Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web

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Summary

1. Despite their documented effects on trophic interactions and community structure, parasites are rarely included in food web analyses. The transmission routes of most parasitic helminths follow closely the trophic relationships among their successive hosts and are thus embedded in food webs, in a way that may influence energy flow and the structure of the web.

2. We investigated the impact of parasitism on the food web structure of a New Zealand intertidal mudflat community. Different versions of the food web were analysed, one with no parasites, one with all parasite species and several other versions, each including a single parasite species. We measured key food web metrics such as food chain length, linkage density and proportions of top, intermediate and basal species.

3. The inclusion of all parasite species in the food web resulted in greatly increased mean and maximum food chain length, but had little impact on linkage density and realized connectance. The main change caused by introduction of parasites was the relegation of a number of species from top predators to intermediate status, although the addition of parasites as top predators left the actual ratio of predators to prey relatively unchanged.

4. When individual parasites were added to the food web, their effect on food web properties was generally minimal. However, one trematode species that affected several host species, because of its complex life cycle and low host specificity, produced food web properties similar to those in the web version including all parasite species.

5. The respective effect of individual parasite species was roughly proportional to the number of host species they affected, and thus the life cycle characteristics of parasites determine to a large extent their impact on food web structure. The next step would be to quantify how they affect energy flow through the web.

Key-words: energy, helminths, host specificity, intertidal mudflat.

Introduction

Food webs are networks of trophic relationships which map the location of energy flows in a community. While there has been criticism levelled at the approach because of historical problems with the quality of data (e.g. Paine 1988; Polis 1994), the best resolved food webs (e.g. Raffaelli & Hall 1992; Schmid-Araya *et al*. 2002; Thompson & Townsend 2003) seem to show attributes that are evocative of real patterning of

ecological systems. Despite the increasing detail that has been incorporated into food webs, some functional groups have remained neglected. Among these are the parasites, which have rarely been incorporated into food web studies (Marcogliese & Cone 1997; but see Huxham, Raffaelli & Pike 1995). Host–parasite interactions, however, are ubiquitous in real systems (Poulin & Morand 2000, 2004) and are known to affect community structure (e.g. Minchella & Scott 1991; Combes 1996; Mouritsen & Poulin 2002), trophic relationships (Lafferty 1999; Marcogliese 2002) and energy flow (e.g. Anderson 1977; Mouritsen & Jensen 1998).

Food web context is also thought to have been important in the evolution of many of the characteristics observed in marine parasites, including complex

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life cycles (Parker *et al*. 2003) and long-lived larval stages (Marcogliese 2002). Complex interactions between productivity, host species richness and parasite species richness have been hypothesized (Marcogliese 2001). Food web context has been hypothesized to have an influence on transmission rates of some parasite species in aquatic systems (Curtis 1984; Marcogliese 2002). The transmission pathways of many parasites are embedded in food webs: just as food webs have exerted strong selective pressures on the evolution of parasite transmission strategies, parasites are now shaping some of the ecological properties of existing food webs.

Parasites have important influences on many of the processes that we evoke to explain food web patterns, and on the metrics that we use to measure those patterns. Cascade models (e.g. Pimm 1982) and derivations such as niche models (e.g. Warren 1994; Woodward & Hildrew 2002) rely on a body size hierarchy from larger predators to smaller prey as a structuring determinant. While these models explain well many of the patterns observed in the food webs described thus far, they are clearly incapable of incorporating feeding links with parasites because parasites as 'predators' are much smaller than their prey. The inclusion of parasites in food webs can create loops (species A eats species B eats species A, and higher order variants), which fundamentally influence metrics such as mean and maximum (Hall & Raffaelli 1993) food chain lengths. Loops in food webs also make inference of energy flows more difficult, as we rarely know the energetic cost of parasitism at a species scale. The importance of food web loops as energy pathways has been little explored.

Here, we investigate the impact of parasitism on the food web structure of a New Zealand intertidal mudflat community. To our knowledge, ours is only the second food web study to attempt an evaluation of the influence of parasitism on overall food web characteristics, providing an independent assessment of the role of parasites that can be compared to that of Huxham *et al*. (1995). In keeping with the approach taken by Huxham *et al*.'s (1995) we measured key food web metrics such as food chain length (number of links from the top to the basal species), linkage density and proportions of top, intermediate and basal species. Specifically, we compare key food web properties between the complete food web and a simpler version from which parasite species were excluded. Our expectations, based on Huxham *et al*.'s (1995) results, are that inclusion of parasites will result in longer food chains, a high percentage of the total links occurring via parasitic species resulting in an increase in linkage density, and a greater proportion of top species.

In addition to an assessment of the generality of the results gained from the previous analysis, we investigate the effects of individual parasite species on food web topology with regard to seeking relationships between parasite life cycle characteristics and their importance in influencing food web structure.

Methods

We chose the intertidal mudflat of Company Bay, in Otago Harbour (South Island, New Zealand) as a model system. The free-living species found at this site are, with minor exceptions, roughly the same as those found in other mudflats within the harbour or in the surrounding area, and the parasite species found in Company Bay also occur at practically all other sites sampled (K.N. Mouritsen & R. Poulin, unpublished data). The species composition of the invertebrate community living in or on the sediment was determined from extensive core sampling (each 0·012 m^2, 15 cm deep, with sediments passed through a 500 μm sieve) and visual detection of larger macrofauna. Fish and birds feeding on the mudflat were identified by direct *in situ* observations. The trophic position of each taxon was determined either from previously published studies performed on these taxa at our study site or elsewhere in New Zealand or Australia, direct observations of predation events at the study site, or from gut content analysis of animals collected at the study site. Hence, the majority of links are established with great certainty. In total, the food web included 67 free-living taxa, with basal taxa (primary producers), bacteria, meiofauna and zooplankton included as broad categories (see Table 1).

The helminth (trematodes, nematodes and acanthocephalans) parasites found in Company Bay and adjacent bays have been the subject of several earlier investigations (Poulin, Steeper & Miller 2000; Latham & Poulin 2002a,b; Moravec *et al*. 2003; Babirat, Mouritsen & Poulin 2004; Fredensborg, Latham & Poulin 2004; Martorelli *et al*. 2004). Their life cycles, i.e. their transmission pathways from invertebrate intermediate hosts to vertebrate definitive hosts, are well understood. The food web included nine parasite species (see Table 1), all infecting one or more of the most abundant free-living species (Table 2). A handful of other parasite species are known from the study site; these are not included here because they are very rare, and their life cycles are yet to be elucidated.

The food web was reduced to a binary matrix of feeding relationships (Cohen, Briand & Newman 1990). A trophic link was indicated in the body of the matrix by a '1'. Simple food web metrics such as number of species, number of links, linkage density (number of links divided by number of species) and realized connectance were calculated directly from the matrix. Linkage density provides some average measure of dietary specialization across the food web. Realized connectance is the proportion of food web links which actually occur divided by the number that could conceivably occur, i.e. basal taxa such as macroalgae, phytoplankton and diatoms are attributed no potential feeding links (Thompson & Townsend 2003). Formally, realized connectance is calculated as $L/[(S \times S)-(b \times S)]$, where L is the number of links observed, S is the number of species in the web, and b is the number of

Table 1. List of taxa in the Company Bay food web; symbols and numeric codes are those used in Fig. 1

Taxon	Code	Taxon	Code
Benthic invertebrates*	●	Pelagic invertebrates	●
Anthopleura aureoradiata	1	Zooplankton	51
Edwardsia spp.	2	Basal taxa	◆
Enopla sp. 1	3	Phytoplankton	52
Enopla sp. 2	4	Macroalgae	53
Abarenicola affinis	5	Benthic diatoms	54
Capitellidae sp. 1	6	Bacteria	●
Capitellidae sp. 2	7	Bacteria	55
Heteromastus filiformis	8	Fish	∇
Decamastus sp.	9	Flatfish sp.	56
Paraonis sp.	10	*Sprattus* sp.	57
Scoloplos johnstonei	11	*Notolabrus celidotus*	58
Macroclymenella stewartensis	12	*Thyrsites atun*	59
Hesionidae sp.	13	Birds	□
Exogone heterosetosa	14	*Haematopus ostralegus*	60
Exogone sp. 2	15	*Haematopus unicolor*	61
Perinereis nuntia	16	*Vanellus miles*	62
Sphaerodorum sp.	17	*Larus dominicanus*	63
Spio sp. 1	18	*Larus novaehollandiae*	64
Spio sp. 2	19	*Ardea novaehollandiae*	65
Boccardia syrtis	20	*Sterna striata*	66
Boccardia acus	21	*Anas platyrhynchos*	67
Malacoceros sp.	22	Parasites**	+
Prinospio sp.	23	*Maritrema novaezealandensis*	68
Colurostylis lemurum	24	*Levinseniella* sp.	69
Diastylopsis thileniusi	25	*Curtuteria australis*	70
Tanaidacidae sp.	26	*Acanthoparyphium* sp.	71
Heterophoxus stephenseni	27	*Gymnophallus* sp.	72
Phoxocephalus regium	28	*Ascarophis* sp.	73
Pontharpinia australis	29	Acuariidae sp.	74
Amphipoda sp. 1	30	*Profilicollis antarcticus*	75
Amphipoda sp. 2	31	*Profilicollis novaezelandensis*	76
Cymodopsis montis	32		
Callianassa filholi	33		
Heterosquilla tricarinata	34		
Macrophthalmus hirtipes	35		
Hemigrapsus crenulatus	36		
Hemigrapsus edwardsii	37		
Notoacmea helmsi	38		
Diloma subrostrata	39		
Zeacumantus subcarinatus	40		
Pyramidellidae sp.	41		
Cominella glandiformis	42		
Nucula dunedinensis	43		
Perrierina turneri	44		
Macomona liliana	45		
Austrovenus stutchburyi	46		
Pelecypoda sp. 1	47		
Pelecypoda sp. 2	48		
Phoronida sp.	49		
Meiofauna	50		

*Anemones, 1–2; nemerteans, 3–4; polychaetes, 5–23; crustaceans, 24–37; molluscs, 38–48; phoronid, 49. **Trematodes, 68–72; nematodes, 73–74; acanthocephalans, 75–76.

Table 2. Life cycle characteristics of parasites found in the Company Bay food web

Parasite species	Type	Intermediate Host 1	Intermediate Host 2	Definitive host
Maritrema novaezealandensis	Trematode	*Zeacumantus* (1 spp.)	Crabs, amphipods (8 spp.)	Shorebirds (6 spp.)
Levinseniella sp.	Trematode	*Zeacumantus* (1 spp.)	Crabs (3 spp.)	Shorebirds (5 spp.)
Curtuteria australis	Trematode	*Cominella* (1 spp.)	*Austrovenus* (1 spp.)	Shorebirds (4 spp.)
Acanthoparyphium sp.	Trematode	*Zeacumantus* (1 spp.)	*Austrovenus* (1 spp.)	Shorebirds (4 spp.)
Gymnophallus sp.	Trematode	*Macomona* (1 spp.)	*Austrovenus* (1 spp.)	Shorebirds (4 spp.)
Ascarophis sp.	Nematode	Crabs (3 spp.)	–	Fish (2 spp.)
Acuariidae sp.	Nematode	Crabs (3 spp.)	–	Shorebirds (5 spp.)
Profilicollis antarcticus	Acanthocephalan	Crabs (3 spp.)	–	Shorebirds (5 spp.)
Profillicolis novaezelandensis	Acanthocephalan	Crabs (3 spp.)	–	Shorebirds (5 spp.)

basal species. Proportions of top, intermediate and basal species were calculated in the manner described by Huxham *et al.* (1995). A top species is a species which is not fed upon by any species. Intermediate species are both predators and prey. Basal species have predators but no prey. Consistent with Huxham *et al.* (1995), we defined all parasites as top species (although the free-swimming larvae of trematodes are eaten by benthic invertebrates) and excluded bacterial links.

Because of the large size and complexity of the food web, network analysis tools were used to extract more complex attributes and to graphically represent the data. UCINET 6.0 (Borgatti, Everett & Freeman 2002) was used to manipulate the data and to generate food web diagrams. PAJEK 0.96 (Batagelj & Mrvar 1998) was used to calculate distributions of food chain lengths. The food web was analysed a number of times, initially with no parasite species included, then with each parasite species separately, and finally with the entire parasite community included. In so doing we were able to correlate the effects of each parasite on food web topology with the parasite's natural history characteristics.

Results

The inclusion of parasites increased the food chain lengths and introduced considerable complexity into the food web architecture (Fig. 1). Maximum food chain length was doubled, from three to six links, by including all parasites (Fig. 2) and average food chain length was also greatly increased (Table 3). Modal food chain length was unchanged, but the inclusion of parasites resulted in a proliferation of possible food chains. Linkage density and realized connectance were similar with and without parasites in the food webs (Table 3). The main change caused by introduction of parasites was in the number of top species. Inclusion of parasites as top predators relegated a number of species from top to intermediate status. However, the addition of parasites as top predators largely compensated for that change, and the actual ratio of predators to prey was relatively unchanged.

The parasites included in the webs affected variable numbers of species depending on their host specificity and their life cycle (Table 2). *Maritrema novaezealandensis* (Martorelli, Fredensborg, Mouritsen & Poulin) alone affected 15 species (nine intermediate hosts and six definitive hosts), 68% of the species affected by all parasites combined (Table 3). Other species showed much higher specificity for intermediate or definitive hosts, thereby affecting fewer species in the web. The most extreme case was the nematode *Ascarophis*, which affected five species in the food web (three crab intermediate hosts and two fish definitive hosts). Species with higher specificity for their definitive hosts relegated fewer of the top species to intermediate species status and thus allowed the web to retain a trophic structure more similar to that without parasites (Table 3).

Table 3. Attributes of the marine food web with and without inclusion of parasite species

|	No parasite included	*Maritrema novaezealandensis*	*Levinseniella* sp.	*Curuteria australis*	*Acanthoparyphium* sp.	*Gymnophallus* sp.	*Ascarophis* sp.	Acuariidae sp.	*Profilicollis antarcticus*	*Profilicollis novaezelandensis*	All included
No. of species	67	68	68	68	68	68	68	68	68	68	76
No. of links	500	523	512	514	514	513	507	510	510	510	613
Linkage density	7·46	7·69	7·53	7·56	7·56	7·54	7·46	7·50	7·50	7·50	8·07
No. of spp. parasitized	0	15	9	6	6	6	5	8	8	8	22
No. of basal species	3	3	3	3	3	3	3	3	3	3	3
No. of intermediate species	49	55	54	53	53	53	50	54	54	54	57
No. of top species (parasites)	15 (0)	10 (1)	11 (1)	12 (1)	12 (1)	12 (1)	15 (1)	11 (1)	11 (1)	11 (1)	16 (9)
Realized connectance	0·117	0·118	0·116	0·116	0·116	0·116	0·115	0·115	0·115	0·115	0·110
Maximum chain length	3	6	6	6	6	6	6	6	6	6	6
Mean chain length	1·675	2·523	2·510	2·690	2·690	2·708	1·804	1·849	1·849	1·849	2·539
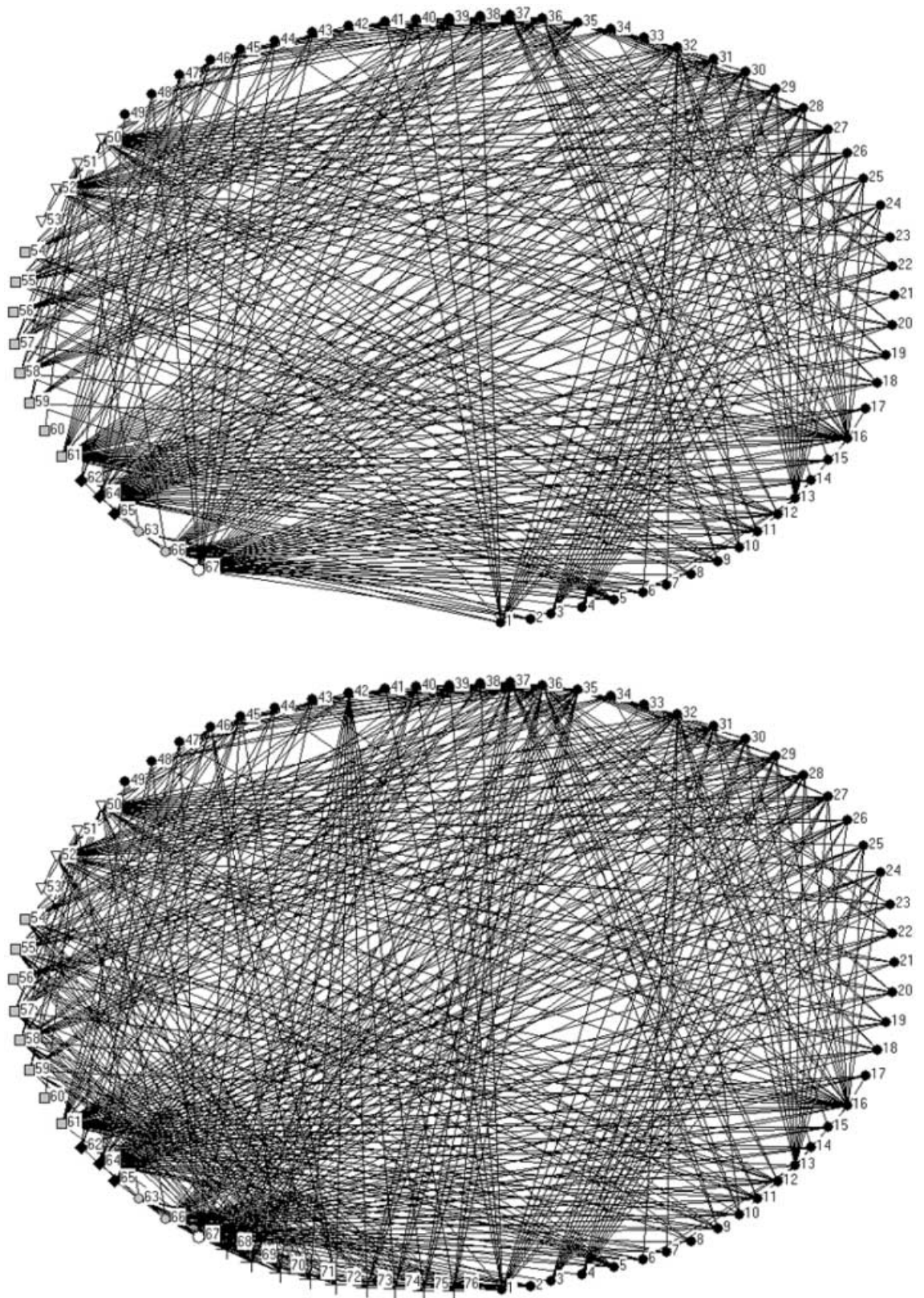
Fig. 1. Food web diagrams for the marine food web with (top) and without (bottom) the inclusion of parasite species. Numbers indicate species or tropho-species, while symbols delineate major groups (see Table 1 for key).

All the parasites, when added to the food web individually, had a minimal effect on realized connectance, which was approximately 11–12% in all versions of the web (Table 3). However, the individual effects of different parasites on linkage density and food chains were different. Linkage density was increased as the number of species parasitized in the food web was increased (Fig. 3, $r^2 = 0.817$, $P < 0.05$). The trematode *M. novaezealandensis* (affecting 15 species) had the greatest effect on this attribute, whereas *Ascarophis*
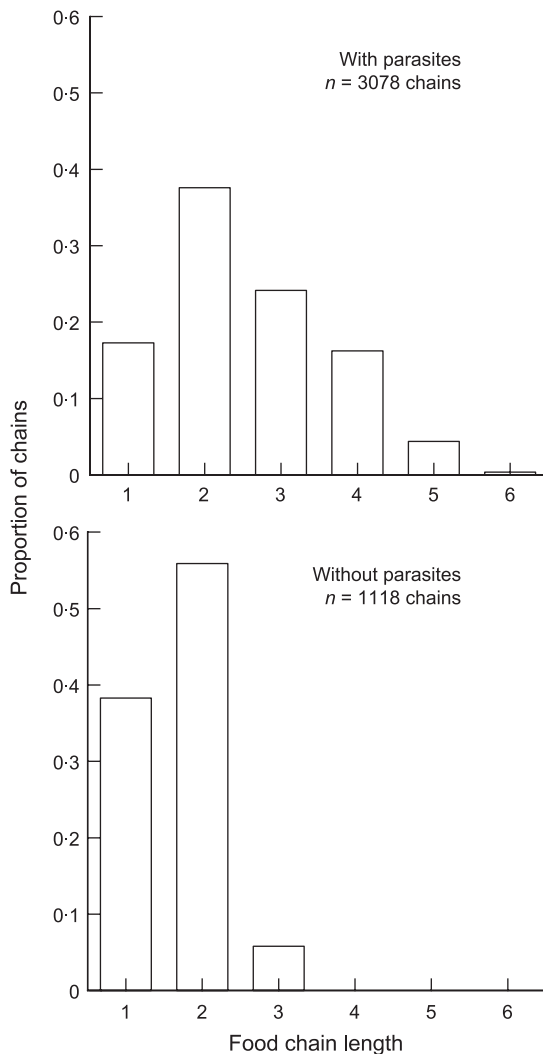
Fig. 2. Frequency distribution of food chain lengths for two versions (with and without parasite species) of the marine food web. The two distributions of food chain lengths are significantly different (Kolmogorov–Smirnov test, $Z = 11 \cdot 21$, $P < 0 \cdot 005$).
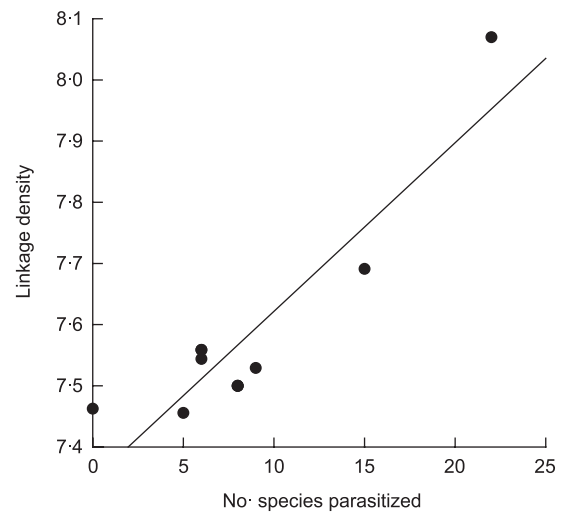

Fig. 3. Relationship between linkage density and the number of species affected by parasitism. The values for no species affected and 22 species affected represent the food webs with no parasites and all nine parasite species, respectively. The intermediate values are obtained when single parasite species are included in the web.

(affecting five species) had no effect on linkage density when introduced into the food web. While the introduction of any parasite species individually into the food web was sufficient to increase the maximum food chain length from three to six links, effects on mean food chain length varied with species (Table 3). The doubling of the maximum food chain length results from predation on the free-living stages of the parasites by non-host organisms, e.g. anemones (Mouritsen & Poulin 2003c), which indirectly joins species in the web that would otherwise not be linked. Parasite species using a single intermediate host with a relatively high trophic position (such as crabs) had a less dramatic effect on mean food chain length than species that introduced links into food chains at a lower trophic level.

Discussion

Parasites are typically left out from analyses of food webs in natural systems (see Marcogliese & Cone 1997;

Morand & Gonzales 1997; Skorping & Högstedt 2001). In soft-sediment intertidal ecosystems, where parasites are particularly prevalent, excluding them can produce an incomplete picture of the community structure (Sousa 1991). Our results are consistent with those from the only other study to incorporate parasites into a marine food web (Huxham *et al.* 1995). This analysis also found that longer food chains resulted from the inclusion of parasites in a Scottish estuarine food web. Inclusion of parasites was also shown to alter other measures of food web structure such as intervality (Huxham, Beaney & Raffaelli 1996), and to reduce linkage density and connectance. We found weak evidence for lower connectance in our food web when parasites were included, but linkage density increased slightly. Our food web showed much higher internal linkage than that of Huxham *et al.* (1995). Logically, the inclusion of parasites affected the number of top species by relegating some top predators to an intermediate status. As the parasite definitive hosts were also top predators, parasite species with a large number of definitive hosts had the greatest effect on the number of top species.

The effects of the individual life cycle characteristics of parasites on food web attributes were particularly interesting. The inclusion of generalist species which affected many host species had the strongest effect on food web attributes. Indeed, the inclusion of the parasite *M. novaezealandensis* was sufficient to produce food web attributes which closely resembled those for the food web with all nine parasites included. As the generalist species are also more likely to be encountered in field sampling, this suggests that detection and incorporation of the most important parasites into food webs may be less problematic than it may appear. There was also evidence that the nature of the parasite

life cycle may affect food web attributes. Species with a single intermediate host which occupied a higher trophic position tended to have a lesser effect on mean food chain lengths.

Some of the species introduced singly into the food web had identical effects on food web topology (e.g. the *Profilicollis* spp. and Acuariidae sp., *Curtuteria australis* (Allison) and *Acanthoparyphium* sp.). Although binary food webs cannot distinguish the relative importance of each of the multiple hosts to each species, our data suggest relatively high overlap in food web position between some parasite species. This may suggest that competition for niches in these species is occurring within the host rather than in the wider arena of the community.

In terms of analysis of patterns in food webs, these results have some important implications. First, the lengthening of food chains shows that the simple hypotheses relating food chain length to primary productivity (Pimm 1982) or ecosystem size (Cohen & Newman 1988) are probably inadequate in settings where parasites are common. Equally this opens the way for new research seeking relationships between parasites and energy supply that may revitalize this area of debate. Secondly, the inclusion of parasites increased food web complexity. It is now becoming clear that, contrary to previous expectation (e.g. May 1973), complex systems are stable. The importance of weak interactions in determining stability has now been identified (McCann, Hastings & Huxel 1998), and the role of parasitic interactions in this scenario merits exploration.

The search for a better understanding of food web structure is driven mainly by a desire to understand the passage of energy through systems. Although our analysis shows clearly that parasites alter the architecture of a marine food web in fundamental ways, it cannot determine whether the pathways identified are energetically significant. Nevertheless, it seems likely that at least some parasites have a significant effect on energy budgets, given the energetic costs that parasites have at an individual (e.g. Munger & Karasov 1989; Kristan & Hammond 2000) and population level (Anderson 1977; Grenfell & Dobson 1995). We also cannot determine the structural or energetic consequences of the presence of parasites on food webs – our analysis can describe only the effects of inclusion or exclusion on the described attributes.

There is, however, considerable evidence that parasites can modulate the passage of energy through the New Zealand intertidal mudflat system. The larval stages of many parasitic helminths can alter the behaviour of their intermediate hosts in ways that make them more susceptible to predation by the parasites' definitive hosts (see Moore 2002). In our system, the trematodes *C. australis* and *Acanthoparyphium* sp. encyst in the foot of cockles, *Austrovenus stutchburyi* (Finlay), and prevent cockles from burrowing normally; cockles stranded at the sediment surface are more likely to be eaten by oystercatchers (Thomas & Poulin 1998;

Mouritsen 2002; Babirat *et al.* 2004). Similarly, the acanthocephalans *Profilicollis* spp. interfere with the normal hiding behaviour of their crab intermediate hosts, *Macrophthalmus hirtipes* (Heller) and *Hemigrapsus* spp., thus increasing the latter's vulnerability to gull predation (Latham & Poulin 2002a). In both examples, prevalence of the parasites in these hosts is about 100%, so their effects on prey choice by birds are potentially important in this system. In the absence of parasites, the relative amount of energy flowing in the food web from cockles-to-oystercatchers, and from crabs-to-gulls, would probably be greatly reduced. Parasites may also open completely new routes of energy transfer in the food web. In the example above, surface-stranded cockles are not only susceptible to higher predation rates by birds than burrowed cockles, they also experience non-lethal predation from the labrid fish *Notolabrus celidotus* (Bloch & Schneider), which crop the foot of surfaced cockles that try to burrow at high tide (Mouritsen & Poulin 2003a). This trophic relationship exists almost exclusively because of the parasite. From the average amount of foot tissue removed by fish, the rate of foot regeneration and the proportion of cockles incurring foot cropping, we estimate that the biomass going from cockles-to-fish may exceed 1000 mg wet weight m^{-2} $week^{-1}$ (Mouritsen & Poulin 2003b; Mouritsen 2004). Although this is only a modest proportion of total cockle biomass, surface-stranded cockles are also exploited by other predators, such as whelks (Ansell 2001), and the total cockle biomass diverted to other members of the food web because of parasitism is probably not negligible. This illustrates clearly that the indirect effects of parasites on their hosts can open new pathways of energy transfer through existing food webs.

The next crucial step will be to obtain actual quantitative estimates of both the direct and indirect effects of parasitism on energy flow through the web, and on interaction strength and food web stability. This is logistically difficult, but not unrealistic for certain ecosystems where parasite diversity is low and field experiments are feasible. It may not even be necessary to quantify the influence of every parasite species on energy flow. Our results indicate that all parasites are not equal: parasites with complex life cycles and low host specificity are likely to have greater impacts on food webs than those using one or few host species. Another interesting direction for future research would be to examine the composition of the parasite fauna in different systems, to determine whether the proportion of parasite species with complex life cycles varies among different types of systems, and how this relates with other ecosystem properties such as biodiversity or productivity.

Acknowledgements

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