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Determination of keystone species in CSM food web: A topological analysis of network structure

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Abstract

The importance of a species is correlated with its topological properties in a food web. Studies of keystone species provide the valuable theory and evidence for conservation ecology, biodiversity, habitat management, as well as the dynamics and stability of the ecosystem. Comparing with biological experiments, network methods based on topological structure possess particular advantage in the identification of keystone species. In present study, we quantified the relative importance of species in Carpinteria Salt Marsh food web by analyzing five centrality indices. The results showed that there were large differences in rankings species in terms of different centrality indices. Moreover, the correlation analysis of those centralities was studied in order to enhance the identifying ability of keystone species. The results showed that the combination of degree centrality and closeness centrality could better identify keystone species, and the keystone species in the CSM food web were identified as, *Stictodora hancocki*, small cyathocotylid, *Pygidiopsoides spindalis*, *Phocitreroides ovale* and *Parorchis acanthus*.

Key words keystone species; topological parameters; centrality indices; biological networks.

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1 Introduction

Food webs are complex ecological networks describing trophic relationships between species in a certain area (Pimm, 1982; Belgrano et al., 2005; Arie et al., 2007). If the entire food web is treated as a graph, the nodes in the graph represent different species (individuals) in the ecosystem and the edges denote the interactions between species (individuals). As a kind of network, food webs provide a new way to study communities (Albert and Barabasi, 2002; Newman, 2003). To some extent, such a network is a formalized description for complex relationships between species within the system.

The concept of keystone species originated from the thought that species diversity of an ecosystem was controlled by the predators in the food chains, and they affected many other creatures in the ecosystem.

Keystone species refer to those that biomass is disproportionate with its impact on the environment, and the extinction of keystone species may lead to the collapse of communities (Paine, 1969; Mills et al., 1993; Springer et al., 2003). The concept of keystone species means that an ecological community is not just a simple collection of species (Mouquet, 2013). As a result, the ecologically important species might not necessarily be the rare species conservation biologists always believed (Simberloff, 1998), because rare species are associated with the little biomass and abundance of species, and the importance of species is a kind of functional properties of the network. Therefore, the traditional protection pattern for rare species should be gradually transformed into the maintenance of keystone species (Wilson, 1987).

Keystone species strongly affect species richness and ecosystem dynamics (Piraino et al., 2002), so the research of keystone species is an important area for predicting and maintaining the stability of ecosystem (Naeem and Li, 1997; Tilman, 2000). Definition of keystone species emphasizes the functional advantages of species in the ecosystem, and whether a species is a keystone species depends upon if it has a consistent effect in ecological function (Power et al., 1996), namely its sensitivity to environmental changes, such as competition, drought, floods and other ecological processes. In the past, researchers used many field experimental methods to study keystone species, but they mainly focused on the impact of changes in the abundance of a species on the other species (Paine, 1992; Wootton, 1994; Berlow, 1999). The main identification methods include control simulation method (Paine, 1995; Bai, 2011), equivalent advantage method (Khanina, 1998; Ji, 2002), competitive advantage method (Yeaton, 1988; Bond, 1989), the relative importance of species interactions method (Tanner and Hughes, 1994), community importance index method (Power et al., 1996), keystone index method (Jordán et al., 1999) and functional importance index method (Hurlbert, 1997). However, these methods mainly concentrated on a few species. Thus researchers need to do an assessment of the interactions between species in the community before the experiment, in order to determine species not important or interesting. So these methods are obvious subjective and produce certain mistake on identifying keystone species (Wootton 1994; Bustamante et al., 1995). Furthermore, monitoring species reaction to changes in the external environment through the above experimental methods requires that experimenters have a high professional quality. And because of the longer experimental time span, greater cost (Ernest and Brown, 2001), as well as other factors during the experiment, they are only suitable for semi-artificial or simple controllable ecosystems. It is more difficult to judge whether a species is a keystone species based on certain characteristics of species (Menge et al., 1994). So far, we don't have a perfect and universally applicable method to identify keystone species.

Research of keystone species has evolved from the initial direct experimental methods to network/software analysis. For example, Libralato et al. (2006) analyzed keystone indicators of functional groups of a species or a group of species in food web model through the ecosystem modeling (the Ecopath with Ecosim, EwE), and then ranked the level of the key indicators to obtain the keystone species. Jordán et al. (2008) pointed out that there were at least two methods to quantitatively assess the importance of species in communities. One was the structural importance of network analysis and another for the functional importance of network analysis. So they calculated the structural importance and the functional importance of species in the food web in Prince William Sound by CosBiLaB Graph software, and evaluated the advantages and disadvantages of the two methods. They believed that the combination of these two methods in the future would be the most important way to research dynamic mechanism. Kuang and Zhang (2011) analyzed the topological properties of the food web in Carpinteria Salt Marsh and found that parasites played a very important role in the food web, and the addition of parasites in the food web would change some properties and greatly increase the complexity of the food web. Therefore, the relationship between keystone species and topological characteristics can provide an effective method to understand and describe the topological structures, dynamic characteristics and the

complexity of functions between species within the food web. And it also can provide valuable theory and evidence for conservation ecology, biodiversity, habitat management, as well as the dynamics and stability of the ecosystem.

Nevertheless, so far we lack of effective methods to identify keystone species and quantify their relative importance, so the quantitative assessment of species importance in the food web is becoming increasingly important and urgent (Paine, 1966; Power et al, 1996; Jordán, 2008). In recent years, there have been some major discoveries about the topological properties of complex systems (Strogatz, 2001; Albert and Barabási, 2002; Newman, 2003), and these also affect the definition and identification of keystone species. For example, the highly connected species were found to have more important influence on sustainability of food webs (Soulé and Simberloff, 1986), which promoted the generation of the concept of degree. Degree of nodes thus become the most widely used topological parameter to measure the keystone species (Dunne et al., 2002a). Degree refers to the direct impacts between species (Callaway et al., 2000; West, 2001; Zhang, 2011, 2012a, 2012b, 2012c, 2012d). However, indirect impacts between species are also important (Wootton, 1994; Huang, et al., 2008). For example, Darwin (1859) described the influence of cats on the clovers. Although indirect effects of chemical and behavioral studies may be difficult to quantify, some indirect impacts of network links have been proposed (Ulanowicz and Puccia, 1990; Patten, 1991). Thus the concept of centrality is proposed to address this problem. Centrality focuses on the indirect effects between species. The impacts of food webs are generally spread through indirect ways, so it may require detailed research and quantitative description on the effective range of indirect interactions from a specific point to the entire network (Jordán, 2001). In other words, it is necessary to determine how relevant these species are in the food web (Yodzis, 2000; Williams et al., 2002). The concept of centrality stemmed from the social network analysis (Wasserman and Faust, 1994), namely the ability of a node communicates with other nodes or the intimacy of a node with the others (Go'mez et al., 2003). These have resulted in a series of topological parameters relating to the relative importance of a node, such as degree centrality, betweenness centrality, closeness centrality, clustering coefficient centrality, eigenvector centrality and information centrality, etc. In present paper, we used various methods to detect and quantify relative importance of species in a famous food web, CSM (Carpinteria Salt Marsh) food web, reported by Lafferty et al. (2006a, 2006b, 2008), and further studied the correlation between topological parameters of the food web, aiming to evaluate the effectiveness of various methods in quantifying relative importance of species and detecting the keystone species in the food webs.

2 Materials and Methods

2.1 Data source

Data were collected from the food web, Carpinteria Salt Marsh, California, reported by Lafferty et al. (2006a, 2006b, 2008) (<http://www.nceas.ucsb.edu/interactionweb/html/carpinteria.html>). CSM food web includes four sub-webs, predator-prey sub-web, predator-parasite sub-web, parasite-host sub-web, and parasite-parasite sub-web.

2.2 Methods

2.2.1 Pajek software

Pajek is a software platform for network analysis, which contains various methods/algorithms/models on analysis of topological properties.

2.2.2 Centrality measures

Centrality indices are used to measure impact and importance of nodes in a network. The most commonly used centrality indices are degree centrality, betweenness centrality, closeness centrality, clustering coefficient

centrality and eigenvector centrality (Navia et al., 2010; Zhang, 2012a, b).

(1) Degree centrality (DC)

DC is the simplest measure which considers the degree of a node (species) only. The degree of species i is: $D_i = D_{in,i} + D_{out,i}$, where $D_{in,i}$: number of prey species of species i , and $D_{out,i}$: number of predator species of species i . The degree of species was calculated by Net/Partitions/DC/All in Pajek.

(2) Betweenness centrality (BC)

BC is calculated by the following formula

$$BC_i = 2 \sum_{j \neq k} g_{jk}(i) / g_{jk} / [(N-1)(N-2)]$$

where $i \neq j \neq k$, g_{jk} : the shortest path between species j and k , $g_{jk}(i)$: number of the shortest paths containing species i , N : total number of species in the food web. A greater BC_i means that the effect of losing species i will promptly disperse across the food web (Zhang, 2012a, b).

(3) Closeness centrality (CC)

CC_i refers to the mean shortest path of species i

$$CC_i = (N-1) / \sum_{j=1}^N d_{ij}$$

where $i \neq j$, d_{ij} is the length of the shortest path between species i and j . A greater CC_i means a more importance of species i .

In Pajek, we use Net/Vector/Centrality/Closeness/All and Net/Vector/Centrality/Betweenness to calculate BC (Wasserman and Faust, 1994).

(4) Clustering coefficient centrality (CU)

Clustering coefficient centrality denotes the ratio of the actual edges E_i of node i connected with its neighbors divided by the most possible edges $D_i(D_i-1)/2$ between them (Watts and Strogatz, 1998). In other words, it refers to the ratio of the directly connected neighboring pairs divided by all the neighboring pairs in the neighboring points of the node, that is

$$CU_i = 2E_i / [D_i(D_i-1)]$$

It measures how close the current node is to its neighboring nodes. The average clustering coefficient of all nodes is the clustering coefficient of the entire network. Obviously, the clustering coefficient of a network is weighted by the clustering coefficient of all nodes whose degree must be at least 2. $0 \leq CU \leq 1$; if $CU=0$, all nodes in the network are isolated, and if $CU=1$, the network is fully connected. Furthermore, studies have shown that clustering coefficient is related to network modularity. Clustering coefficient of the entire network reflects the overall trend of all the nodes gathering into a module (Eisenberg and Levanon, 2003; Ravasz et al, 2002).

(5) Eigenvector centrality (EC)

Eigenvector centrality is the dominant eigenvector of the adjacency matrix A of the network (Bonacich, 1987), i.e., the extent of a node connected to the node with the highest eigenvector centrality. In the word of social networks, a person tends to occupy the central place more likely if he (she) has contacted more people in the center position. Eigenvector centrality reflects the prestige and status of nodes. This measure tries to find the keystone node in the entire network rather than in the local structure. Here, eigenvector is e , and $\lambda e = Ae$, where A is the adjacency matrix of a food web. Therefore, the EC of node i is

$$EC_i = e_1(i)$$

where e_1 is the eigenvector corresponding to the maximum eigenvalue λ_1 . A greater value of EC_i means a greater number of the neighboring nodes connected with node i , and it indicates that the node is in the core

position.

3 Results

3.1 Degree centrality

As shown in Fig. 1, 2 and Table 1, the species with the greater DC values in the full CSM food web are largely consistent with that in the predator-parasite sub-web, parasite-parasite sub-web and parasite-host sub-web. And these species are substantially parasites. The species with the maximum DC value in the predator-prey sub-web is *Pachygrapsus crassipes*, and the species with the fourth DC value is *Willet*. Although DC values of the two species are larger, they are slightly lower than nine parasite species, such as *Mesostephanus appendiculatoides*, etc. In addition, the basal species, Marine detritus, is of greater importance also.

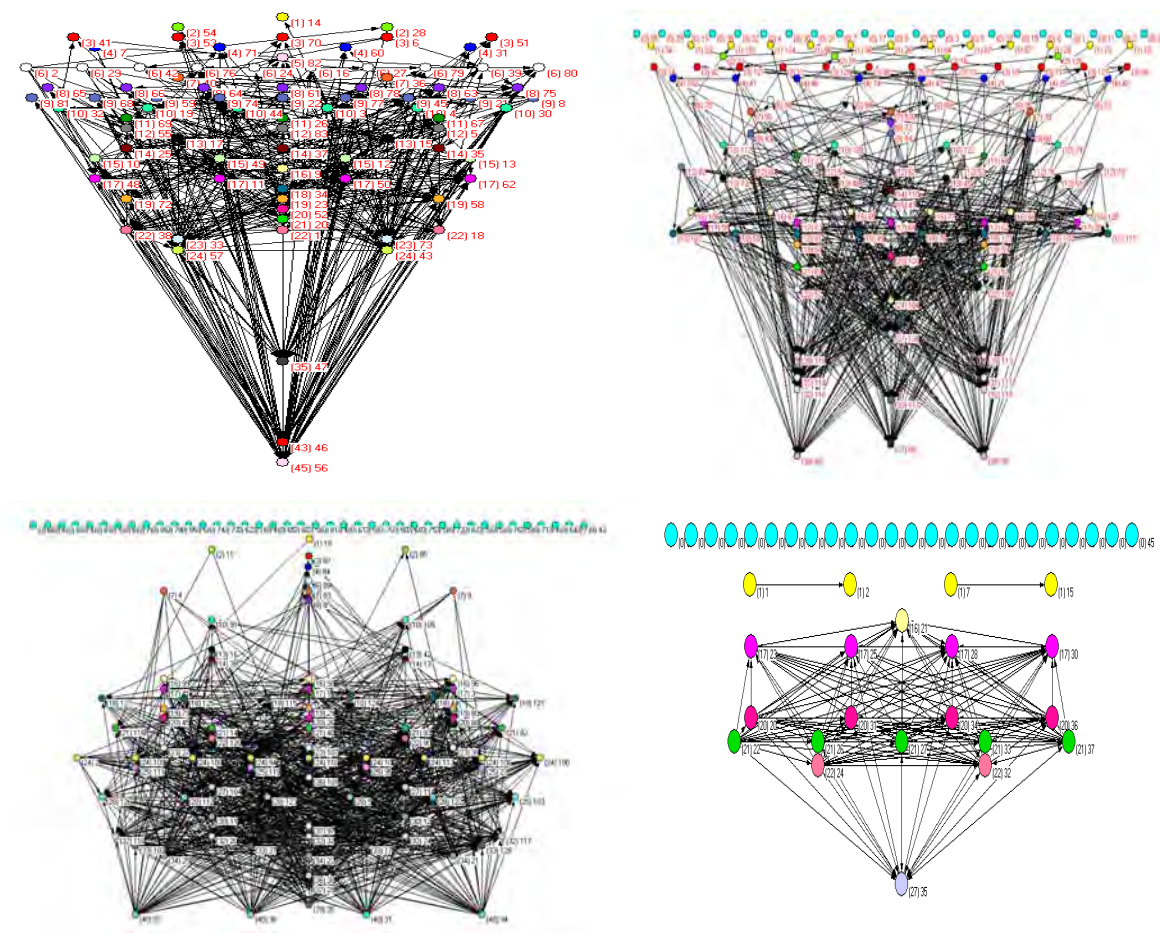


Fig. 1 Results of degree centrality for the four sub-webs of CSM food web (upper left: predator-prey sub-web; upper right: predator-parasite sub-web; bottom right: parasite-parasite sub-web; bottom left: parasite-host sub-web). The numbers in parentheses are total links (degree, or incoming degree + outgoing degree) and the numbers outside parentheses are species ID codes. The ID codes of different sub-webs are different from the original species.

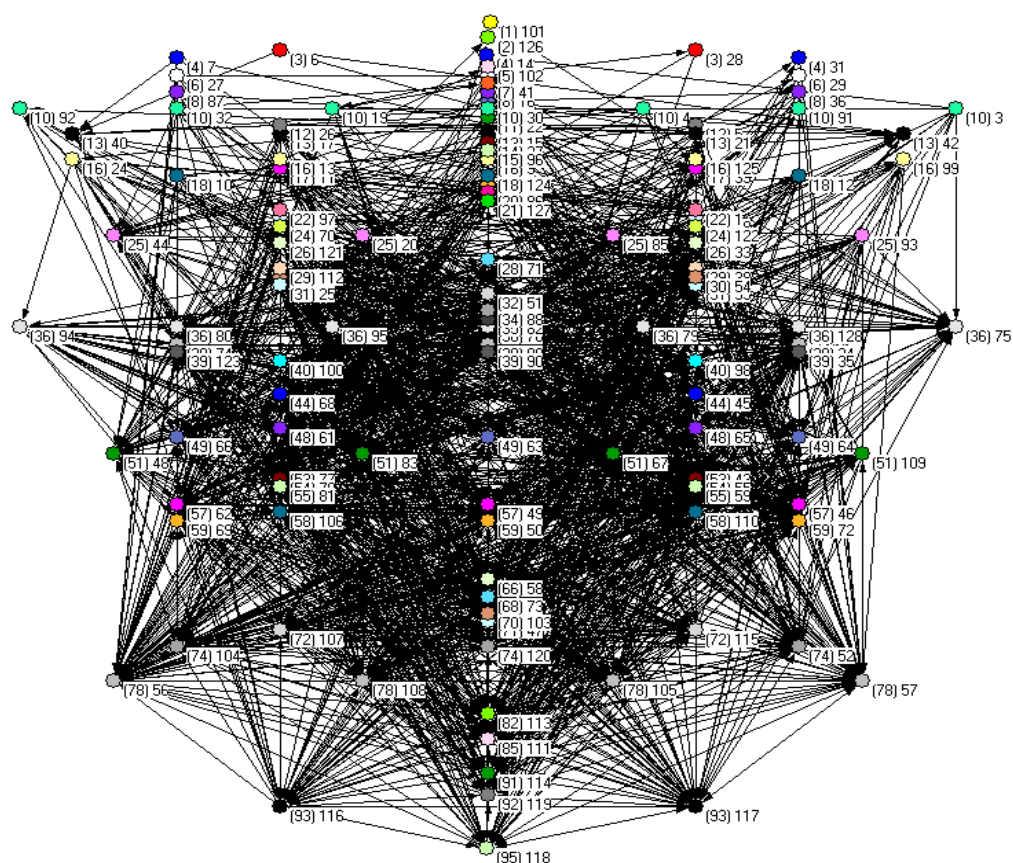


Fig. 2 Results of degree centrality for the full CSM food web. The numbers in parentheses are total links (degree, or incoming degree + outgoing degree) and the numbers outside parentheses are species ID codes.

Table 1 Species with greater DC values in the full CSM food web and four sub-webs.

Predator-prey sub-web		Predator-parasite sub-web		Parasite-parasite sub-web		Parasite-host sub-web		Full CSM food web	
ID	Species	ID	Species	ID	Species	ID	Species	ID	Species
56	<i>Pachygrapsus crassipes</i>	90	<i>Culex tarsalis</i>	118	<i>Mesostephanus appendiculatoides</i>	117	<i>Stictodora hancocki</i>	118	<i>Mesostephanus appendiculatoides</i>
46	<i>Hemigrapsus oregonensis</i>	89	<i>Aedes taeniorhynchus</i>	115	<i>Renicola cerithidicola</i>	114	<i>Phocitrema ovale</i>	117	<i>Stictodora hancocki</i>
47	<i>Fundulus parvipinnis</i>	98	Plasmodium	107	<i>Renicola buchmanani</i>	119	<i>Pygidiopsoides spindalis</i>	116	Small cyathocotyloid
57	Willet	117	<i>Stictodora hancocki</i>	120	Microphallid 1	116	Small cyathocotyloid	119	<i>Pygidiopsoides spindalis</i>
43	<i>Cleavlandia ios</i>	119	<i>Pygidiopsoides spindalis</i>	116	Small cyathocotyloid	118	<i>Mesostephanus appendiculatoides</i>	114	<i>Phocitrema ovale</i>
73	<i>Gillycthyis mirabilis</i>	116	Small cyathocotyloid	110	Large xiphideocercaria	111	<i>Parorchis acanthus</i>	111	<i>Parorchis acanthus</i>
33	<i>Macoma nasuta</i>	114	<i>Phocitrema ovale</i>	109	<i>Catantropis johnstoni</i>	113	<i>Cloacitrema michiganensis</i>	113	<i>Cloacitrema michiganensis</i>
18	<i>Anisogammar</i>	111	<i>Parorchis</i>	105	<i>Probolocoryphe</i>	104	<i>Himasthla</i>	105	<i>Probolocoryphe</i>

	<i>us confervicolus</i>		<i>acanthus</i>		<i>uca</i>		<i>rhigedana</i>		<i>uca</i>
1	Marine detritus	118	<i>Mesostephanus appendiculatoides</i>	119	<i>Pygidiopsoidea spindalis</i>	105	<i>Probolocoryphe uca</i>	108	<i>Acanthoparyphium sp.</i>
38	<i>Geonemertes</i>	113	<i>Cloacitrema michiganensis</i>	117	<i>Stictodora hancocki</i>	108	<i>Acanthoparyphium sp.</i>	56	<i>Pachygrapsus crassipes</i>
		31	Mosquito larva					57	Willet

3.2 Betweenness centrality

As illustrated in Fig. 3 and 4, the BC values of all nodes in the predator-parasite sub-web and parasite-host sub-web are 0, because these species do not locate between other species in the network. But the radius of *Mesostephanus appendiculatoides* in the parasite-parasite sub-web is very obvious, indicating that some species in the parasite-parasite sub-web need to go through *Mesostephanus appendiculatoides*. Once this species is removed, all the interaction chains will collapse and largely destruct the whole sub-web. From Table 2, the BC values of the top four species in the CSM food web are identical with that in the predator-prey sub-web, while some parasites with larger DC values, such as *Mesostephanus appendiculatoides*, etc., whose BC values are lower than that of some free-living species, such as *Hemigrapsus oregonensis*. It indicates that the nutritional flow of free-living species in the food web has a greater effect than parasites.

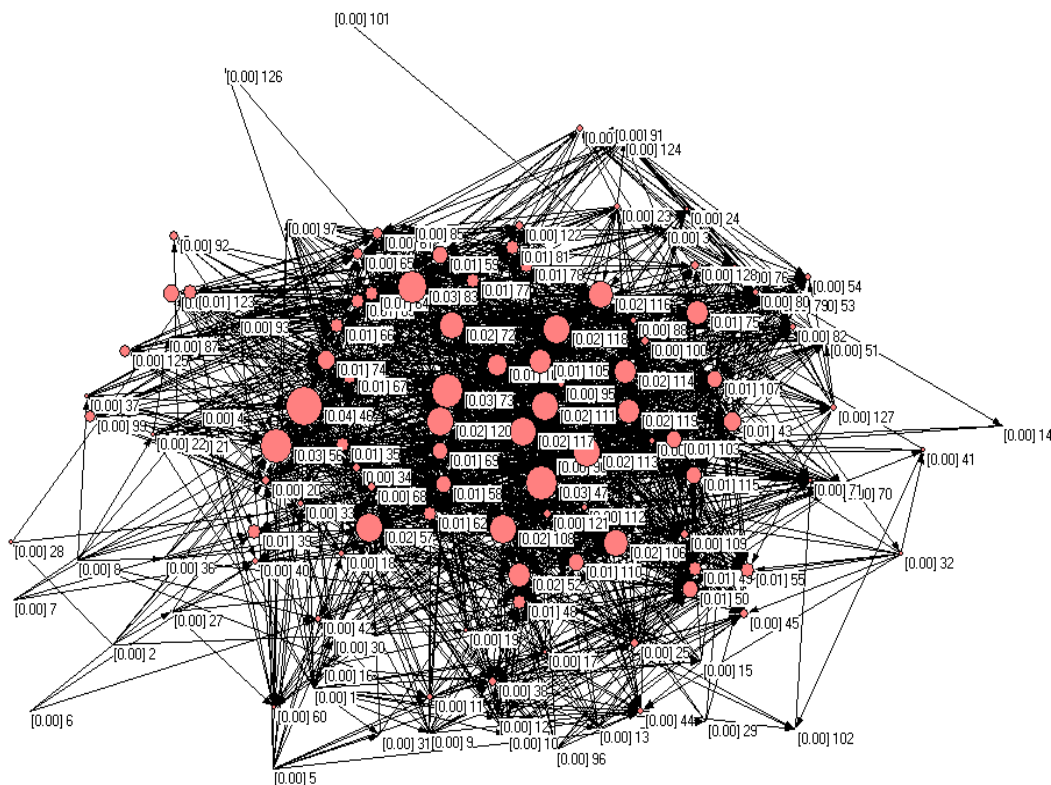


Fig. 3 Results of betweenness centrality for the full CSM food web. The numbers in parentheses are betweenness centralities and the numbers outside parentheses are species ID codes.

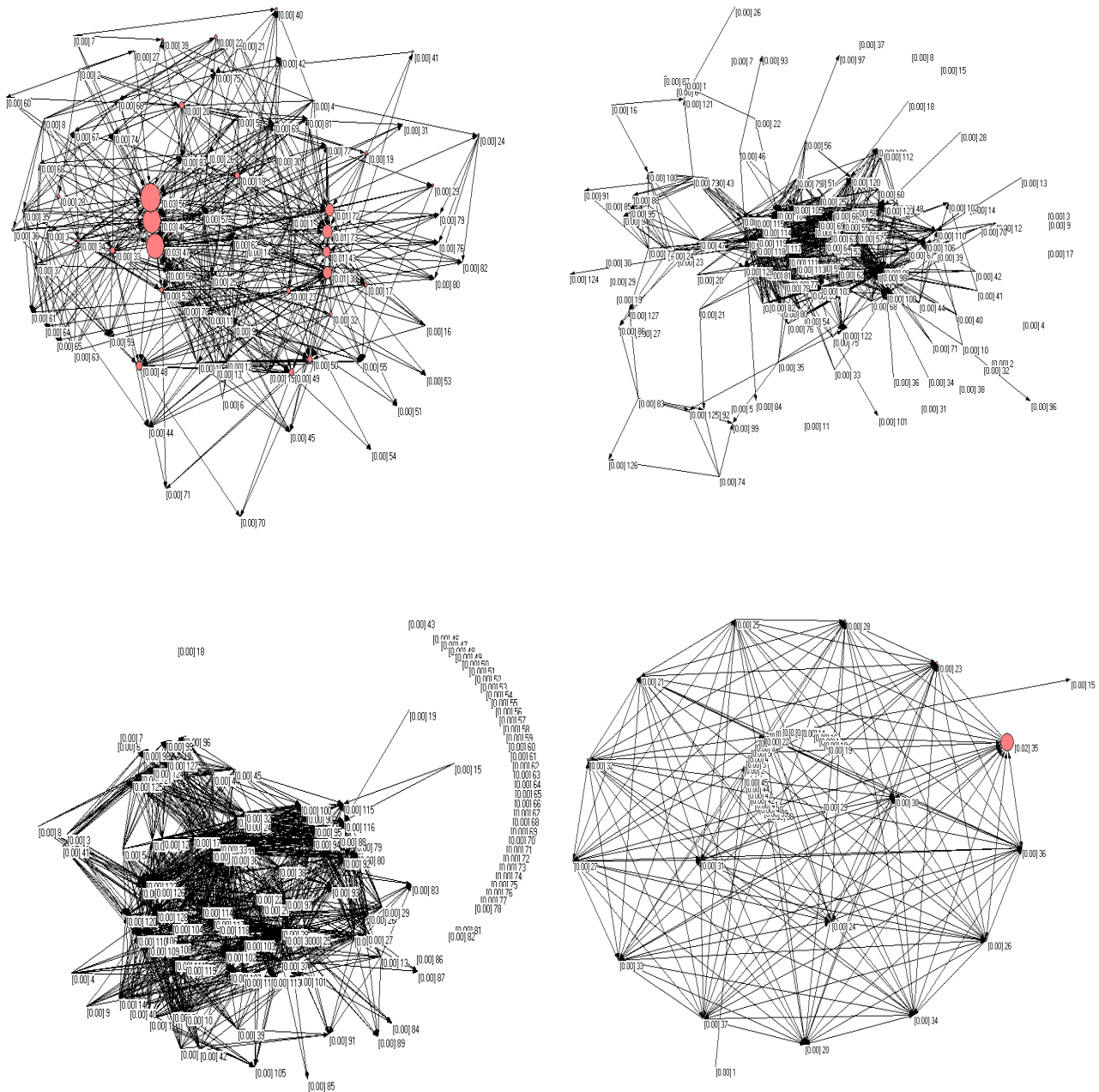


Fig. 4 Results of betweenness centrality for the four sub-webs of CSM food web (upper left: predator-prey sub-web; upper right: predator-parasite sub-web; bottom right: parasite-parasite sub-web; bottom left: parasite-host sub-web). The numbers in parentheses are betweenness centralities and the numbers outside parentheses are species ID codes. The ID codes of different sub-webs are different from the original species. The size of the node relates to the value of BC; the greater BC is, the bigger the node radius is. The species ID codes of different sub-webs are different from the original species, and the magnification of each figure is different.

Table 2 Species with greater BC values in the full CSM food web and four sub-webs.

Predator-prey sub-web		Predator-parasite sub-web		Parasite-parasite sub-web		Parasite-host sub-web		Full CSM food web	
ID	Species	ID	Species	ID	Species	ID	Species	ID	Species
46	<i>Hemigrapsus oregonensis</i>			118	<i>Mesostephanus appendiculatoides</i>	46	<i>Hemigrapsus oregonensis</i>		
56	<i>Pachygrapsus crassipes</i>			106	Himasthla species B	56	<i>Pachygrapsus crassipes</i>		
47	<i>Fundulus parvipinnis</i>			109	<i>Catatropis johnstoni</i>	47	<i>Fundulus parvipinnis</i>		
73	<i>Gillychthys mirabilis</i>			111	<i>Parorchis acanthus</i>	73	<i>Gillychthys mirabilis</i>		
72	<i>Leptocottus armatus</i>			115	<i>Renicola cerithidicola</i>	83	<i>Triakis semifasciata</i>		
38	Geonemertes			105	<i>Probolocorypha uca</i>	72	<i>Leptocottus armatus</i>		
43	Cleavlandiaios			110	Large xiphideocercaria	57	Willet		
48	Western Sandpiper			116	Small cyathocotylid	108	<i>Acanthoparyphium sp.</i>		
50	Least Sandpiper			120	Microphallid 1	52	Dowitcher		
18	<i>Anisogammarus confervicolus</i>					113	<i>Cloacitrema michiganensis</i>		
11	Phoronid					115	<i>Renicola cerithidicola</i>		
						106	Himasthla species B		
						118	<i>Mesostephanus appendiculatoides</i>		
						116	Small cyathocotylid		
						117	<i>Stictodora hancocki</i>		
						111	<i>Parorchis acanthus</i>		
						119	<i>Pygidiopsoides spindalis</i>		
						120	Microphallid 1		

3.3 Closeness centrality

CC values of species in food webs increases with the increase of species richness and completeness of food web. Connection between species in the full CSM food web is closer than the other four sub-webs (Fig. 5 and 6, Table 3). Combined with Table 2, the species with the maximum CC value is *Pachygrapsus crassipes* (species 56) in the full CSM food web, and it is also the greatest in the predator-prey sub-web, indicating it is closer than other species in food web. The species with the tenth CC value is *Fundulus parvipinnis* (species 47)

in the full CSM food web, but it is the third in the predator-prey sub-web, just following behind *Pachygrapsus crassipes* and *Hemigrapsus oregonensis*.

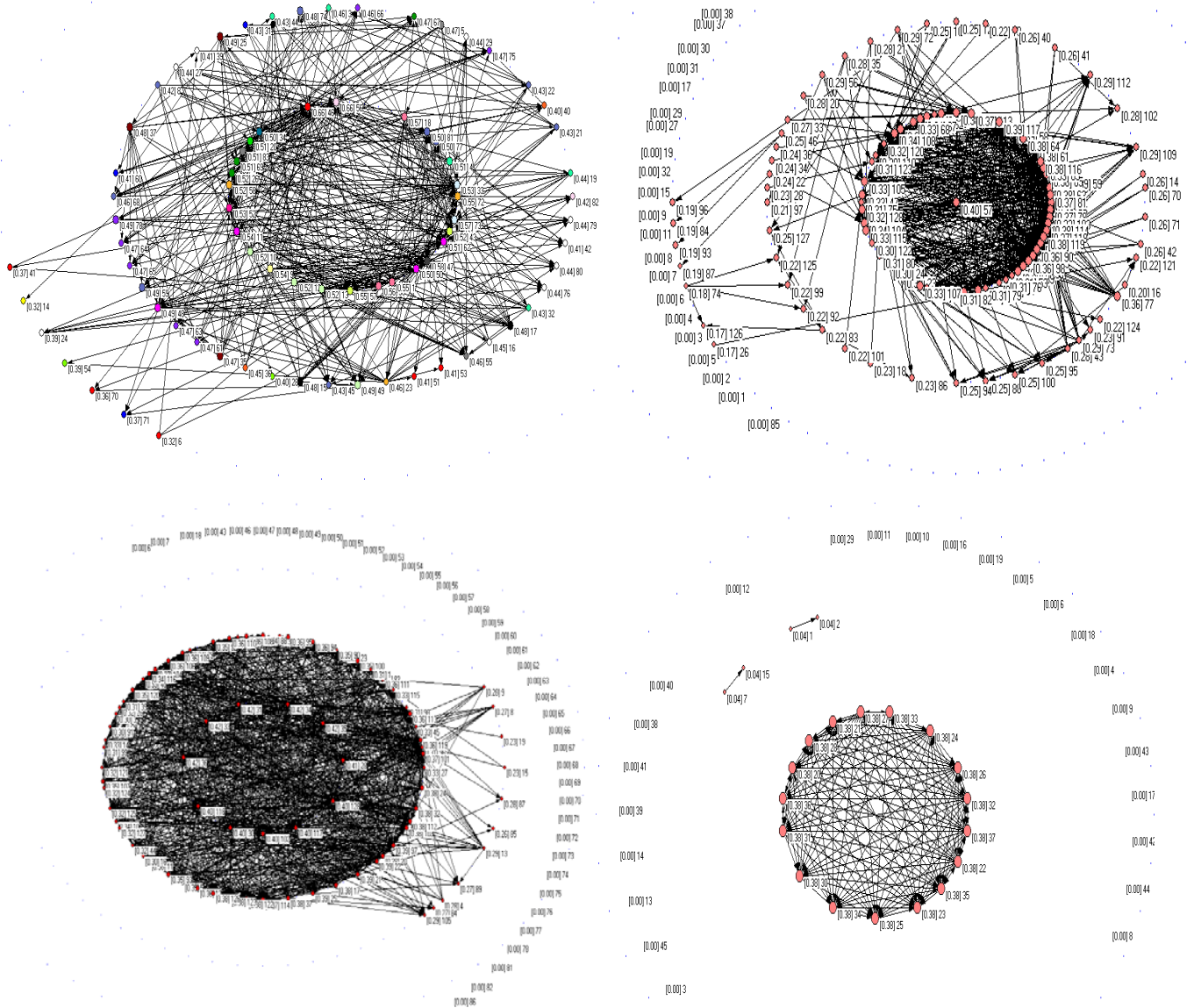


Fig. 5 Results of closeness centrality for the four sub-webs of CSM food web (upper left: predator-prey sub-web; upper right: predator-parasite sub-web; bottom right: parasite-parasite sub-web; bottom left: parasite-host sub-web). The numbers in parentheses are closeness centralities and the numbers outside parentheses are species ID codes. Species ID codes of different sub-webs are different from the original species.

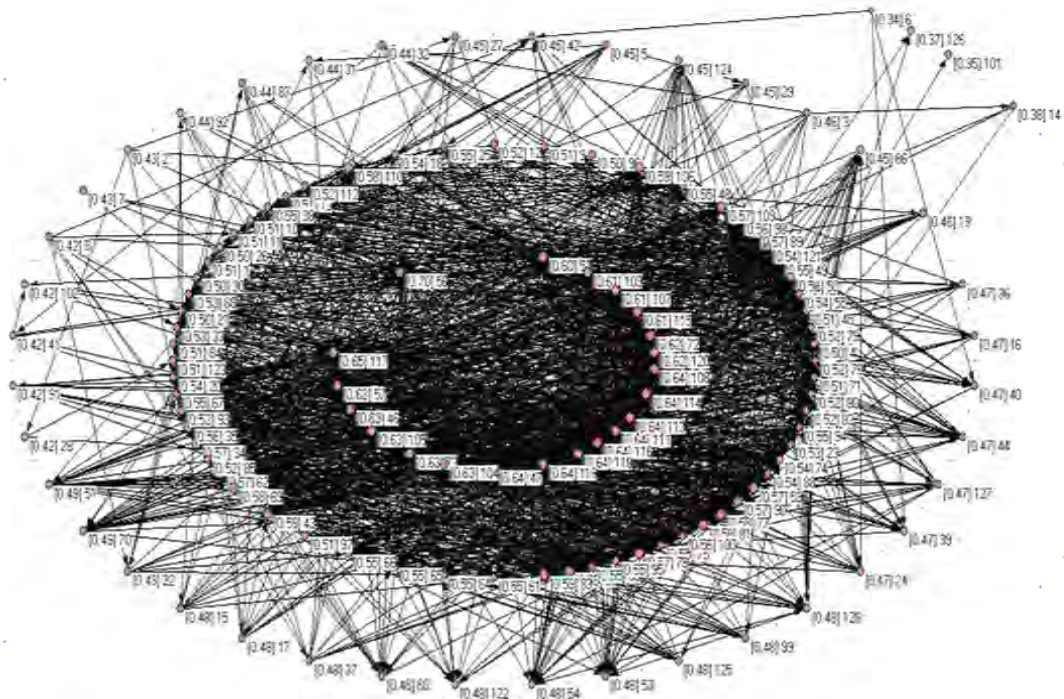


Fig. 6 Results of closeness centrality for the full CSM food web. The numbers in parentheses are closeness centralities and the numbers outside parentheses are species ID codes.

Table 3 Species with greater CC values in the full CSM food web and four sub-webs.

Predator-prey sub-web		Predator-parasite sub-web		Parasite-parasite sub-web		Parasite-host sub-web		Full CSM food web	
ID	Species	ID	Species	ID	Species	ID	Species	ID	Species
56	<i>Pachygrapsus crassipes</i>	52	Dowitcher	116	Small cyathocotylid	119	Pygidiopoides spindalis	56	<i>Pachygrapsus crassipes</i>
46	<i>Hemigrapsus oregonensis</i>	57	Willet	107	<i>Renicola buchmanii</i>	116	Small cyathocotylid	117	<i>Stictodora hancocki</i>
47	<i>Funduluspar vipinnis</i>	58	Black-bellied Plover	109	<i>Catatropis johnstoni</i>	114	<i>Phocitremaoides ovale</i>	116	Small cyathocotylid
73	<i>Gillythys mirabilis</i>	59	California Gull	115	<i>Renicola cerithidicola</i>	117	<i>Stictodora hancocki</i>	119	<i>Pygidiopoides spindalis</i>
18	<i>Anisogammarus confervicolus</i>	69	Clapper rail	120	Microphallid 1	118	<i>Mesostephanus appendiculatoides</i>	114	<i>Phocitremaoides ovale</i>
38	Geonemertes	117	<i>Stictodora hancocki</i>	105	<i>Probolocoryphe uca</i>	111	<i>Parorchis acanthus</i>	111	<i>Parorchis acanthus</i>
33	Macomanasuta	62	Marbled Godwit	118	<i>Mesostephanus appendiculatoides</i>	83	<i>Triakis semifasciata</i>	113	<i>Cloacitrema michiganensis</i>
72	<i>Leptocottus armatus</i>	63	Ring-billed gull	106	Himasthla species B	72	<i>Leptocottus armatus</i>	118	<i>Mesostephanus appendiculatoides</i>
1	Marine detritus	64	Western Gull	108	<i>Acanthoparyphium sp.</i>	57	Willet	108	<i>Acanthoparyphium sp.</i>

57	Willet	65	Bonaparte's Gull	117	<i>Stictodora hancocki</i>	113	<i>Cloacitremamic higanensis</i>	47	<i>Fundulus parvipinnis</i>
9	Oligochaete	111	<i>Parorchis acanthus</i>	113	<i>Cloacitrema michiganensis</i>	73	<i>Gillythys mirabilis</i>		
11	Phoronid	114	<i>Phocitre moi des ovale</i>	114	<i>Phocitre moi des ovale</i>				
		116	Small cyathocotyled	119	<i>Pygidiopsoi des spindalis</i>				
		119	<i>Pygidiopsoi des spindalis</i>	111	<i>Parorchis acanthus</i>				
		111	<i>Parorchis acanthus</i>						

3.4 Clustering coefficient centrality

CU values of predator-parasite sub-web and parasite-host sub-web appear in two patterns: one for the degree values of some nodes are less than 2, and the CU values of these nodes are 999999998 in the Pajek; another for the neighboring nodes of one node are less than 2, and the CU values of these nodes are 0. From Table 4, we can find that the CU rankings of nodes in the full CSM food web and predator-prey sub-web are really different.

Table 4 Species with greater CU values in the full CSM food web and four sub-webs.

Predator-prey sub-web		Predator-parasite sub-web		Parasite-parasite sub-web		Parasite-host sub-web		Full CSM food web	
ID	Species	ID	Species	ID	Species	ID	Species	ID	Species
60	Whimbrel			104	<i>Himasthla rhigedana</i>			25	<i>Cerithidea californica</i>
81	Pied Billed Grebe			106	Himasthla species B			109	<i>Catatropis johnstoni</i>
38	Geonemertes			108	<i>Acanthoparyphium sp.</i>			70	Cooper's Hawk
78	Black-crowned Night heron			111	<i>Parorchis acanthus</i>			34	Protothaca
61	Mew Gull			113	<i>Cloacitrema michiganensis</i>			110	Large xiphideocercaria
63	Ring-billed gull			103	<i>Euhaplorchis californiensis</i>			35	<i>Tagelus spp.</i>
64	Western Gull			114	<i>Phocitre moi des ovale</i>			106	Himasthla species B
65	Bonaparte's Gull			117	<i>Stictodora hancocki</i>			71	Northern Harrier
36	Cryptomya			119	<i>Pygidiopsoi des spindalis</i>			115	<i>Renicola cerithidicola</i>
77	Snowy Egret			105	<i>Probolocoryphe uca</i>			103	<i>Euhaplorchis californiensis</i>
68	Bufflehead			107	<i>Renicola buchanani</i>			107	<i>Renicola buchanani</i>

3.5 Eigenvector centrality

Species with greater EC values in the full CSM food web are largely consistent with that in the predator-prey sub-web (Table 5; Fig. 7, 8). Species with greater EC values in the full CSM food web and predator-prey sub-web are free-living species, rather than parasites. Willet (species ID 57) has the largest EC value. Otherwise, species with larger EC values in predator-parasite sub-web and parasite-parasite sub-web are parasites.

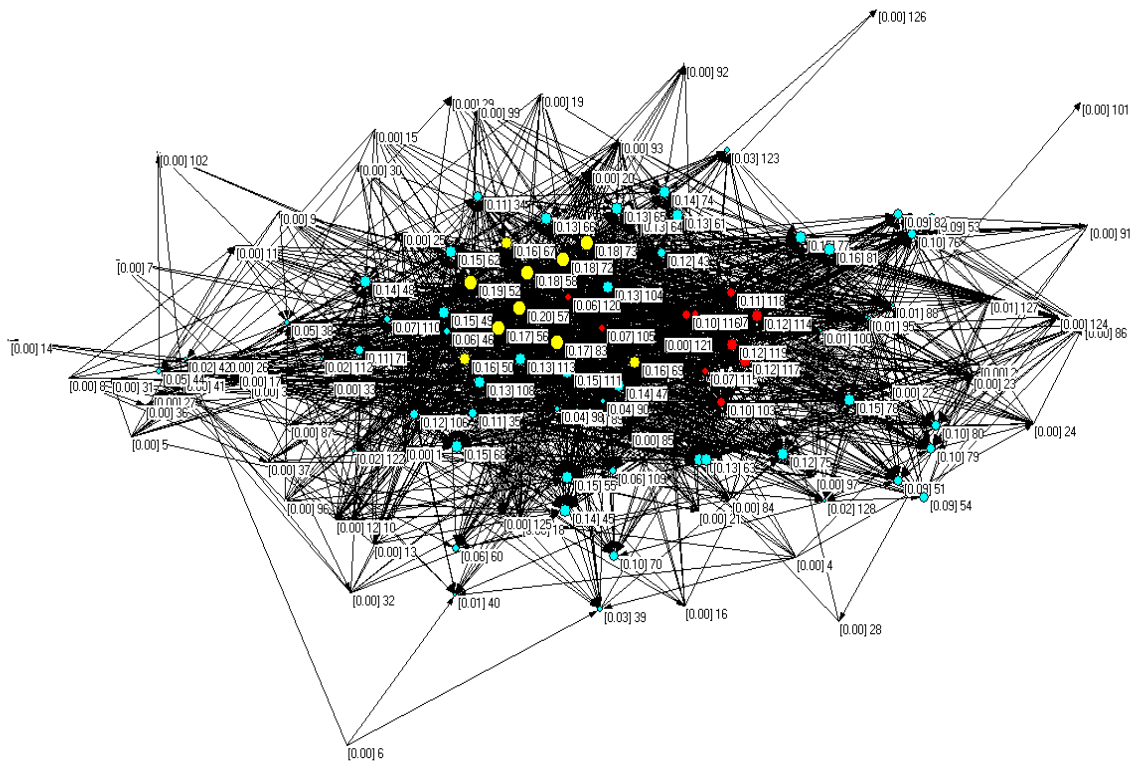
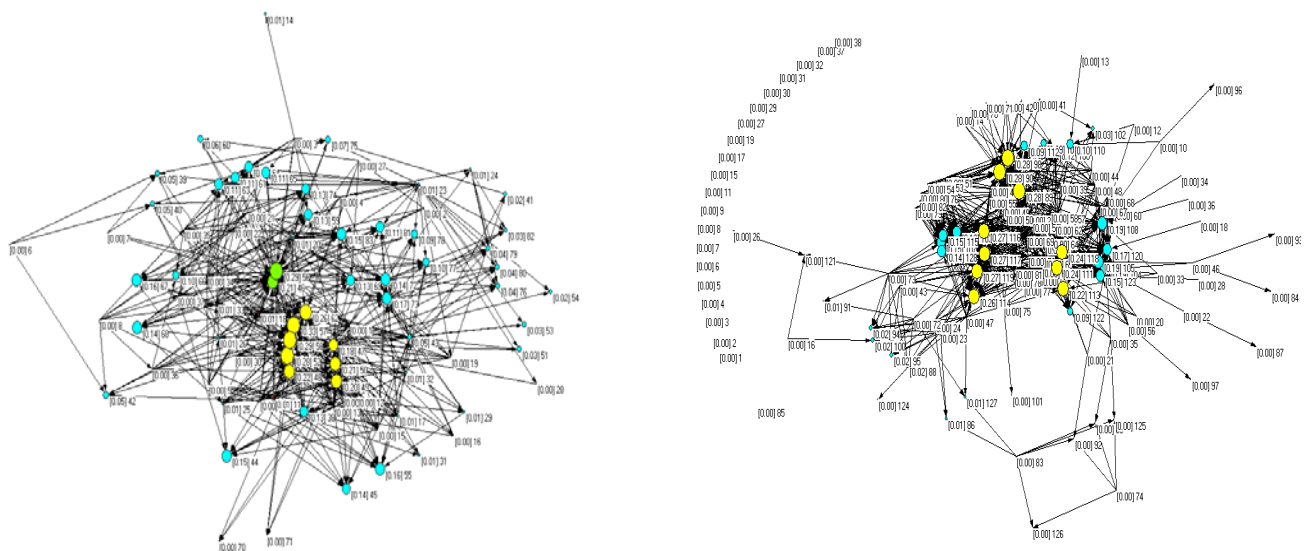


Fig.7 Results of eigenvector centrality for the full CSM food web. The numbers in parentheses are eigenvector centralities and the numbers outside parentheses are species ID codes.



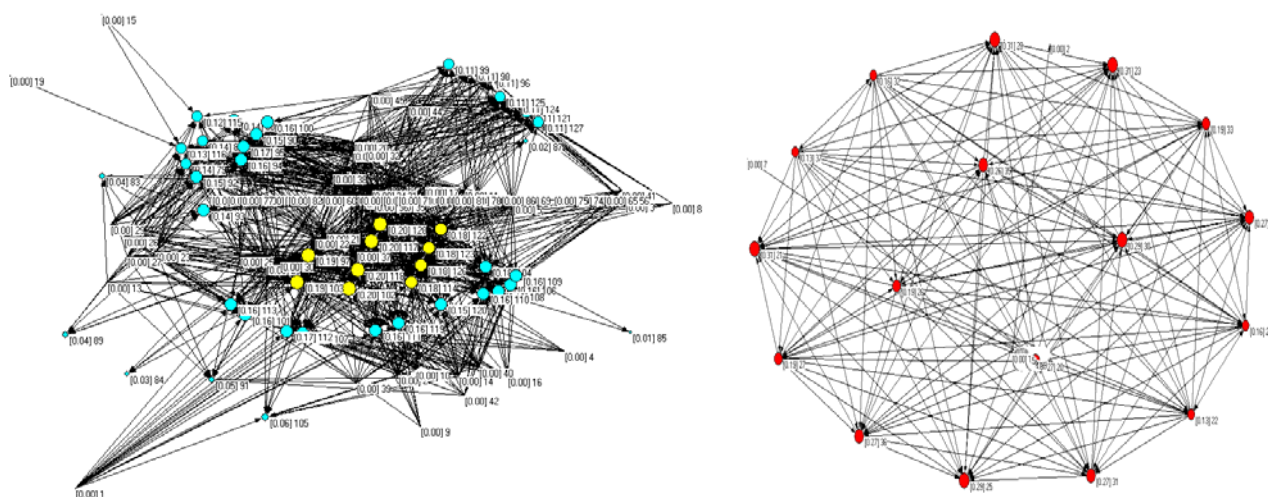


Fig. 8 Results of eigenvector centrality for the four sub-webs of CSM food web (upper left: predator-prey sub-web; upper right: predator-parasite sub-web; bottom right: parasite-parasite sub-web; bottom left: parasite-host sub-web). The numbers in parentheses are eigenvector centralities and the numbers outside parentheses are species ID codes. Species ID codes of different sub-webs are different from the original species.

Table 5 Species with greater eigenvector values in the full CSM food web and four sub-webs.

Predator-prey sub-web		Predator-parasite sub-web		Parasite-parasite sub-web		Parasite-host sub-web		Full CSM food web	
ID	Species	ID	Species	ID	Species	ID	Species	ID	Species
57	Willet	98	Plasmodium	111	<i>Parorchis acanthus</i>	83	<i>Triakis semifasciata</i>	57	Willet
58	Black-bellied Plover	90	<i>Culex tarsalis</i>	106	Himasthla species B	72	<i>Leptocottus armatus</i>	52	Dowitcher
56	<i>Pachygrapsus crassipes</i>	89	<i>Aedestaeniorhynchus</i>	104	<i>Himasthla Rhigedana</i>	73	<i>Gilylthys mirabilis</i>	58	Black-bellied Plover
52	Dowitcher	116	Small cyathocotylid	113	<i>Cloacitrema michiganensis</i>	57	Willet	72	<i>Leptocottus armatus</i>
62	Marbled Godwit	117	<i>Stictodora hancocki</i>	108	<i>Acanthoparyphium sp.</i>	52	Dowitcher	73	<i>Gilylthys mirabilis</i>
48	Western Sandpiper	119	<i>Pygidiopsoides spindalis</i>	119	<i>Pygidiopsoides Spindalis</i>	58	Black-bellied Plover	56	<i>Pachygrapsus crassipes</i>
46	<i>Hemigrapsus oregonensis</i>	114	<i>Phocitrema ovale</i>	117	<i>Stictodora Hancocki</i>	77	Snowy Egret	83	<i>Triakis semifasciata</i>
50	Least Sandpiper	118	<i>Mesostephanus Appendiculatoides</i>	114	<i>Phocitrema Ovale</i>	78	Black-crowned Night heron	67	Surf Scoter
59	California Gull	111	<i>Parorchis acanthus</i>	103	<i>Euhaplorchis californiensis</i>	81	Pied Billed Grebe	50	Least Sandpiper
47	<i>Fundulus parvipinnis</i>	113	<i>Cloacitrema michiganensis</i>	118	<i>Mesostephanus Appendiculatoides</i>	69	Clapper rail	69	Clapper rail

3.6 Analysis of DC, BC, CC, CU and EC

According to Table 6, the change of species ranking with CU is larger: the top ten species are totally different with species ranking by remaining four indices. The DC and CC analysis in the full CSM food web (species ID No. 1 to No. 128) showed that the parasites are more important than free-living species, while reverse results were obtained from BC and EC analysis. The more important parasites calculated from DC and CC analysis are *Stictodora hancocki*, small cyathocotylid, *Pygidiopsoides spindalis*, *Phocitreroides ovale* and *Parorchis acanthus* (species No. 117, 116, 119, 114, and 111, respectively). Species ranking by BC, DC and CC in the full CSM food web (species ID No. 1 to No. 83) are basically consistent with the species in the predator-prey sub-web, and the relative important species are *Pachygrapsus crassipes*, *Hemigrapsus oregonensis* and *Fundulus parvipinnis* (species ID No.56, 46, and 47, respectively). These results show that parasites in the full CSM food web do not change the relative importance of free-living species, but increase the DC value of free-living species.

Table 6 The top ten species (ID codes) ranking by DC, BC, CC, CU and EC in the full CSM food web and predator-prey sub-web, respectively.

	DC	BC	CC	CU	EC
Full CSM food web (Species ID No.1 to No. 128)	118	46	56	25	57
	117	56	117	109	52
	116	73	116	70	58
	119	83	119	34	72
	114	47	114	110	73
	111	72	111	35	56
	113	57	113	106	83
	105	108	118	71	67
	108	52	108	115	50
	56	113	47	103	69
Full CSM food web (Species ID No.1 to No. 83)	56	46	56	25	57
	57	56	47	70	52
	52	73	46	34	58
	47	83	57	35	72
	73	47	73	71	73
	58	72	72	43	56
	68	57	52	19	83
	50	52	58	16	67
	72	75	43	12	50
46	74	83	23	69	
Predator-prey sub-web (Species No.1 to No. 83)	56	56	56	60	57
	46	46	46	81	58
	47	47	47	38	56
	43	73	73	78	52
	57	72	18	61	62
	73	38	38	63	48
	33	43	33	64	46
	18	48	72	65	50
	1	50	1	36	59
38	18	57	77	47	

3.7 Pearson correlation of five topological indices

As can be seen from Table 7, the Pearson's correlations of DC and CC are the largest in the full CSM food web and predator-prey sub-web (0.917 and 0.877, respectively), so DC and CC are strongly correlated. DC mainly measures the importance of a node in the local scope, and thus denotes the self-correlation of the node. CC is a measure of the ability of one node for controlling the other nodes, and denotes the centralization extent of a node. Therefore, DC and CC analysis synthesizes the importance of a node locally and globally. Table 6 demonstrates that the keystone species in the CSM food web are *Stictodora hancocki*, small cyathocotylid, *Pygidiopsoides spindalis*, *Phocitremonoides ovale* and *Parorchis acanthus* (species ID No. 117, 116, 119, 114, and 111, respectively).

Table 7 Pearson's correlation coefficients of five topological indices.

Pearson's correlation coefficient analysis		DC	BC	CC	CU	EC
DC	Full CSM food web	1.000	0.773	0.917	0.483	0.800
	predator-prey sub-web	1.000	0.789	0.877	0.053	0.498
BC	Full CSM food web	0.773	1.000	0.754	0.338	0.625
	predator-prey sub-web	0.789	1.000	0.595	-0.032	0.402
CC	Full CSM food web	0.917	0.754	1.000	0.525	0.695
	predator-prey sub-web	0.877	0.595	1.000	0.360	0.478
CU	Full CSM food web	0.483	0.338	0.525	1.000	0.307
	predator-prey sub-web	0.053	-0.032	0.360	1.000	0.205
EC	Full CSM food web	0.800	0.625	0.695	0.307	1.000
	predator-prey sub-web	0.498	0.402	0.478	0.205	1.000

3.8 Efficiency analysis of the full CSM food web

Table 8 indicates the changes of topological properties after removing different keystone species from the full CSM food web. The major topological changes before and after removing keystone species include

- (1) Number of top species and basal species does not change. The top species are not necessarily the keystone species of the food web.
- (2) Number of links and cycles reduces significantly. It means that the keystone species play an important role in the food web. There are less cycles between predators and preys due to the removal of parasites.
- (3) Number of total links and maximum links, and link density and connectance decreases respectively.
- (4) The maximum chain length did not change significantly.

Compared with the results of removing important species, the changes of the full food web are not significant in terms of all indices.

In conclusion, the topological structure of the full food web changed significantly after removing the keystone species, which further validates the results achieved previously.

Table 8 Comparison of topological properties of the full CSM food web with removed different keystone species.

	Removed species No.117	Removed species No.116	Removed species No.119	Removed species No.114	Removed species No.111	Removed species No.56	Full CSM food web
Number of species, S	127	127	127	127	127	127	128
Number of links, L	2197	2197	2198	2199	2205	2212	2290
Number of top species, T	3	3	3	3	3	3	3
Number of intermediate species, I	116	116	116	116	116	116	117
Number of basal species, B	8	8	8	8	8	8	8
Number of Chain cycles	71142	70472	71111	71526	74331	80450	85214
Link density, L/S	17.299	17.299	17.307	17.315	17.362	17.417	17.891
Connectance, L/S ²	0.13621	0.13621	0.13628	0.13634	0.13671	0.13714	0.13977
Mean connectance, D	34.598	34.598	34.614	34.630	34.724	34.835	35.781
Maximum chain length	No.1-5: 3 No.6: 5 No.7-8: 4	No.1-5, 7: 3 No.6: 5 No.8: 4	No.1-5, 7: 3 No.6: 5 No.8: 4	No.1-5, 7: 3 No.6: 5 No.8: 4	No.1-5, 7: 3 No.6: 5 No.8: 4	No.1,3-5,7: 3 No.2,6,8: 4	No.1-5,7: 3 No.6: 5 No.8: 4

4 Discussion

Since the concept of keystone species was first proposed by Paine (1969), the importance of them for conservation biology has been widely studied. However, due to the limitations of field experimental methods and the temporal and spatial variation (Menge et al., 1994; Paine, 1995; Estes et al., 1998), more and more researchers questioned the original concept of keystone species, and have developed various definitions of keystone species (Mills et al., 1993; Bond, 2001; Davic, 2003). So far, quantitative methods to identify keystone species remain to be little (Menge et al., 1994; Bond, 2001).

The traditional definitions of keystone species closely related to the richness and biomass of species, however, the definitions can be considered by combining the topological importance (Jordán et al., 1999, Jordán et al., 2003). Although the definitions of keystone species from network perspective and traditional definition are not fully consistent, they provide a quantitative and complementary view for the importance of species, and stress that the network theory and species conservation practices are highly correlated (Memmott, 1999; Dunne et al., 2002a). The identification of keystone species in food webs using network analysis depends on the topological characteristics of the network. In present study, we calculated the five centrality indices of nodes in the full CSM food web and its four sub-webs, and found that species rankings using different centrality indices were different. Species importance ranking by the degree centrality and betweenness centrality is based on their direct connection in the network. Degree considers the direct impact of

a species with its neighboring species directly connected. Betweenness centrality represents the influence of a species in the "communication" process. On the other hand, closeness centrality, clustering coefficient centrality and eigenvector centrality take the influence of a species in the global network into consideration (Borgatti, 2005). In all of these indices, the importance of a species in the global or local network is equally important, so the different rankings using different centrality indices should be taken as the comprehensive measure of different topological properties, which are likely relevant to the direct target analysis of theoretical ecology and conservation ecology (Estrada, 2007).

Studies have indicated that there is a significant correlation between different topological parameters of a complex network (Wutchy and Stadler, 2003). Our results showed that DC and CC correlated significantly. Thus the combined use of DC and CC can better reflect the importance ranking of species in the global and local network.

Power et al. (1996) proposed that a quantitative and predictive generalization is a primary task for identifying keystone species. Research on complex networks will give us new thoughts and methods to further understand ecosystems (Abrams et al., 1996; Yodzis, 2001; Piraino et al., 2002). In this article, we identify keystone species by only using Pajek software, so the analytical method may be more unitary and lack of comparative study statistically. More methods, as Ecosim networks (Dunne et al., 2002b; Jordán et al., 2008), CosBiLaB Graph software (Jordán et al., 2008), etc., are suggested using in the future. In addition, we have used the conventional definition, i.e., taxonomical species, and simplify the life stages of species. In the further studies, we may distinguish species in different life stages and then integrate their relationship.

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