12	**24**	89	**4**	1.13	**4**	0.38	**6**	2.37	**4**	1.13	**22**	2.12
4	Swordfish	*Xiphias gladius*	**4**	7	**4**	47.76	**6**	90	**10**	1.09	**10**	0.36	**22**	2.12	**10**	1.09	**25**	1.58
5	Blue marlin	*Makaira mazara*	**6**	7	**22**	44.52	**12**	90	**18**	1.06	**18**	0.35	**25**	1.97	**18**	1.06	**27**	1.02
6	Shortbill spearfish	*Tetrapturus angustirostris*	**22**	7	**3**	42.60	**2**	92	**5**	1.01	**5**	0.34	**4**	1.63	**5**	1.01	**30**	0.98
7	Wahoo	*Acanthocybium solandri*	**8**	6	**25**	42.53	**3**	92	**3**	0.99	**3**	0.33	**8**	1.37	**3**	0.99	**28**	0.89
8	Albacore	*Thunnus alalunga*	**2**	5	**8**	41.10	**8**	94	**9**	0.98	**9**	0.33	**10**	1.09	**9**	0.98	**29**	0.84
9	Striped marlin	*Kajikia audax*	**3**	5	**18**	35.00	**9**	94	**2**	0.87	**2**	0.29	**18**	1.06	**2**	0.87	**23**	0.82
10	Snake mackerel	*Gempylus serpens*	**10**	5	**2**	33.54	**25**	95	**1**	0.7	**1**	0.23	**27**	1.02	**1**	0.7	**32**	0.81
11	Sunfish	*Mola mola*	**12**	5	**9**	28.85	**7**	96	**15**	0.64	**12**	0.21	**5**	1.01	**15**	0.64	**26**	0.7
12	Pelagic thresher	*Alopias pelagicus*	**27**	5	**12**	26.50	**14**	96	**12**	0.63	**15**	0.21	**3**	0.99	**12**	0.63	**35**	0.58
13	Crocodile shark	*Pseudocarcharias kamoharai*	**1**	4	**5**	24.71	**15**	96	**19**	0.58	**19**	0.19	**9**	0.98	**19**	0.58	**33**	0.57
14	Bigeye thresher	*Alopias superciliosus*	**5**	4	**10**	22.73	**1**	98	**11**	0.48	**11**	0.16	**30**	0.98	**11**	0.48	**4**	0.5
15	Oceanic whitetip shark	*Carcharhinus longimanus*	**9**	4	**15**	22.04	**10**	98	**17**	0.45	**17**	0.15	**28**	0.89	**17**	0.45	**34**	0.42
16	Scalloped hammerhead	*Sphyrna lewini*	**23**	4	**1**	16.05	**5**	100	**13**	0.42	**13**	0.14	**2**	0.87	**13**	0.42	**31**	0.14
17	Silky shark	*Carcharhinus falciformis*	**29**	4	**27**	15.62	**17**	100	**25**	0.39	**25**	0.13	**29**	0.84	**25**	0.39	**1**	0
18	Blue shark	*Prionace glauca*	**30**	4	**32**	11.66	**22**	101	**7**	0.29	**7**	0.1	**23**	0.82	**7**	0.29	**2**	0
19	Dolphinfish	*Coryphaena hippurus*	**7**	3	**30**	11.06	**16**	102	**14**	0.29	**14**	0.1	**32**	0.81	**14**	0.29	**3**	0
20	Sailfish	*Istiophorus platypterus*	**14**	3	**28**	11.05	**27**	103	**16**	0.2	**16**	0.07	**1**	0.7	**16**	0.2	**5**	0
21	Cephalopods	–	**15**	3	**29**	10.75	**18**	104	**20**	0.08	**20**	0.03	**26**	0.7	**20**	0.08	**6**	0
22	Unidentified fishes	–	**17**	3	**17**	8.77	**29**	105	**21**	0	**21**	0	**15**	0.64	**21**	0	**7**	0
23	Crustacean	–	**28**	3	**23**	6.41	**23**	109	**22**	0	**22**	0	**12**	0.63	**22**	0	**8**	0
24	Scomber	*Scomber* sp.	**32**	3	**7**	6.34	**30**	111	**23**	0	**23**	0	**19**	0.58	**23**	0	**9**	0
25	Longnose lancetfish	*Alepisaurus ferox*	**33**	3	**14**	6.34	**28**	113	**24**	0	**24**	0	**35**	0.58	**24**	0	**10**	0
26	Flyingfish	*Cypselurus comatus*	**11**	2	**19**	5.04	**33**	113	**26**	0	**26**	0	**33**	0.57	**26**	0	**11**	0
27	Barracuda	*Barracuda* sp.	**13**	2	**13**	4.38	**13**	114	**27**	0	**27**	0	**11**	0.48	**27**	0	**12**	0
28	Sardine	*Clupeidae*	**16**	2	**16**	3.00	**32**	115	**28**	0	**28**	0	**17**	0.45	**28**	0	**13**	0
29	Silver spinyfin	*Diretmus argenteus*	**18**	2	**33**	2.84	**34**	119	**29**	0	**29**	0	**13**	0.42	**29**	0	**14**	0
30	Puffer	–	**19**	2	**26**	2.14	**19**	122	**30**	0	**30**	0	**34**	0.42	**30**	0	**15**	0
31	Surgeonfish	*Acanthuridae*	**26**	2	**11**	2.10	**20**	124	**31**	0	**31**	0	**7**	0.29	**31**	0	**16**	0
32	Hatchetfish	*Sternoptyx* sp.	**34**	2	**35**	1.15	**26**	125	**32**	0	**32**	0	**14**	0.29	**32**	0	**17**	0
33	Hammerjaw	*Omosudis lowii*	**35**	2	**34**	0.96	**31**	125	**33**	0	**33**	0	**16**	0.2	**33**	0	**18**	0
34	Rays bream	*Brama brama*	**20**	1	**20**	0	**35**	125	**34**	0	**34**	0	**31**	0.14	**34**	0	**19**	0
35	Tunas	*Thunnus* sp.	**31**	1	**31**	0	**11**	128	**35**	0	**35**	0	**20**	0.08	**35**	0	**20**	0

Note: The species number is in bold, ranked according to the value of each index.

deliver information to other species in the food web at the fastest speed.

TI^1 expresses the direct effects among species, and the ranking results of TI^1 demonstrated that Shortbill spearfish (TI^1=2.37), Albacore tuna (TI^1=1.37) and Swordfish (TI^1=1.13) had the greatest impacts on the whole food web network. The maximum step length in our study is 3 (Fig. 2), and TI^3 can accurately express the indirect effects among species. Based on TI^3, the top three species were Shortbill spearfish (TI^3=0.79), Albacore tuna (TI^3=0.46) and Swordfish (TI^3=0.38), which were the same top species suggested by TI^1. The intensity of indirect topological importance indices' effects usually weakens with the increases of steps as shown by TI^1 and TI^3. There was little difference in the ranking results of most species with the increase of steps n, and the weakening trend of intensity is consistent.

The top-down keystone index of Shortbill spearfish was the largest among species (K_t=2.37), which suggests that Shortbill spearfish had the greatest impact on the exchange of information in the food web by preying on other species, followed by Albacore tuna (K_t=1.37) and Swordfish (K_t=1.13). Cephalopods had the highest ranking in the bottom-up keystone index (K_b=4.69), indicating that the number of direct predators of cephalopods was the largest, and they were the most influential prey in the food web.

Five species were selected as key species using Key-Player algorithms. With KPP-1 algorithm, the key species selected by F index were Swordfish, Blue marlin, Shortbill spearfish, cephalopods and scomber (F=0.632, Fig. 3); and the key species selected

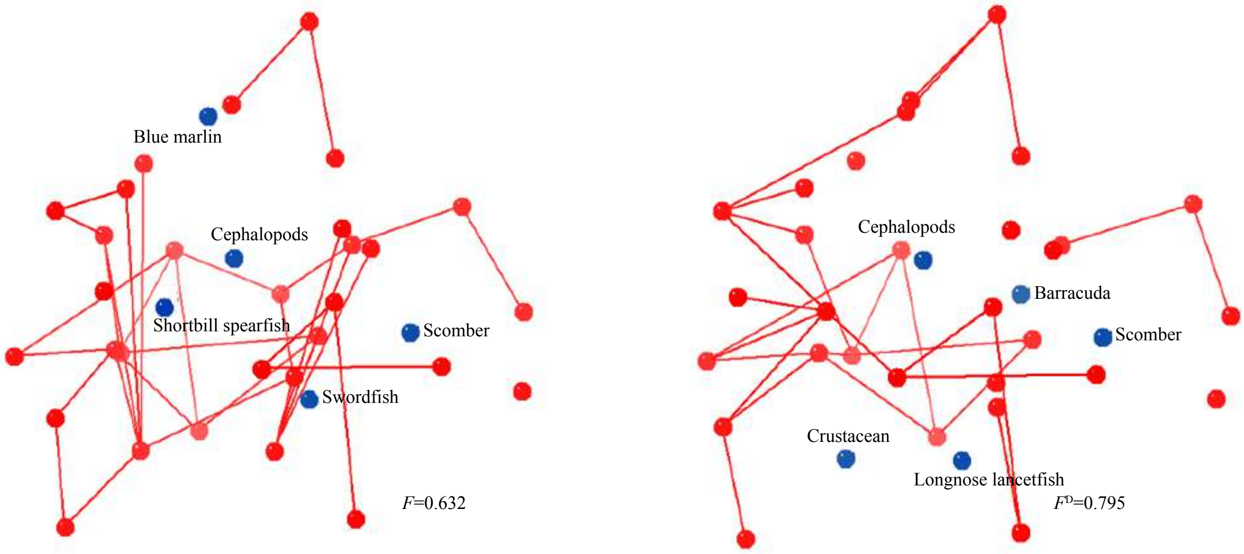

Fig. 3. The disconnected graph based on KPP-1 algorithm with fragmentation index (F) and distance-weighted fragmentation index (F^{D}), repectively. Blue nodes represent the key species being removed, and red nodes represent the remaining species in the food web.

by F^{D} index were cephalopods, scomber, Longnose lancetfish, barracuda and crustaceans (F^{D} = 0.795, Fig. 3). Accordingly, the components or the average distance between the remaining species tend to increase with the removal of these species, which can greatly disconnect the food web.

With KPP-2 algorithm, the five key species selected by R^{D} index were Opah, Shortbill spearfish, Albacore tuna, Cephalopods and Scomber (R^{D}=0.957, Fig. 4), which indicated that these species can reach other species the fastest in the network. The lack of key species reduces the stability of the topological network structure and makes the food web more susceptible to environmental changes. Most of the species with high rank (Table 2) were also selected as key species by the Key-Player, suggesting that the Key-Player algorithms provided consistent information with topological indices.

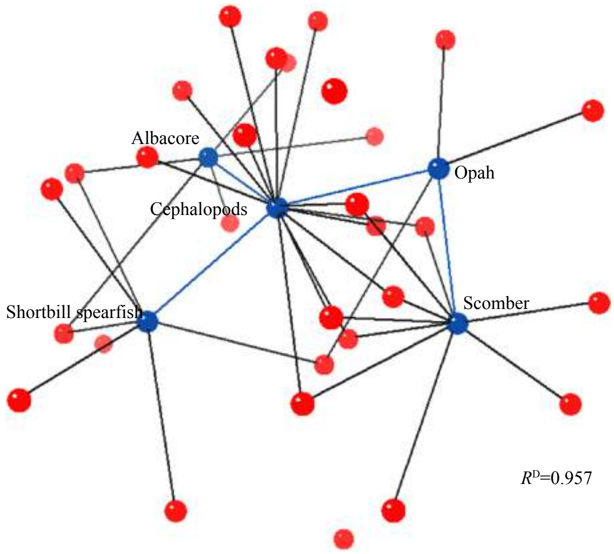

Fig. 4. The disconnected graph based on KPP-2 algorithm with Distance-weighted Reach index (R^{D}). Blue nodes represent the selected key species, and red nodes represent other species in the food web.

3.3 *Relationship between different indices*

The ranking results of different topological indices showed basic similarity, which can be seen in Table 3. There was a significant positive correlation among the indices of D, BC, CC and K, hence most of the top species ranked by D, BC, CC and K were the same in our study, including cephalopods, scomber, and Shortbill spearfish. The correlation between TI^1 and TI^3 was high (0.998), which suggested that the distance was short between the two indices (Fig. 5). The indirect effects which can spread in the pelagic food web contained only three steps and there were few intra-guild predations. This was why the ranking results of TI^1, TI^3, and K_{t} showed little differences.

Table 3. Kendall rank correlation coefficients between eight indices among 35 fish species in the central and eastern tropical Pacific food web

Index	BC	CC	TI^1	TI^3	K	K_{t}	K_{b}
D	0.791*	−0.676*	0.202	0.202	0.724*	0.202	0.288
BC		−0.672*	0.358*	0.359*	0.718*	0.358*	0.135
CC			−0.377*	−0.377*	−0.435*	−0.377*	0.024
TI^1				0.998*	0.259	1.000*	−0.574*
TI^3					0.256	0.998*	−0.575*
K						0.259	0.376*
K_{t}							−0.574*

Note: The correlation ranges from –1 to 1, and * indicates significance at 0.05 level.

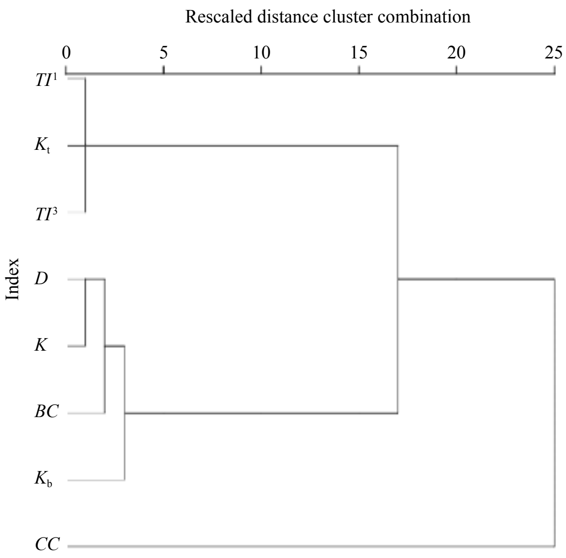

Fig. 5. Hierarchical clustering dendrogram of eight indices based on the Euclidean distance. There were three groups separated by similarity: a=(TI^1, K_t, TI^3), b=(D, K, BC, K_b), c=(CC).

These indices can be divided into three groups based on the similarity in hierarchical clustering shown in Fig. 5, including a=(TI^1, K_t, TI^3), b=(D, K, BC, K_b), c=(CC). The grouping results were consistent with the ranking results in Table 2. The value represents positive and negative correlation, and the greater the absolute value is, the higher the correlation between the two indices.

3.4 *Simplified food web based on key species and body size*

Fifteen species were determined as key species by topological analysis and Key-Player algorithms, including six prey species: cephalopods, scomber, Longnose lancetfish, barracuda, Silver spinyfin (*Diretmus argenteus*) and puffer, and nine predators: Shortbill spearfish, Swordfish, Albacore tuna, Bigeye tuna, Opah (*Lampris guttatus*), Blue marlin (*Makaira mazara*), Striped marlin (*Tetrapturus audax*), Snake mackerel (*Gempylus serpens*) and Pelagic thresher (*Alopias pelagicus*).

The simplified continuous food web based on key species and size data is shown in Fig. 6. Because of the differences in body size range and fishing selectivity-at-size, the size distributions of different species in this study differed greatly. For example, the length range of Albacore tuna was narrow (between 80 cm and 110 cm); whereas the length range of billfish was wide (between 70 cm and 350 cm). Therefore, the common length range of predators was used in this study. All the predations in this study occurred because of a larger predator preying on a smaller prey. The medium-sized Albacore tunas (80–95 cm) could prey on cephalopods ranging 15–25 cm and Silver spinyfin ranging 5–10 cm, whereas the large-sized billfishes could prey on Longnose lancetfish ranging 30–60 cm. Larger predators eat prey with a wider range of body sizes in contrast with the smaller predators. Also, considering only the body size, each species potentially has the behavior of cannibalism.

Numbers 1–5 shown in Fig. 6 represent the predator’s preference on different prey. Shortbill spearfish usually prey on cephalopods and rarely prey on Silver spinyfin. Swordfish can choose to prey on many species, including cephalopods, barracuda, scomber and Longnose lancetfish. The preference of species depends on both prey and predators which can tell how the predation interactions vary with the food web structure changes, such as the abundance loss of some species. As shown in Fig. 6, if cephalopods are removed in the community, bigeye tuna will prey more scomber and Longnose lancetfish. The new order of feeding relationships tends to be determined by body size and preference of remaining species in the food web.

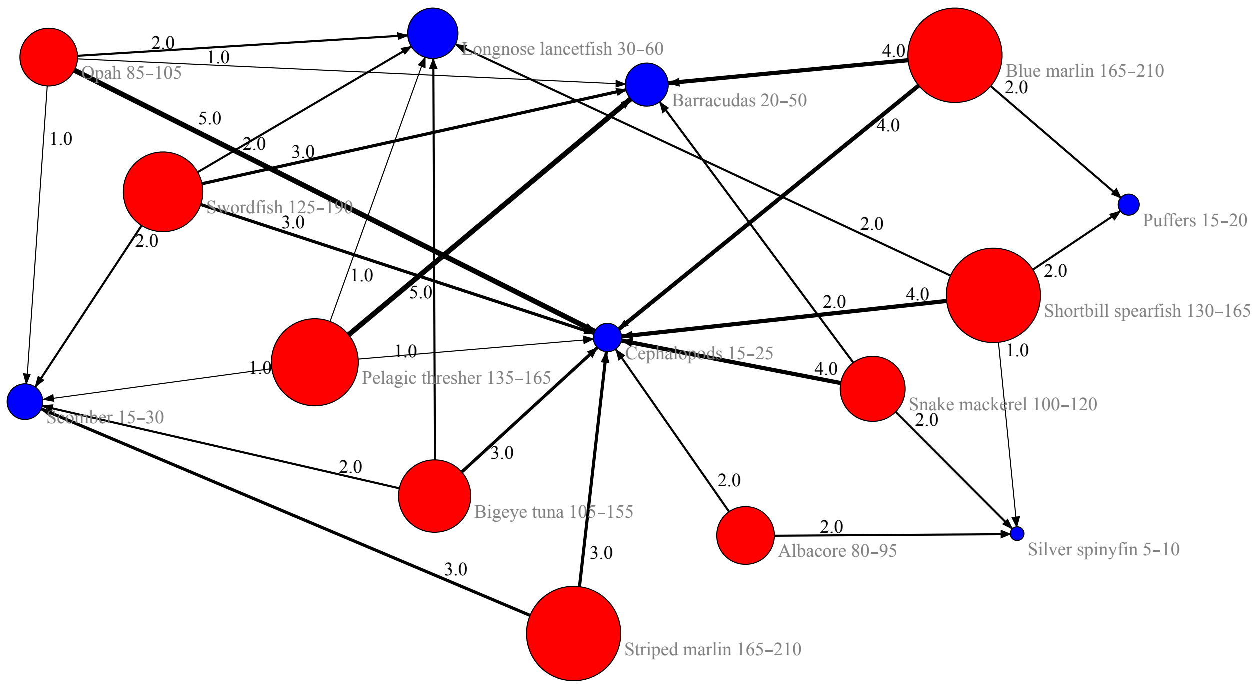

Fig. 6. The simplified food web based on key species and size structure in the central and eastern tropical Pacific food web. Red nodes represent predators, blue nodes represent prey, and the size of nodes represents the species’ length range. The thickness of links (1.0–5.0) represents the preference of predators on prey.

4 Discussion

The trophic relationships were analyzed using stomach contents of fish species caught by pelagic longline. Thus, the trophic relationships in this study may only reflect the pelagic food web. The benthic organisms can be important components of the region, although the main pathway of energy flow was found to be through pelagic food web (Vander Zanden and Vadeboncoeur, 2002; Sánchez-Hernández et al., 2015). The stomach contents were rinsed before returned to lab in this study, due to the difficulty of sending back the whole stomach by fishery observers. This may cause the loss of a small amount of tiny prey items. In addition, many items in the stomach were highly digested and some species were unable to be identified. These uncertainties need to be considered when explaining the food-web developed in this study.

Different criteria for the same ecosystem will result in different determination of key species, and thus the different food web structure. Navia et al. (2016) used two criteria to identify the species to be removed, including the commercial value and the topological importance of the species in the food web. However, species of high topological importance do not necessarily have significant economic value in fisheries. As suggested by Dambacher et al. (2010), species that were identified as key species in the southwest Pacific and the central and western Pacific are cephalopods and Longnose lancetfish; Yellowfin tuna and cephalopods are key species in the central and eastern Pacific. Some studies also demonstrated that sharks were the key species in the central Pacific (Stevens et al., 2000; Kitchell et al., 2002). Although some large predators in this study were not identified as key species, e.g., Yellowfin tuna, they were targeting species for large-scale longline fisheries. This study only considered the topological position of species; therefore, it is needed to complete a comprehensive analysis with other indices if the data allow.

Food web stability has been defined to reflect the response of a population or ecosystem to perturbations (McCann, 2000). A general view seems to be that stability in communities with more species and interactions is easier to achieve. However, the traditional idea was challenged by some subsequent empirical studies by May (1972, 1973), which showed that complex communities were not necessarily stable. In this study we removed species that were not found to be relatively important and established a simplified food web based on key species. Reducing links among species can improve the ability of communities to resist external disturbances and also the resilience (Pimm, 1980). The disconnected graph in Fig. 3 showed that removal of five species (F=0.632, F^{D}=0.795) greatly increased the dispersion of food web. The information transmission can be performed normally as shown in Fig. 4 (R^{D}=0.957) and thus the food-web can be stable. Besides, stability of an ecosystem also depends on the feeding relationships and the different types of interaction, such as competition, predation, or mutualism (Allesina and Tang, 2012; Mougi and Kondoh, 2012). From Fig. 6 we can see that each predator preys on more than one prey species, these competitions and interactions among species can affect the function of energy and the spread of perturbations and thus maintain food web stability. Our research does not prove that the simplified food web is more stable than the whole food web, but its stability can be confirmed to maintain the normal function in a community.

The variations in size distribution of individual species play a key role in topological food webs and ecological processes (Shin et al., 2005). We selected the length range of each species and used different node sizes to represent size range in the food web we constructed, which would enable easier and more effective analysis (Fig. 6). Previous studies also used maturation size or mean size to characterize each species' trait (Hartvig et al., 2011; Shin et al., 2005), and the size-based indicators vary with data requirements and research objectives. However, as Navia et al. (2016), our study did not analyze temporal variations of the food web (Fig. 6). In addition, we only identified one size group for each species, and some information was overlooked in the size-based food web. For example, the fork length of swordfish (125–190 cm) in our study can be divided into three size groups, including 125–150 cm, 150–175 cm and 175–190 cm. Therefore, more attention should be paid to the whole life history of each species and it's necessary to subdivide the length group of each species if data is available.

Whether it is coastal or marine ecosystems, the average sizes of most prey are less than the average predator sizes, and there is always a positive correlation between them (Cohen et al., 1993). We found that the sizes of all predators were larger than prey in our study, which supports the view that size is the important factor in determining predation relationships. The effects of predator sizes in biological communities are much greater than prey sizes (Cohen, 1980; Williams and Martinez, 2000), and the size range of prey that predators can eat determines the food web topology (Law and Morton, 1996; Spencer and Warren, 1996). Most predators are more important in constructing food web, compared with prey based on the rankings of topological importance. For example, cephalopods can be replaced by other prey in the food web; whereas there may be no other species that can perform similar functions of top predators (e.g., Swordfish and Blue marlin). Thus, it is necessary to improve the understanding of the role of body size in ecological network, especially the key predators' size.

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