Article

Some effects of parasitism on food web structure: a topological analysis

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Abstract
So far most of the food webs lack parasitism. It has been found that parasites can profoundly affect food web properties. In this study we tried to consider parasitism in the food web analysis in order to provide a basis for further and more complete theory development. The data for topological analysis of food webs was from the food web studies of Lafferty et al. Pajek software was used to conduct topological analysis on food webs. The results revealed that in the food web the number of base species kept to be constant but the number of top species declined remarkably and the number of intermediate species increases sharply when parasitism was considered. Parasitism increased the food chain cycles. There were 508 cycles in the parasite-parasite sub-web but not any cycle was found in the predator-prey sub-web. The connectance and link density increased after parasitism was added. The links between predators and parasites were greater than the links between predators and preys. The connectance of predator-prey sub-web, predator-parasite sub-web, parasite-host sub-web, and parasite-parasite sub-web is 0.29, 0.16, 0.24, and 0.34, respectively. The link density of predator-prey sub-web, predator-parasite sub-web, parasite-host sub-web, and parasite-parasite sub-web is 11.95, 9.84, 15.5, and 7.64, respectively. Chain length increased slightly and omnivorous species and omnivory increased also. The present study revealed that parasitism would yield substantial effects on food web structure.

Keywords parasitism; parasites; food web; structure; topology; links; connectance; omnivory.

1 Introduction

A food web is a network to describe between-species trophic relationships. It also represents how the energy and materials flow through species. In the food web, the interacted species are connected by lines and arrows (i.e., links), and a species in the graph is a node (i.e., vertex).

In the food web all species occupying the same trophic position make up a trophic level. For example, all plants in the food web constitute a trophic level called the first or "primary producers", all herbivores comprise the second or "primary consumer" trophic level, and all carnivorous animals constitute a third or "secondary consumer" trophic level. In addition, if there are more advanced carnivores that eat other carnivores, they will constitute an even higher trophic level.

To study food webs helps to further understand the patterns of ecosystem organization and their relationship with ecological stability (Pimm, 1991; Pimm et al., 1991; Warren, 1994; Morin and Lawler, 1996; McCann, 2000). However, many of these results look like non-natural laws because the data used is incomplete and the error produced (Polis, 1991; Cohen et al., 1993; Winemiller et al., 2001).

The basic properties of the food web, including the actual number of links L, connectance C and their relationships should be fully taken into account in the food web study (Sugihara et al., 1989). So far a few of studies address between-species trophic links, degree distribution (i.e., hierarchical distribution; Bollobás, 1985), etc. These topological properties stress the importance of species in the stability of food web, which consider species' roles as both producer (incoming link) and consumer (outgoing link). Removing the prominent species, which have most links to other species, will lead to direct or indirect effects on other species (Pimm, 1980; Solé and Montoya, 2001; Dunne et al., 2002; Montoya and Solé, 2002).

Early studies on food webs began with MacArther (1955). The main works during the period are: (1) food webs were in text and graphically expressed; (2) spatial uniformity, relationship linearity, and abstract between-species trophic relationships were assumed to study the stability and equilibrium of food webs. The food web studies during 1990s to 2000s focused on the general principles of link distributions. How to find general and stable patterns from food webs is one of the focuses in those studies (Cohen et al., 1993). Most of the studies on community assembly have based on between-species competition and stochastic linear aseembly principles (May, 1983; Case, 1990; Morton et al., 1996). The most recent studies on trophic networks are exploiting how between-species relationships affect the dynamics and stability of ecosystem (Navia, et al., 2010).

Through topological analysis on two food webs, predator-prey and parasitoid-host networks, Pimm et al. (1991) found the general model of the food webs. However, the conclusions drawn from parasitoids or predators may not fully represent the truth of typical parasites' role in the food webs. Unlike predators, parasites are very efficient in the food web's flow of energy and matter. The energy and matter flow of the large numbers of parasites from a host will profoundly affect the patterns and dynamics of the food web (Lafferty et al., 2006b).

Recent studies have found that parasites can profoundly affect food web properties, such as nestedness (nestedness), chain length and link density. Further, although most of the food web studies show that the vulnerability at the highest trophic level is the smallest, but if the parasites are included the species at the intermediate trophic level, rather than at the lowest trophic level, those species will have the highest vulnerability to natural enemies' attack. These results indicate that the food web not containing parasites is very incomplete. Parasitic links are so important to ecosystem stability because they can increase the links and nestedness (Lafferty et al., 2006a).

It is obvious that the topological analysis of Pimm et al. was not enough to draw a perfect reliable food web model. In this study we tried to consider parasitism in the topological analysis of food web structure, in order to provide a basis for further research and more complete model development.

2 Materials and Methods

2.1 Materials

2.1.1 Data source

The data for topological analysis of food webs was from the food web studies of Lafferty et al ., conducted in Carpinteria Salt Marsh (CSM), California (Lafferty et al., 2006a,b). The purpose of their study was to investigate the effects of parasites on the food web topology (Interaction Web Database: http://www.nceas.ucsb.edu/interactionweb/html/carpinteria.html).

2.1.2 Data description

CSM food web included four sub-webs. It is made of four sub-webs expressed as matrices. Four sub-webs are in the clockwise direction the predator-prey sub-web, parasite-host sub-web, predator-parasite sub-web, and parasite-parasite sub-web. In the predator-parasite sub-web, a predator-parasite link was determined if a predator eats a prey who has been parasitized by parasite(s). Parasite-parasite sub-web includes hyperparasites

(Kuris, 1990; Lafferty et al., 1994; Huspeni and Lafferty, 2004). Six trophic levels are included in the predator-prey sub-web.

2.1.3 Data Conversion

Before the analysis, species were labeled by ID codes (the following table). After conversion, open Data/data editors/matrix editor in the UCINET software and then paste the coded data. Use Matrix Editor to save them as files in “.##h” format. Finally use File/Open/Ucinet dataset/network in Netdraw software to select and open the “.##h” file, and then save it to the file in “.net” format by File/Save data as/Pajek/Net file. The resultant four “.net” files formed the basis for topological analysis using Pajek.

1	Marine detritus	33	*Macoma nasuta*	65	Bonaparte's Gull	97	Eugregarine
2	Terrestrial detritus	34	Protothaca	66	Long-billed Curlew	98	Plasmodium
3	Carrion	35	*Tagelus spp*.	67	Surf Scoter	99	Nematode in tagelus
4	Macroalgae	36	Cryptomya	68	Bufflehead	100	*Spirocamellanus perarai*
5	Epipellic flora	37	*Mytilus galloprovincialis*	69	Clapper rail	101	*Baylisascaris procyonis*
6	Emergent vascular plants	38	Geonemertes	70	Cooper's Hawk	102	Acanthocephalan in Gillichthys
7	Sumergent vascular	39	American Coot	71	Northern Harrier	103	*Euhaplorchis californiensis*
8	Phytoplankton	40	Mallard	72	*Leptocottus armatus*	104	*Himasthla rhigedana*
9	Oligochaete	41	Killdeer	73	*Gillycthys mirabilis*	105	*Probolocoryphe uca*
10	*Capitella capitata*	42	Green-winged teal	74	*Urolophus halleri*	106	*Himasthla species* B
11	Phoronid	43	*Cleavlandia ios*	75	Procyon locator	107	*Renicola buchanani*
12	Spionidae	44	Semipalmated Plover	76	Great Blue Heron	108	*Acanthoparyphium* sp.
13	*Eteone lightii*	45	Greater Yellowlegs	77	Snowy Egret	109	*Catatropis johnstoni*
14	Turkey Vulture	46	*Hemigrapsus oregonensis*	78	Black-crowned Night heron	110	Large xiphideocercaria
15	*Corophium sp*	47	*Fundulus parvipinnis*	79	Double Crested Cormorant	111	*Parorchis acanthus*
16	Harpacticoid	48	Western Sandpiper	80	Great Egret	112	Austrobiharzia
17	Ostracods	49	Dunlin	81	Pied Billed Grebe	113	*Cloacitrema michiganensis*
18	*Anisogammarus confervicolus*	50	Least Sandpiper	82	Osprey	114	*Phocitremoides ovale*
19	Traskorchestia	51	Forster's Tern	83	*Triakis semifasciata*	115	*Renicola cerithidicola*
20	*Uca crenulata*	52	Dowitcher	84	*Portunion conformis*	116	Small Cyathocotylid
21	Neotrypaea	53	Green Heron	85	Picornavirus	117	*Stictodora hancocki*
22	Upogebia	54	Belted Kingfisher	86	*Nerocila californica*	118	*Mesostephanus appendiculatoides*
23	*Atherinops affinis*	55	American Avocet	87	Orthione	119	*Pygidiopsoides spindalis*
24	*Mugil cephalus*	56	*Pachygrapsus crassipes*	88	*Ergasilus auritious*	120	Microphallid 1
25	*Cerithidea californica*	57	Willet	89	*Aedes taeniorhynchus*	121	Hysterolecitha
26	*Acteocina inculcata*	58	Black-bellied Plover	90	*Culex tarsalis*	122	Parvatrema
27	Melampus	59	California Gull	91	Leech (glossiphonidae)	123	Microphallid 2
28	Assiminea	60	Whimbrel	92	Proleptus	124	Galactosomum
29	Trichocorixia	61	Mew Gull	93	Carcinonemertes	125	Tetraphyllidean
30	Ephydra larva	62	Marbled Godwit	94	Gyrodactylus	126	Tetraphyllid fish
31	Mosquito larva	63	Ring-billed gull	95	Trichodina	127	Trypanorynch
32	Ephydra adult	64	Western Gull	96	Eugregarine	128	Dilepidid

2.2 Methods

2.2.1 Pajek software

Pajek is the software to analyze large and complex networks. It is a fast and visualized program. It is unique to calculate the networks with millions of nodes. It is mainly used to conduct global analysis on complex networks.

2.2.2 Some properties of food webs

2.2.2.1 Classification of species

Species were classified into three categories, top (trophic) species, intermediate (trophic) species and base (trophic) species (Pimm et al., 1991).

2.2.2.2 Degree

Degree is the most basic property for a complex network. The degree of a node is defined as the number of its connected nodes. In general the more the degree of a node, the more important the node is. In an oriented network, the degree is the sum of incoming degree and outgoing degree. Use In/Out/All commands of Net/ Partitions/Degree menu of Pajek, the degree, incoming degree and outgoing degree can be calculated. The proportions of three categories of species can be obtained by calculating degrees of these species.

2.2.2.3 Chain cycle

Chain cycle is a closed loop in the food chain. Cannibalism is a kind of chain cycle. Chain cycle can be obtained by using Net/Count/4-rings/directed/cyclic in Pajek.

2.2.2.4 Connectance and link density

Connectance is the ratio of realized trophic interactions to possible interactions. In the calculation of connectance, the number of possible interactions is S^2 if cannibalism is considered, or else it is $S(S-1)$. Link density is equal to the ratio of total number of links to the total number of species.

2.2.2.5 Chain length

Chain length refers to the number of links of the path between the base species and the top species through the chain of two adjacent species. The chain length or between- species distances can be calculated by Net/k-neigbours/output in Pajek.

2.2.2.6 Omnivorous species

An omnivorous species is dependent upon more than one trophic levels. Omnivorous species make the boundaries between trophic levels blurred. Omnivory is the ratio of the number of closed omnivorous links to the number of top species (Sprules and Bowerman, 1988). A closed omnivorous link refers to that a predator feeds on the two preys with different trophic levels along the same food chain.

3 Results

3.1 Species analysis

The results of species analysis on four sub-webs are indicated in Table 1. Pimm et al. (1991) pointed out that the proportions of top species, intermediate species and base species are generally constants. According to our results, however, the number of base species keeps constant but the number of top species declines remarkably (from 33 species to 3 species) when parasites are added. Thus the proportions change sharply (Fig. 1).

Table 1 Species analysis of complete food web

(Sub-)Food web	Category	Number	Total No. Species	Percent (%)	Species ID code
Predator-Prey	T	33	83	39.76	14,42,44,45,51,53-55,57-71,74-83
	I	42		50.60	9-13,15-41,43,46-50,52,56,72,73
	B	8		9.64	1,2,3,4,5,6,7,8
	O	0		0	-
Predator-Parasite	T	44	128	34.38	84,86-128
	I	0		0	-
	B	63		49.22	10,12-14,16,18,20-26,28,33-36,39-83
	O	21		16.41	1-9,11,15,17,19,27,29-32,37,38,85
Parasite-Host	T	47	128	36.72	34,35,38-40,42-83
	I	0		0	-
	B	41		32.03	84-88,91-100,102-125,127,128
	O	40		31.25	1-33,36,37,41,89,90,101,126
Parasite-Parasite	T	2	45	4.44	85,98
	I	17		37.78	103-111,113-120
	B	2		4.44	84,90
	O	24		53.33	86-89,91-97,99-102,112,121-128
Complete food web	T	3	128	2.34	89,101,126
	I	117		91.41	9-88,90-100,102-125,127,128
	B	8		6.25	1,2,3,4,5,6,7,8
	O	0		0	-

Note: T-top species; I-intermediate species; B-base species; O-species outside web (Lafferty et al., 2006a,b). There are not intermediate species in the predator-parasite and parasite-host sub-food webs due to the incomplete data.

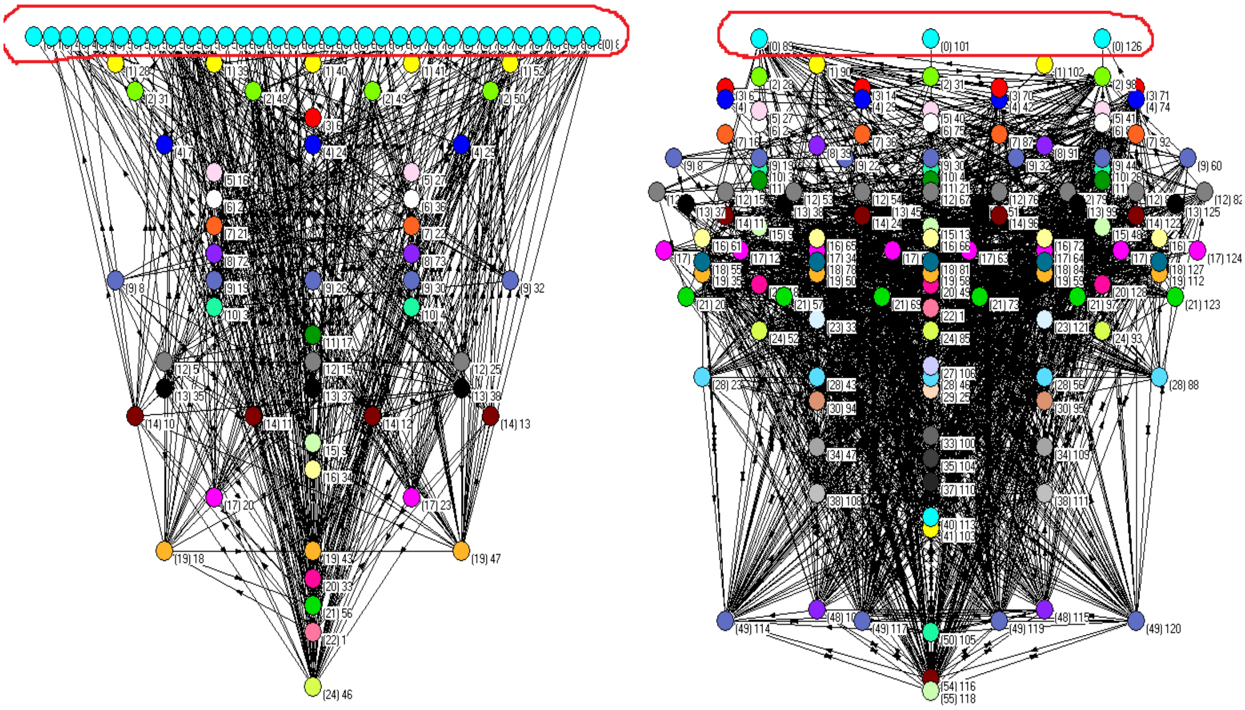
3.2 Cycle analysis

There is not any cycle in the predator-prey, predator-parasite, and parasite-host sub-webs. Contrarily there are 508 cycles in the parasite-parasite sub-web, and there are 85,214 cycles in the complete food web. In the studies of Pimm et al. (1991), however, rare cycles appeared for food webs without parasites.

3.3 Link analysis

There are 992 links in predator-prey sub-web. The connectance and link density is 0.29 and 11.95 respectively (Fig. 2).

Fig. 2 shows that the species *Pachygrapsus crassipes* and *Hemigrapsus oregonensis*, with 45 and 43 links respectively, are the two most significant species in the predator-prey sub-web. Second by *Fundulus parvipinnis* (35 links). Turkey vulture has only one link.



(A) (B)

Fig. 1 Comparison of food webs with (B) and without (A) parasites. The number in parentheses is total links (degree, or incoming degree+outgoing degree) and the number outside parentheses is species ID code. From top to bottom layers the number of links of each species increase.

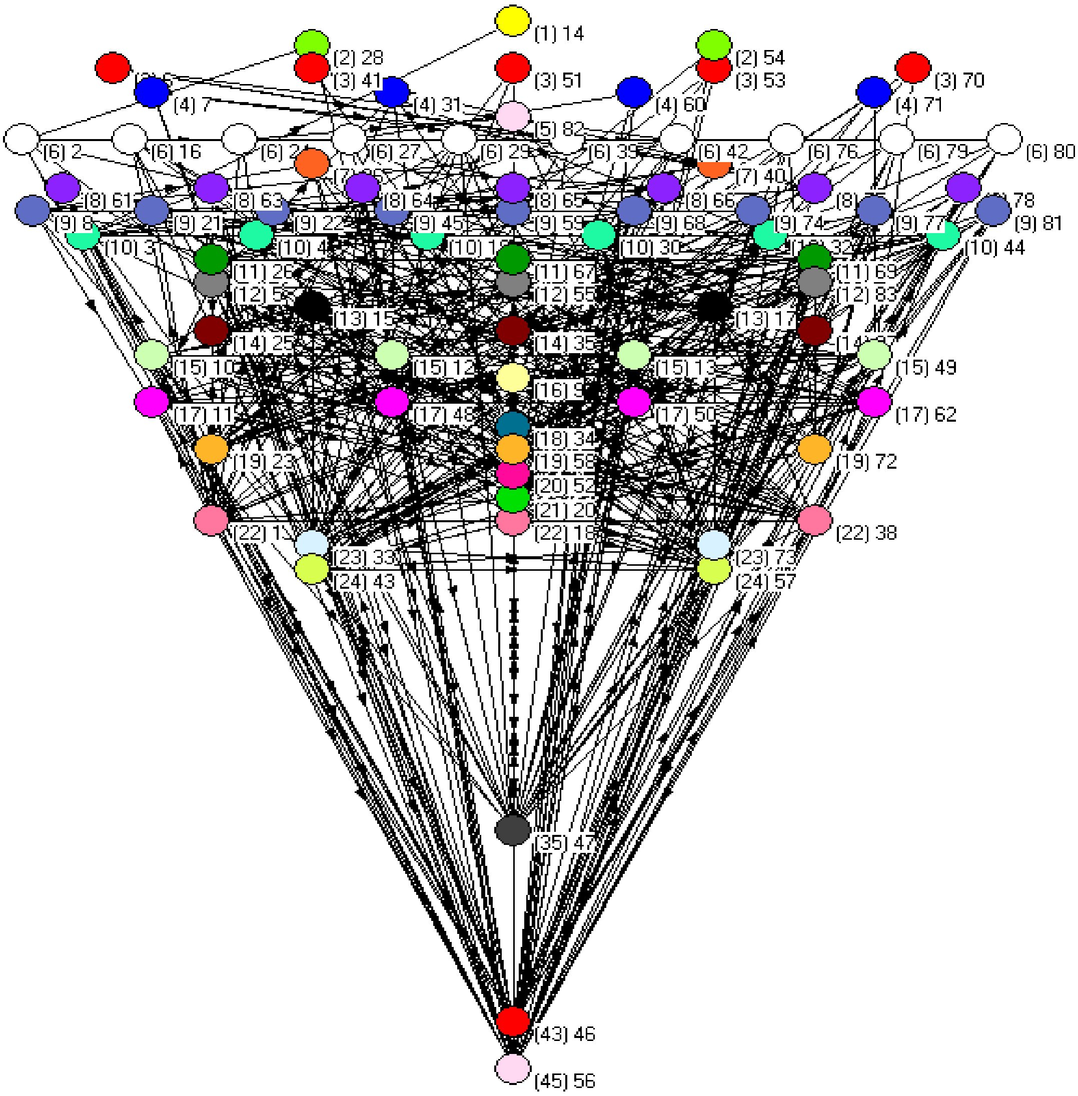


Fig. 2 Predator-prey sub-web.

There are 1,260 links in the predator-parasite sub-web. The connectance and link density of this sub-web is 0.16 and 9.84 respectively (Fig. 3).

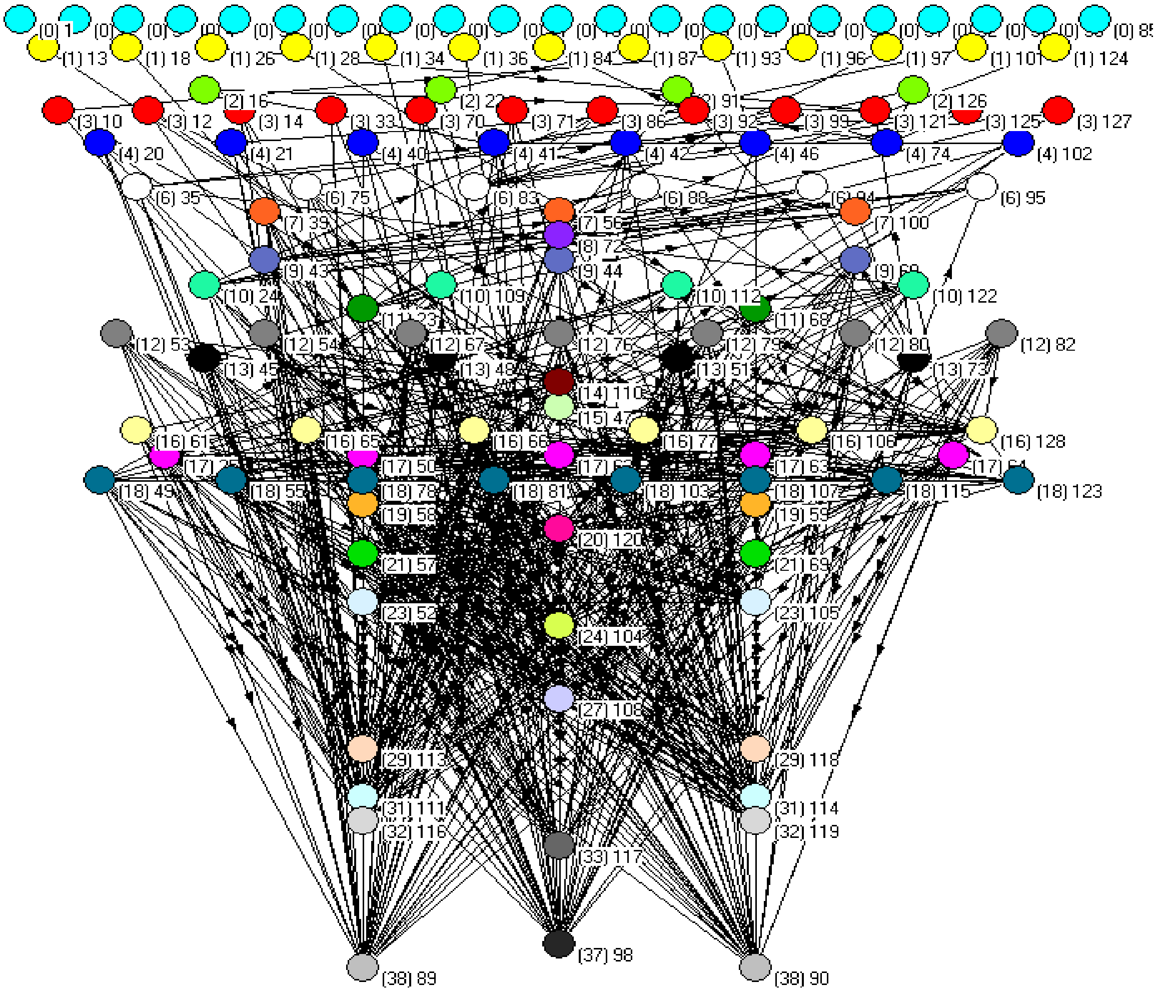


Fig. 3 Predator-parasite sub-web.

Fig. 3 shows that the species *Aedes taeniorhynchus* and *Culex tarsalis*, with 38 links respectively, are the two most significant species in the predator-parasite sub-web, seconded by Plasmodium (37 links). Some species, such as marine detritus and Picornavirus, have not links. They are isolated species.

There are 1,984 links in the parasite-host sub-web, and the connectance and link density of this web is 0.24 and 15.5 respectively (Fig. 4). *Himasthla rhigedana*, *Himasthla* species B, *Renicola buchanani*, and *Catatropis johnstoni* have the most links (40 links) in the parasite-host sub-web. Species, such as Killdeer, etc., have no links.

In total 344 links are found in the parasite-parasite sub-web and the connectance and link density is 0.34 and 7.64 respectively (Fig. 5). In parasite-parasite sub-web, *Mesostephanus appendiculatoides* has the most links (27 links) and *Himasthla rhigedana* has the least links (16 links).

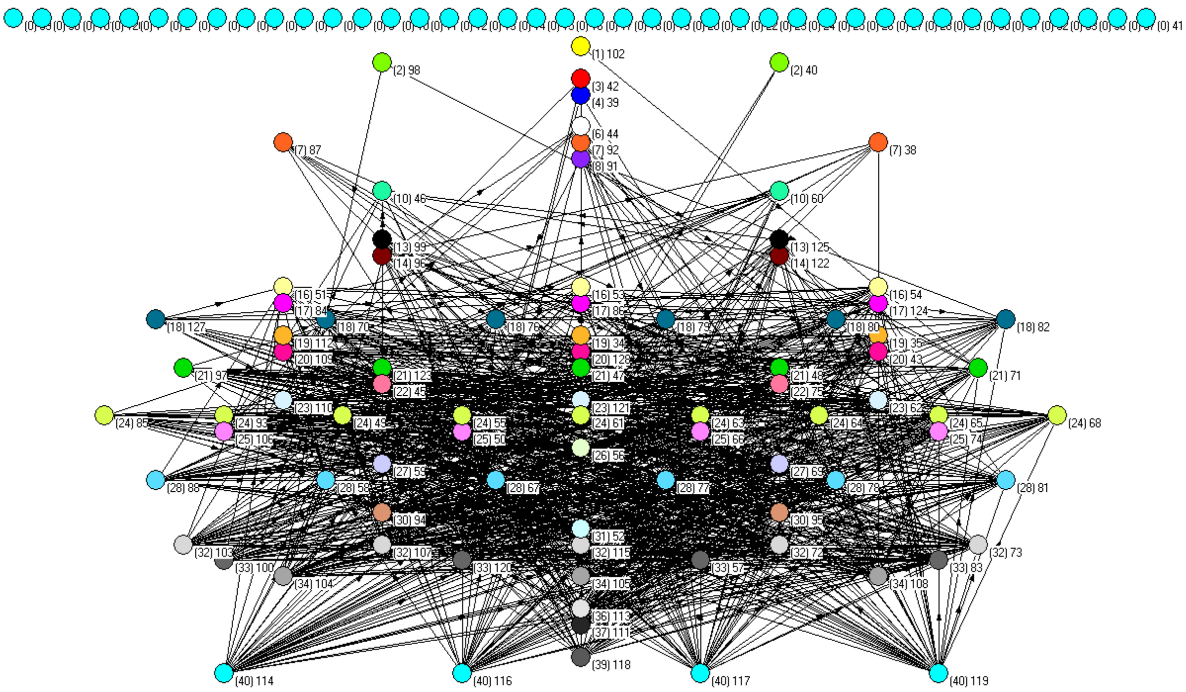


Fig. 4 Parasite-host sub-web.

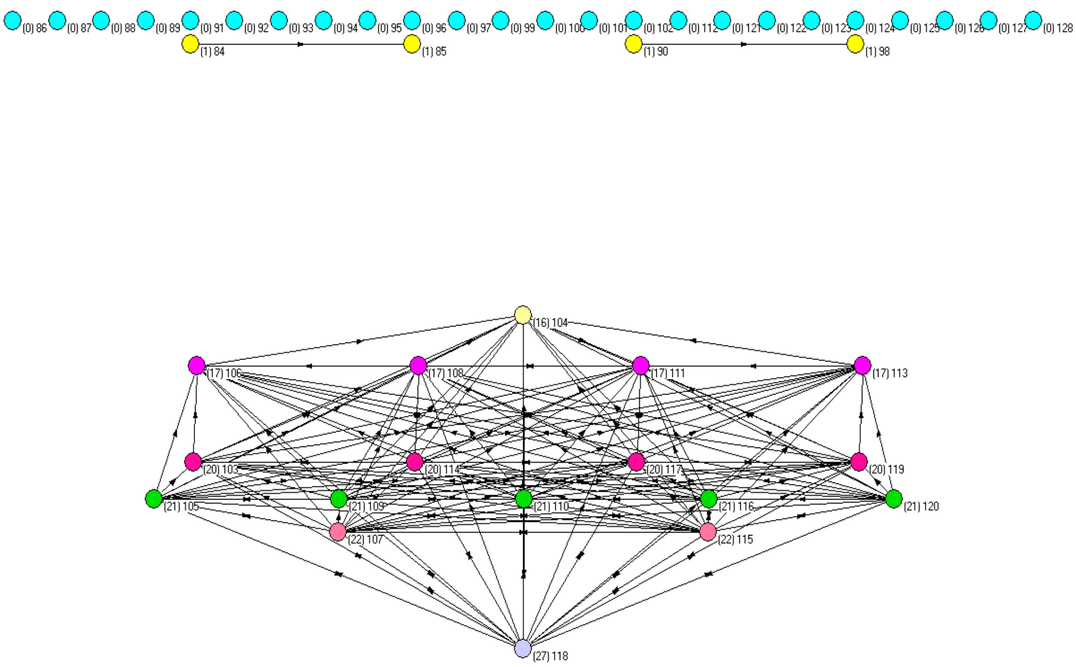


Fig. 5 Parasite-parasite sub-web.

Totally there are 4,580 links in the complete food web. The connectance and link density for the food web is 0.56 and 35.78 respectively (Fig. 6). In the complete food web, small cyathocotylid (93 links), *Stictodora hancocki* (93 links), *Mesostephanus appendiculatoides* (95 links), and *Pygidiopsoides spindalis* (92 links) are the most significant species. *Baylisascaris procyonis* has one link only.

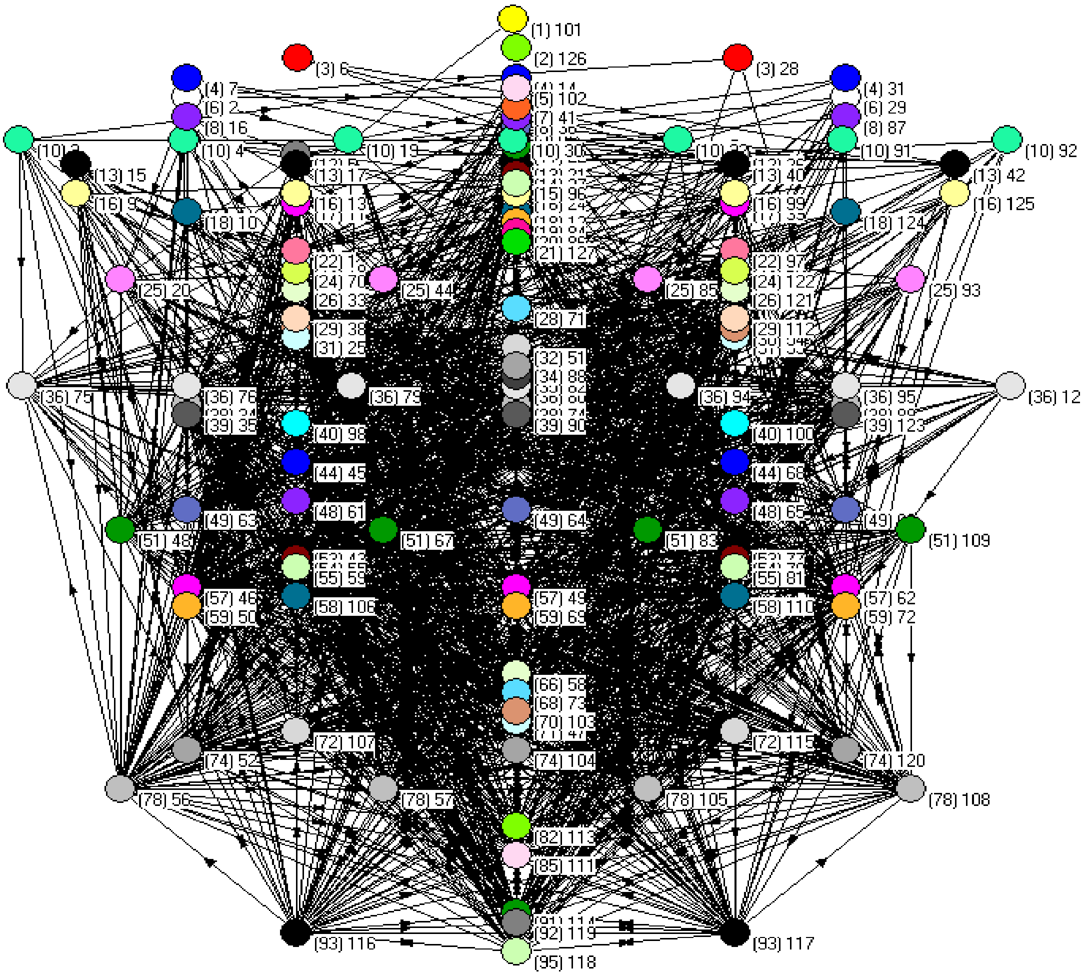


Fig. 6 Complete food web.

Table 2 Parameters of web links

(Sub-)Food web	Total links	Percent (%)	Connectance	Link density	Maxi. No. links	Total No. Species
Predator-Prey	992	21.66	0.29	11.95	45	83
Predator-Parasite	1260	27.51	0.16	9.84	38	128
Parasite-Host	1984	43.32	0.24	15.5	45	128
Parasite-Parasite	344	7.51	0.34	7.64	27	45
Complete food web	4580	100	0.56	35.78	95	128

From Table 2 we can find that the links of predator-prey sub-web accounts for only 21.66% of the total links of complete food web, while the links of parasite-host sub-web (43.32%) and predator-parasite sub-web (27.51%) account for 70.83% of the total. This result stresses the importance of parasitism in the food web.

The link density of predator-prey sub-web is 11.95, greatly less than the 35.78 of complete food web, which means the addition of parasitism in the food web will remarkably increase link density. The number of top species, intermediate species and base species in the predator-prey sub-web is 275, 641 and 76, respectively, much different from the number of 41, 4463, and 76 in complete food web. We may find from these results that top species decline and intermediate species increase sharply after parasitism is added.

3.4 Chain length

For both predator-prey sub-web and complete food web, the base species are species with ID code 1 to 8.

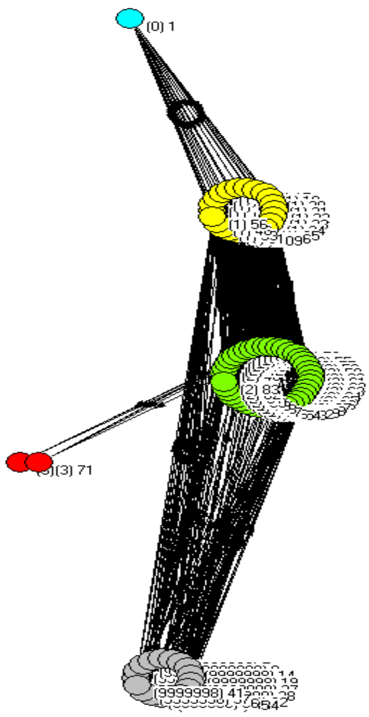


Fig. 7 K-neighbour/output analysis of ID No. 1 species in the predator-prey sub-web. The species No. 9,999,998 means that it is not reachable to No. 1species. Among species reachable to No. 1 species, the maximum chain length is 3.

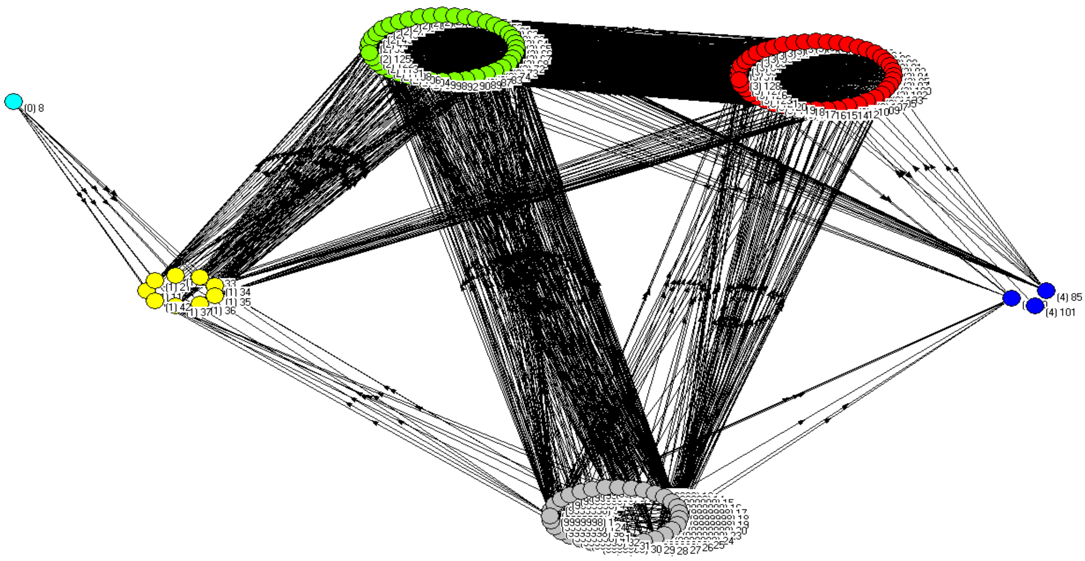
Similar to the analysis on the No. 1 species, as indicated in Fig. 7, the K-neighbour/output analysis on No.2 to No. 8 in the predator-prey sub-web is conducted, as shown in Table 3.

Table 3 Distribution of chain length for No.1 to No. 8 species in the predator-prey sub-web

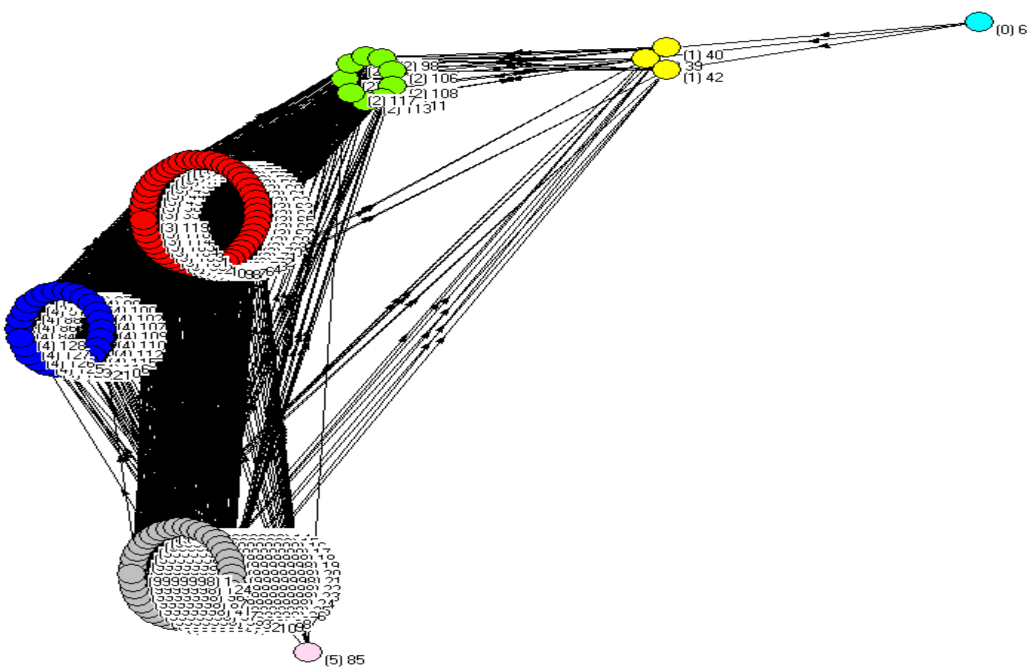
(Sub-) Food web	1	2	3	4	5	6	7	8	Maximum Chain length
Predator-Prey	3	3	3	3	3	2	3	3	3
Complete food web	3	3	3	3	3	5	3	4	5

Pimm et al. (1991) pointed out that chain length for top species is typically 2 or 3, and 1 is relatively rare (led by incomplete information), and the chain length larger than 3 occurs seldom. The corresponding number of trophic levels is 3 or 4. In present analysis there are 6 trophic levels and most chain lengths are 3. The results are in accordant with the Pimm et al. (1991).

For the complete food web, most of the chain lengths are 3 and some are more than 3 (Fig. 8; No. 8 and No. 6 species).



(A)



(B)

Fig. 8 K-neighbour/output analysis of ID No. 8 (A) and No. 6 (B) species in the complete food web. Among species reachable to No. 8 (No. 6) species, the maximum chain length is 4 (5).

As can be seen from Fig.8, the chain lengths for the food web with parasitism are larger slightly than the web without parasitism.

3.5 Analysis on omnivorous species

There are many omnivorous species in the food web. In the predator-prey sub-web, the omnivory increased as the rising of trophic level (Lafferty et al., 2006b; Table 4).

Table 4 Change of omnivory with trophic level

Trophic level	1	2	3	4	5	6
Omnivory	1.0	1.5	2.5	3.0	3.6	4.4

4 Conclusions and Discussion

Most of the food webs so far lack parasitism. Actually once parasitism is added in the network the traditional top species would not still be at the highest trophic level because most of the species are parasitized by one or more parasites (Polis, 1991). The addition of parasitism greatly increases the complexity of food web and alters some properties of food web. As indicated in present study, the major changes include the following aspects:

(1) Structural changes in species. The proportions of top species, intermediate species and base species change after parasitism is added. The number of top species declines and the number of intermediate species increases sharply. The number of base species will not change as the addition of parasitism. If all parasite species are treated as top species, however, the proportion of top species will increases and the proportions of intermediate species and base species will decline (Huxham et al., 1995).

(2) Increase in chain cycles. Rare chain cycles were found in the food web with predators and preys only (Pimm et al., 1991). Different from the observation of Pimm et al. (1991), the between-parasite cycles increase largely once parasitism is added. Moreover, there will be more cycles between predators and preys due to the addition of parasites.

(3) Increase in links. If the parasitism is added, the number of links and link density will increase, and the proportions of top species, intermediate species and base species will be altered. In average the links between parasites and hosts are much more than that between predators and preys (Lafferty et al., 2006b). The links between predators and parasites are greater than the links between predators and preys due to the remarkable existence of parasites in hosts.

The links between parasites and hosts increase more than the total number of links, thus the link density increases. Another study has proved also that link density increases from 5.36 to 8.64 (Amundsen et al., 2009).

A large numbers of parasites serve as both consumers and producers, thereby the number of intermediate species increases greatly, which results in the significant changes of the proportions of top species, intermediate species and base species.

(4) A slight increase in the chain length. According to Pimm et al. (1991), most chain lengths are 2 or 3. Average chain length increases after parasitism is added (Thompson et al., 2005), as proved in present study.

(5) Increase in omnivory. Parasites can consume several trophic levels, thereby omnivorous species and omnivory increase (Huxham et al., 1995). Some research proved that omnivory increases from 1.86 to 2.07 (Amundsen et al., 2009).

Further research may center on the following aspects:

(1) This study has based on the food web data collected from Carpinteria Salt Marsh, and some other data that have been published. However, to obtain complete results we need more data and use some model as cascade model, etc., to validate conclusions or exploit mechanism. More interaction types, e.g., mutualism (Callaway, 1995; Bruno et al., 2003; Bascompte and Jordano, 2007; Dormann, 2011), etc., should also be considered. The occurrence of parasitism will largely increase the complexity of food chains and in particular food cycles and these food cycles and chains will vary with the climates and other environmental conditions. Network structure would therefore change with locations and time (Zhang, 2011), and should be studied based on different locations and time.

(2) Predator and prey overlap graphs are suggested to be developed to analyze topological holes for species with lower abundance.

(3) Dynamic analysis, such as agent-based modeling (Zhang, 2011, 2012), etc., is suggested for using in the dynamic analysis of network structure.

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