Food web topology and parasites in the pelagic zone of a subarctic lake

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Summary

1. Parasites permeate trophic webs with their often complex life cycles, but few studies have included parasitism in food web analyses. Here we provide a highly resolved food web from the pelagic zone of a subarctic lake and explore how the incorporation of parasites alters the topology of the web.

2. Parasites used hosts at all trophic levels and increased both food-chain lengths and the total number of trophic levels. Their inclusion in the network analyses more than doubled the number of links and resulted in an increase in important food-web characteristics such as linkage density and connectance.

3. More than half of the parasite taxa were trophically transmitted, exploiting hosts at multiple trophic levels and thus increasing the degree of omnivory in the trophic web.

4. For trophically transmitted parasites, the number of parasite–host links exhibited a positive correlation with the linkage density of the host species, whereas no such relationship was seen for nontrophically transmitted parasites. Our findings suggest that the linkage density of free-living species affects their exposure to trophically transmitted parasites, which may be more likely to adopt highly connected species as hosts during the evolution of complex life cycles.

5. The study supports a prominent role for parasites in ecological networks and demonstrates that their incorporation may substantially alter considerations of food-web structure and functioning.

Key-words: connectance, ecological networks, linkage density, parasitism, trophic transmission

Introduction

On his 1732 expedition to subarctic Lapland, Carl von Linnè found the lake fish so heavily infected with parasitic worms that he refused to eat them (*Iter Lapponicum*; published posthumously). The fish were Arctic charr *Salvelinus alpinus* (L.) of which the most conspicuous parasites are tapeworm larvae of the genus *Diphyllobothrium* living in the viscera and muscles. These cestodes have a complex life cycle. They are transmitted from copepods to fish (an intermediate host), and then transfer and develop into their adult stage when a suitable final host, bird or mammal, consumes an infected fish. Some species may even establish as adults in the intestine of those humans who, unlike Linnaeus, eat undercooked fish (Vik 1957; Halvorsen 1970). As for Linnaeus, the abundant

parasites of Arctic charr captured our attention, and we sought to understand their role in the food web of a subarctic lake.

Food webs depict ecological communities via networks of trophic relationships (e.g. Cohen *et al*. 1990; Martinez 1991, 1992; Pimm, Lawton & Cohen 1991; Williams & Martinez 2000; Winemiller *et al*. 2001; Montoya & Solé 2003). The relationship between food-web complexity and ecosystem stability has been of particular interest (e.g. Bascompte *et al*. 2003; Dunne *et al*. 2005; May 2006; Allesina & Pascual 2008). Topological (who eats whom) webs (Martinez 1991, 1992; Williams & Martinez 2000; Borer *et al*. 2002; Montoya & Solé 2003) assess food-web characteristics using species richness (S; also referred to as the number of nodes in the network) and the number of species interactions or links (L). Other properties of topological webs include connectance (C), often defined as L divided by the maximum possible number of links, i.e. L/S^2 (directed connectance; Martinez 1991), and linkage density

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(L/S). Such metrics, quantifying complexity, are also important determinants of web stability (Dunne 2006; Allesina & Pascual 2008).

Food webs of freshwater lakes are well studied, especially in relation to trophic cascades in the pelagic zone (Carpenter, Kitchell & Hodgson 1985, Carpenter *et al*. 2001; Shurin *et al*. 2002). Several high-resolution food webs exist from small lakes and ponds (Warren 1989; Martinez 1991; Havens 1992; Jonsson, Cohen & Carpenter 2005), and a few large systems (Kitchell *et al*. 2000; Mills *et al*. 2003). Analyses of lacustrine food webs have contributed substantially to the development of food-web theory (Martinez 1992; Williams & Martinez 2000; Cohen, Jonsson, & Carpenter 2003). Several recent studies indicate important interactions between predators and parasites of zooplankton and phytoplankton in lakes (e.g., Johnson *et al*. 2006; Duffy 2007; Kagami *et al*. 2007). However, except for a survey of metazoan endoparasites in fish and birds which was included in the food-web analyses of Loch Leven, Scotland (Huxham, Raffaelli & Pike 1995), the role of parasites in lake food webs is generally unexplored.

Parasites permeate food webs with their often complex life cycles (Marcogliese & Cone 1997; Lafferty & Kuris 2002; Lafferty, Dobson & Kuris 2006a; Hernandez & Sukhdeo 2008). Trophically transmitted parasites are particularly embedded in the networks, as they use trophic interactions to transfer up through a food chain. A growing awareness of the role of parasitism in ecosystems has included an increasing interest in the role of parasites in food webs (Huxham *et al*. 1995; Marcogliese & Cone 1997; Marcogliese 2003; Thompson, Mouritsen & Poulin 2005; Dobson, Lafferty & Kuris 2006; Lafferty *et al*. 2006a,b, 2008; Wood 2007; Hernandez & Sukhdeo 2008, Kuris *et al*. 2008). Adding parasites to food webs results in increases in parameters such as species richness, links, trophic levels, and food chain length (Huxham *et al*. 1995; Memmott, Martinez & Cohen 2000; Thompson *et al*. 2005). In salt marshes, parasites have furthermore been shown to increase linkage density, connectance and nestedness, and they disproportionately increase the vulnerability of top trophic levels to natural enemies (Lafferty *et al*. 2006b). In a stream food web, the inclusion of parasites similarly increased linkage density and connectance, whereas nestedness decreased (Hernandez & Sukhdeo 2008).

As an overall result, parasites appear to increase the food-web complexity and may thus potentially enhance biodiversity and production (Hudson, Dobson & Lafferty 2006), and alter ecosystem stability (Dobson *et al*. 2006; Wood 2007; Allesina & Pascual 2008). There is, however, an apparent demand for further examination of the generality of these findings, as the role of parasitism for the topology of food webs has been thoroughly explored only in a few ecosystems, including estuary, mudflat, salt marsh and stream systems (Hernandez & Sukhdeo 2008). Here we provide a high-resolution topological food web with parasites from the pelagic zone of a subarctic lake in northern Scandinavia. We investigated how parasitism influenced the topology of the food web, hypothesizing that the inclusion of parasites alters important metrics related to network complexity such as linkage density, connectance, and nestedness. As many parasites use trophic interactions to transfer between hosts, we also asked whether the linkage density of host species affected the linkage density of their parasites, particularly in respect to trophically transmitted parasites.

Methods

ENVIRONMENTAL CHARACTERISTICS OF THE STUDY AREA

The study lake Takvatn (69°07′ N, 19°05′ E) is a subarctic, oligotrophic and dimictic lake situated in northern Norway, 300 km north of the Arctic Circle and at an altitude of 214 m. Mountains and a landscape dominated by birch (*Betula pubescens* Ehrh.) with scattered pine trees (*Pinus sylvestris* L.) and patches of farmland surround the watershed. The area of the lake is 14·2 km², and there are two main basins, both with a maximum depth of about 80 m. The climate is subarctic with an average air temperature in July of 13·2 °C. Winter temperatures are low, averaging –10 °C in January. The polar night lasts from late November to late January and the period with midnight sun lasts from late May until late July. The ice-free season normally extends from June to November, with summer stratification from mid-July to the end of August. The maximum epilimnetic temperature is approximately 14 °C, and the thermocline occurs at 10–14 m depth (Primicerio & Klemetsen 1999; Primicerio 2000). Secchi depth ranges between 14 m and 17 m, and total phosphorus concentration does not exceed 5 µg L^{-1} (Primicerio & Klemetsen 1999). The pH is neutral to slightly alkaline.

DEFINING THE STUDY SYSTEM

Takvatn (the suffix 'vatn' means 'lake') has been investigated annually since 1979. The bulk of the research has been on the population dynamics, feeding and parasite ecology of the fish community (e.g. Amundsen & Klemetsen 1988; Klemetsen *et al*. 1989, 2002; Amundsen, Klemetsen & Grotnes 1993; Jørgensen & Klemetsen 1995; Knudsen 1995; Knudsen, Klemetsen & Staldvik 1996; Amundsen, Knudsen & Klemetsen 2007; Persson *et al*. 2007). The zooplankton community has also been extensively studied (e.g. Dahl-Hansen, Rubach & Klemetsen 1994; Dahl-Hansen 1995; Primicerio & Klemetsen 1999; Primicerio 2000, 2005), and the composition and abundance of phytoplankton have been explored (Primicerio 2000). A few systematic bird censuses are available for the breeding season (A. Klemetsen & R. Knudsen, unpublished data). The availability of such detailed information provides the opportunity to develop a comprehensive and accurate topological food web for the pelagia of the lake. This is a source web (*sensu* Cohen 1978), including only trophic relationships among species that arise from phytoplankton as the basal energy source. We further constrained the food web spatially to species utilizing the open-water limnetic zone as a feeding habitat and temporally to comprise the ice-free season of the lake. With respect to parasites, we only included taxa that use pelagic dwelling species as their hosts.

THE NODES AND LINKS

Information about the nodes and links of the Takvatn pelagic food web was integrated from studies carried out from 1986 to 2007. We used species as our preferred taxonomic unit, and all consumers,

most phytoplankton and all parasites except fungi have been identified to the species or genus level. Although different life stages of parasites differ substantially in their ecology and could be treated as separate trophic species (Huxham *et al.* 1995; Dobson *et al.* 2006), for most analyses, the splitting of species into trophic species may produce artificial results for linkage density, connectance and omnivory (Huxham *et al.* 1995). For this reason, we treated different life-cycle stages of a parasite as one species, just as we have not separated different ontogenetic stages of free-living species with distinct niche shifts (like e.g. the copepods) into trophic species. We primarily used information from Ruttner samplers (phytoplankton), zooplankton net hauls, fish gillnetting, and bird surveys to compile our species list. For each sampling method, we excluded species that comprised < 1% of the individuals sampled. A few top predators [in particular, the loons *Gavia arctica* (L.) and *Gavia stellata* (Pont.)] that failed the abundance criterion were included because higher trophic levels can be relatively important in food webs even if relatively rare (Lafferty *et al.* 2006b).

Topological food webs consist of an $n \times n$ matrix on n species, with predators as columns and prey as rows (Cohen 1978). Binary entries (e.g. 0 or 1) in the matrix indicate whether a predator eats a prey species. Most carnivorous predator–prey links were documented from our own dietary observations, whereas for other consumers, we consulted published information on diets. Parasites can also be useful indicators of host diets (Knudsen *et al.* 1996; Marcogliese & Cone 1997; Bertrand, Marcogliese & Magnan 2008). For parasites acquired with food, the living parasite resides in the host far longer than the digested food item stays in the gut, providing a robust indicator of host diet (Marcogliese 2003). Accordingly, a species that serves as an intermediate host for a parasite known to occur in a specific predator is likely to be a prey for that predator (Huxham *et al.* 1995; Marcogliese 2003; Lafferty *et al.* 2006b). A few predator–prey links (1·5% of the total number of predator–prey links) were thus logically inferred from the presence of a trophically transmitted parasite in species at adjacent trophic levels.

Information on parasites came from extensive parasite studies on the fish populations of the lake, more restricted parasite surveys of invertebrates and birds, as well as from a comprehensive literature review of taxa that are potential parasites of the free-living organisms present in the study system. Tentative host–parasite links were only included in the web when the parasite was known to be able to develop or reproduce successfully in the specific host. For bird parasites, we only included intestinal helminths present in their intermediate stages in pelagic organisms in the lake (exclusively fish), and excluded parasites species that complete their life cycles in other habitats (e.g., during winter migrations). Similarly, for fish, we only included parasite species acquired in the pelagic zone. Helminths and other macroparasites have been thoroughly covered by our parasite surveys, whereas less complete resolution and information are available with respect to protozoan and fungal parasites. Protozoa and fungi probably parasitize most invertebrates. Fungi, for example, have been observed on some of the crustacean zooplankton species in the lake, but as they are taxonomically poorly understood (Ebert 2005), we grouped them into a single group. A similar consideration was made with respect to fungal parasites of phytoplankton (Ibelings, de Bruin & Van Donk 2003; Kagami *et al.* 2007). Because fungal species frequently parasitize rotifers (e.g. Barron 1980, 1991), we also assumed that this link occurred in the lake (including or excluding this hypothetical group did not alter our conclusions). Crustacean zooplankton, in particular *Daphnia*, were screened for microsporidians and other microparasites according to the procedure described by Ebert (2005; and Ebert, D. Web-guide to *Daphnia* parasites), but none were observed.

INCORPORATING PARASITES INTO THE WEB

We organized the food web into four subwebs, after Lafferty *et al.* (2006a,b). Predator–prey and parasite–host subwebs are obvious and have been included in earlier studies (Huxham *et al.* 1995; Memmott *et al.* 2000; Thompson *et al.* 2005; Hernandez & Sukhdeo 2008). Less obvious are predator–parasite and parasite–parasite subwebs. The predator–parasite web describes links when a predator eats a parasite. This is most likely to happen when a predator consumes an infected prey and digest the included parasite. It also includes potential predation of free-living stages such as trematode cercariae (Lafferty *et al.* 2006a,b). The parasite–parasite subweb includes hyperparasites and parasites that prey on other parasites, for example intraguild predation among larval trematodes (Kuris 1990; Lafferty, Sammond & Kuris 1994; Huspeni & Lafferty 2004). In the present pelagic trophic web, the first three subwebs were present, whereas no parasite–parasite interactions have been identified.

FOOD-WEB METRICS

To assess the effects of parasitism on food-web properties, we calculated several metrics of webs with and without parasites, including species richness (S), number of links (L) and linkage density ($D = L/S$). The potential number of links, L_P, in a symmetrical matrix of $S \times S$ species (such as a predator–prey subweb or a complete web) is equal to the number of cells in the matrix (S^2). For a subweb comprised of two separate species lists (such as X parasites and Y hosts), the number of cells in the matrix is XY and not S^2, and hence $L_P = XY$ (Lafferty *et al.* 2006b). Connectance (C) is the realized number of links as a proportion of the potential number of links, i.e. $C = L/L_P$. Nestedness (a measure borrowed from island biogeography) describes the extent to which specialist consumers eat a subset of the prey eaten by generalists. To estimate the nestedness of Takvatn, we first calculated matrix temperature (a measure of absolute nestedness) using software described by Rodríguez-Gironés & Santamaría (2006) that compares the extent to which a food web is significantly nested with randomized matrices. To allow easier comparison among networks, we then estimated relative nestedness after Bascompte *et al.* (2003).

We also explored the variation in parasite richness per host in the web. Here, the number of parasite species per host was the dependent variable and the type of parasitism (expressed as percentage of links involving trophic transmission), and the number of links with free-living species (predator–prey links) were the independent factors. Because assumptions of a general linear model could not be met, we used a generalized linear model (log-link function with Poisson distribution). The initial model also considered interaction between these main effects, but the interaction was nonsignificant and removed. To consider how vulnerability to predation affected parasite diversity, we also plotted the association between predator–prey links and parasite–host links for two types of host species: those parasitized mostly by trophically transmitted parasites and those not parasitized by trophically transmitted parasites.

Results

The total pelagic food web included 50 nodes, consisting of eight basal species, 29 free-living predators and 13 parasitic taxa (Fig. 1; See Table S1–S4, Supporting information for details). The basal species were represented by the dominant phytoplankton taxa (Ph1–Ph8). The free-living predators

(a)

(b)
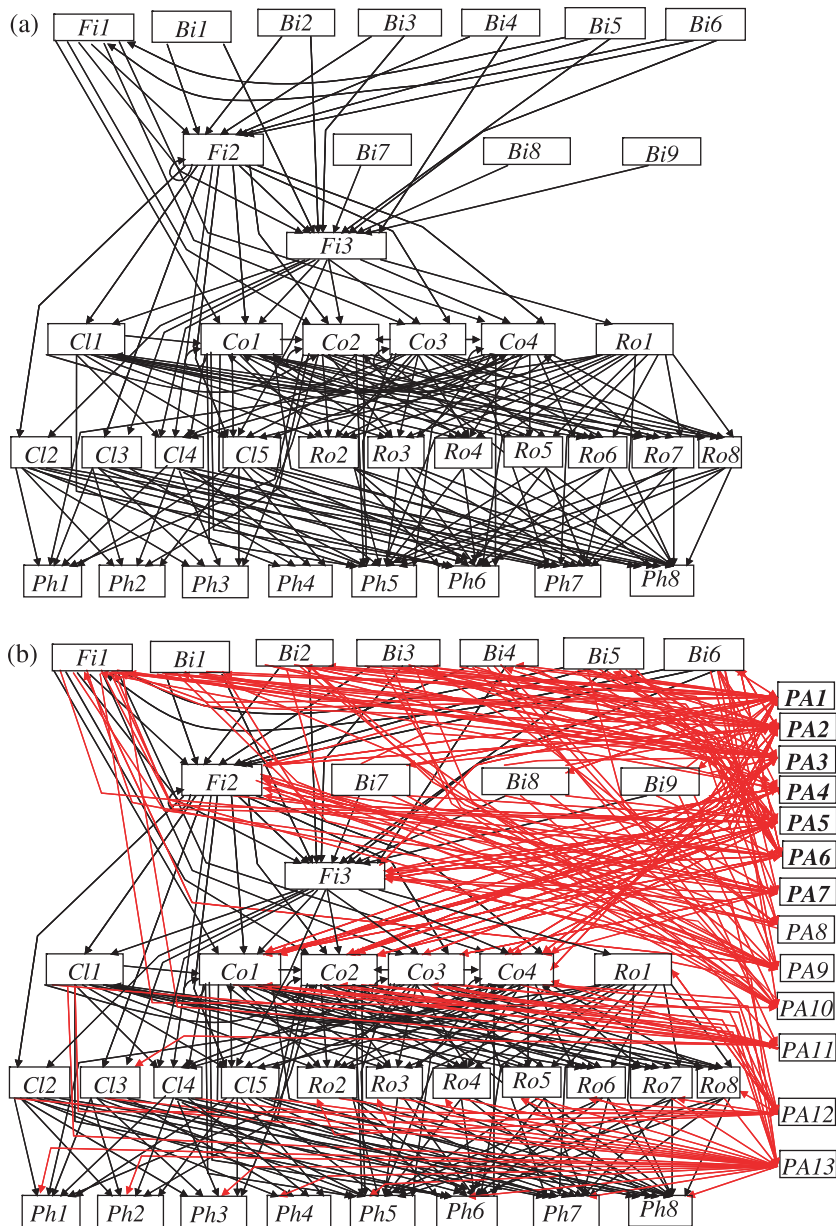
Fig. 1. Pelagic food web of the subarctic lake Takvatn (a) without and (b) with parasite-related links included. Predator–prey links are indicated by black lines whereas parasite–host and predator–parasite links are indicated by red lines. Nodes include: **Phytoplankton** (*Asterionella formosa* Ph1, *Cyclotella comensis* Ph2, *Cyclotella kützingiana* Ph3, *Stephanodiscus medius* Ph4, Chrysomonads Ph5, *Ceratium hirundinella* Ph6, *Gymnodinium helveticum* Ph7, *Elakatothrix genevensis* Ph8); **Rotifers** (*Asplanchna pridonta* Ro1, *Keratella cochelearis* Ro2, *Kellicottia longispina* Ro3, *Polyarthra* sp. Ro4, *Synchaeta* sp. Ro5, *Ascomorpha* sp. Ro6, *Conochilus unicornis* Ro7, *Filinia gr. longiseta-terminalis* Ro8); **Cladocerans** (*Polyphemus pediculus* Cl1, *Holopedium gibberum* Cl2, *Daphnia galeata* Cl3, *Bosmina longispina* Cl4, *Bosmina longirostris* Cl5); **Copepods** (*Cyclops scutifer* Co1, *Eudiaptomus graciloides* Co2, *Acanthocyclops gigas* Co3, *Heterocope appendiculata* Co4); **Fish** (brown trout *Salmo trutta* Fi1, Arctic charr *Salvelinus alpinus* Fi2, three-spined sticklebacks *Gasterosteus aculeatus* Fi3); **Birds** common gull *Larus canus* Bi1, Arctic tern *Sterna paradisaea* Bi2, red-breasted merganser *Mergus serrator* Bi3, long-tailed duck *Clangula hyemalis* Bi4, Arctic loon *Gavia arctica* Bi5, red-throated loon *Gavia stellata* Bi6, common scoter *Melanitta nigra* Bi7, tufted duck *Aythya fuligula* Bi8, goldeneye *Bucephala clangula* Bi9); **Parasites** (*Diphyllobothrium dendriticum* PA1, *Diphyllobothrium ditremum* PA2, *Eubothrium salvelini* PA3, *Eubothrium crassum* PA4, *Proteocephalus* sp. PA5, *Schistocephalus solidus* PA6, *Philonema oncorhynchi* PA7, *Salmincola edwardsii* PA8, *Gyrodactylus arcuatus* PA10, Saprolegnia PA9, Fungi on crustacean zooplankton PA11, Rotiferophthora PA12, Chytridiomycetes PA13). Trophic transmitted parasites are indicated in bold.

were distributed over five trophic levels, including seven top and 22 intermediate predators (Fig. 1a). The first and second consumer levels comprised rotifers (Ro1–Ro8) and crustacean zooplankton (including cladocerans, Cl1–Cl5, and copepods, Co1–Co5), whereas the upper three levels included three fish (Fi1–Fi3) and nine bird species (Bi1–Bi9). Parasites (including cestodes, PA1–PA6; nematodes, PA7; parasitic copepods, PA8; monogenenans, PA10; and fungi, PA9 and PA11–13) infected hosts at all trophic levels, including the basal and top-predator species (Fig. 1b). There was an average of 6·8 prey species per predator species and 5·8 host species per parasite species.

The predator–prey subweb included 37 species and had 1369 potential links of which 198 links were observed, resulting in a directed connectance of 0·145 (Table 1). Like many pelagic ecosystems, the food web was 'wasp-waisted', with high diversity in the low and high trophic levels, whereas one of the

intermediate levels was represented only by a single species, the three-spined stickleback, *Gasterosteus acculeatus* L. (Fi3, Fig. 1a). Diet breadth peaked at the second consumer level and declined towards the top trophic levels (Fig. 2a), a pattern that partly resulted from the exclusion of benthic and terrestrial species in our pelagic source web analysis. The degree of omnivory also peaked at the second consumer level, but was high at the top level as well (Fig. 2b). Cannibalistic links occurred, but at a low frequency (approx. 2% of all predator–prey links). A few horizontal links (Fig. 1a) resulted from the consumption of early ontogenetic stages of some species, e.g. adult *Cyclops scutifer* Sars (Co1) preying upon nauplii of *Heterocope appendiculata* Sars (Co4), and vice versa.

The parasite–host and the predator–parasite subwebs both had 481 potential links of which 75 parasite–host and 159 predator–parasite links were observed, for a directed

Table 1. Summary of food web metrics. No parasite–parasite links were observed, so statistics for this subweb are not presented. Connectance for the predator–prey + parasite–host subweb were calculated using an asymmetrical matrix (limiting the potential number of links to the two subwebs)
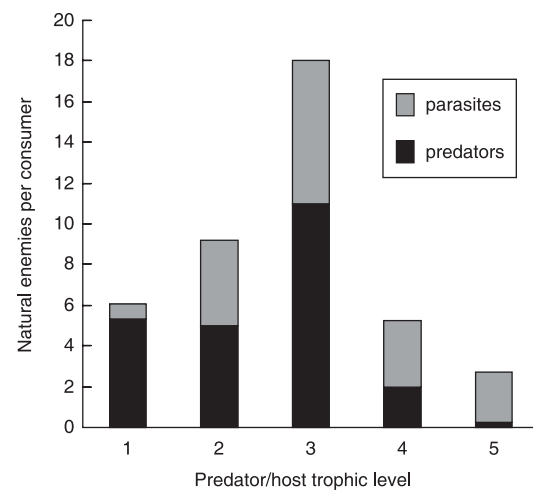
Parameters	Total food web	Predator–prey subweb	Parasite–host subweb	Predator–Prey + Parasite-host subweb	Predator–parasite subweb
Number of species; S	50	37	50	50	50
Potential no. of links; L_p	2500	1369	481	1850	481
Observed no. of links; L	432	198	75	273	159
Linkage density; L/S	8·64	5·36	1·50	5·46	3·18
Connectance; C	0·173	0·145	0·156	0·148	0·331
Omnivory*	2·05	1·86	2·46	2·05	–
Relative nestedness	0·23	0·10	–	0·24	–

*Omnivory = average no. of trophic levels being fed on.
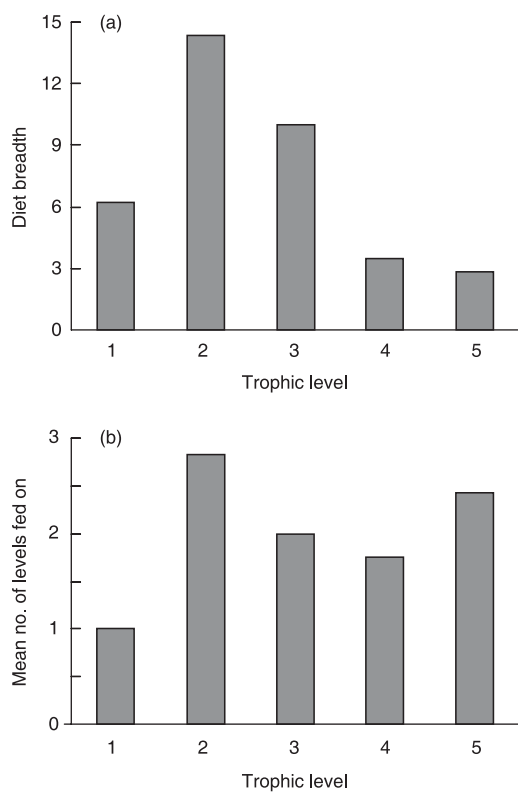
Fig. 2. Diet breadth (a) and omnivory (b) (i.e., the mean number of trophic levels that are fed on) of free-living species at different trophic levels of the Takvatn pelagic food web.

Fig. 3. Vulnerability to natural enemies at different trophic levels of the Takvatn pelagic food web.

connectance of 0·156 and 0·331, respectively. The inclusion of parasites in the total food web increased the number of nodes from 37 to 50 (Fig. 1b), but also substantially increased the number of links from 198 to 432, resulting in an overall increase in directed connectance from 0·145 to 0·173 (Table 1). Thus, 54·2% of the links in the total food web were parasite-related, even though parasites constituted only 26% of the total number of species. The linkage density increased from 5·35 in the predator–prey food web to 8·64 in the total web including parasites, whereas the mean (± SE) degree

of omnivory increased from 1·86 (± 0·18) to 2·07 (± 0·16). Trophically transmitted parasites (PA1–PA7) were involved in a higher number of links and contributed more to the increased connectance and linkage density than nontrophically transmitted parasites (PA8–PA13). Hence, an inclusion of only the trophically transmitted parasites in the food web resulted in a directed connectance and linkage density of 0·178 and 7·82, respectively, compared to 0·155 and 6·65 when only the nontrophically transmitted parasites were included.

The vulnerability to predators (i.e. the number of predator species using each prey species) generally decreased with increasing trophic level of the consumer species (Fig. 3) with the exception of sticklebacks at the mid-trophic level (Fi3; Fig. 1a). In contrast, the vulnerability to parasites (i.e. the number of parasite species using each host species) was lowest at the first consumer level, increased towards the mid-trophic level and thereafter decreased. The overall result was that the intermediate trophic levels were the most vulnerable to natural enemies (Fig. 3).

The degrees of a node increased distinctly from the predator–prey subweb to the total trophic web including parasites
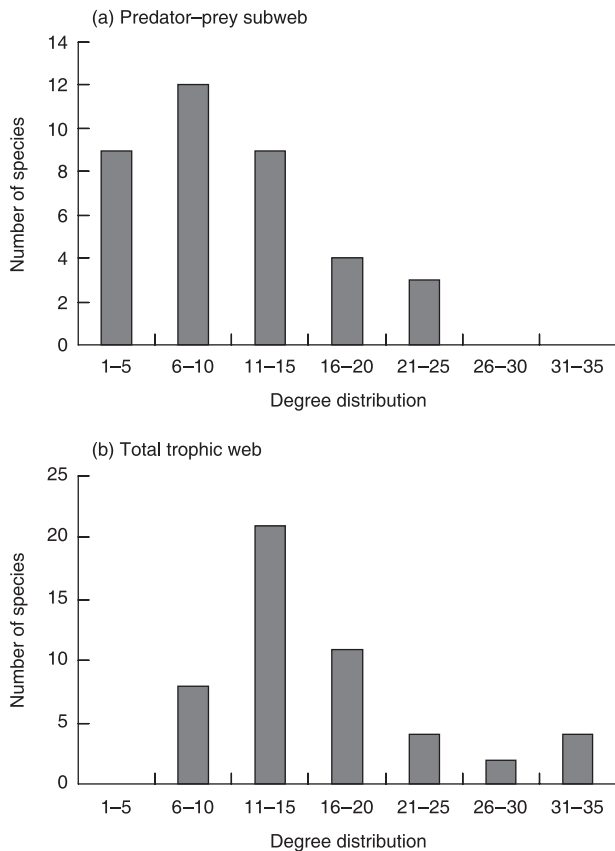
(a) Predator–prey subweb

(b) Total trophic web

Fig. 4. Frequency distributions of links in (a) the predator–prey subweb, and (b) the total pelagic food web including parasites.

Fig. 5. The relationship between the number of predator–prey links around a host species and the number of parasite–host links observed. To illustrate the effect of parasite type in the analysis (see Results for information on the generalized linear model), for the purpose of the figure, we divided host species along a bimodal distribution for those exclusively parasitized by nontrophically transmitted parasites (white circles) and those parasitized mostly by trophically transmitted parasites (dark circles). The stippled line indicates the linear regression relationship between the numbers of predator–prey and parasite–host links for host species parasitized mostly by trophically transmitted parasites ($y = 1·416x + 0·138$; $R^2 = 0·85$, $P < 0·001$). No significant relationship occurred for host species parasitized exclusively by nontrophically transmitted parasites ($P > 0·05$).

(Fig. 4), with the mean (± SE) number of links per node being 10·5 (± 1·07) links for the predator–prey subweb and 16·1 (± 0·99) links for the total web. The most highly linked species in the predator–prey subweb were the two copepod species *C. scutifer* and *Eudiaptomus graciloides* (Lilljeborg) (Co1 and Co2; both with 24 links) as well as three-spined sticklebacks (Fi3; 21 links) and Arctic charr (Fi2; 19 links). After the inclusion of parasites in the total web, these four species were still, by far, the most connected nodes, with 32–34 links around each species. Some parasite species were also highly connected (> 20 links), including the trophically transmitted *Diphyllobothrium dendriticum* (Nitzsch) (PA1), *Diphyllobothrium ditremum* (Creplin) (PA2), *Protocephalus* sp. (PA5) and *Schistocephalus solidus* (Müller) (PA6). The trophically transmitted parasites had an average (± 95% CI) of 2·72 (± 0·18) hosts at each stage in their life cycle, for a total of 7·0 (± 1·1) hosts, on average, per parasite species.

The number of parasite taxa present in a host species was well explained by the types of parasites in the host and the number of links between the host and other free-living species (generalized linear model, $N = 33$, d.f. = 2, $\chi^2 = 43·46$, $P < 0·0001$). In this analysis, the parasite richness in a host increased with the number of free-living links (d.f. = 1, $\chi^2 = 27·13$, $P < 0·0001$). In addition, hosts with many parasites tended to have a high proportion of trophically transmitted parasites (d.f. = 1,
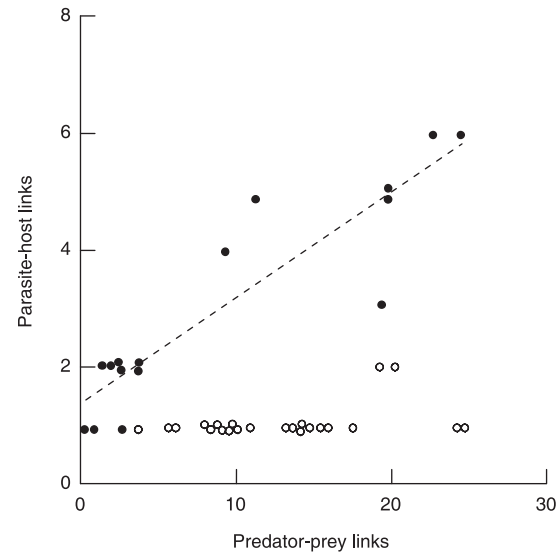
$\chi^2 = 22·57$, $P < 0·0001$). There was no significant interaction between these effects in the generalized linear model. However, plotting parasite diversity as a function of vulnerability to parasites revealed that a strong positive relationship existed only for those host species infected primarily by trophically transmitted parasites (Fig. 5).

All webs were significantly nested in comparison to randomized matrices (Monte Carlo re-sampling, $P < 0·0001$). Adding the parasite–host web to the predator–prey web more than doubled relative nestedness from 0·10 to 0·24. Adding the predator–parasite matrix did not affect nestedness.

Discussion

The present study clearly demonstrates that parasites are important constituents of the pelagic food web of a subarctic lake and have a large impact on the structure and function of the trophic web. The inclusion of parasites more than doubled the number of links and resulted in an increase in important food web characteristics such as linkage density, connectance, omnivory, food chain length, relative nestedness, and the number of trophic levels. Moreover, the intermediate trophic levels were most vulnerable to natural enemies as also observed in a salt marsh web (Lafferty *et al.* 2006a). Our main

findings also support the most evident conclusions of the few other studies that have integrated parasites in food-web analyses, including increased food chain lengths and number of trophic levels (Huxham *et al.* 1995, Memmott *et al.* 2000; Thompson *et al.* 2005; Lafferty *et al.* 2006a,b; Hernandez & Sukhdeo 2008). The most comparable analysis to ours is the food web of the Carpinteria Salt Marsh, California (Lafferty *et al.* 2006a,b), for which the effects of parasites appeared even more dramatic than what we report for Takvatn. For instance, parasites were involved in a higher proportion of links in the salt marsh than in the Takvatn food web (78% vs. 54%), and the former study also found a greater increase in connectance following the inclusion of parasites (93% vs. 19% increase). Adding parasites quadrupled nestedness in the salt marsh web, as opposed to the doubling seen in Takvatn (parasites affected relative nestedness in Takvatn through the addition of the parasite–host subweb, while in the salt marsh it was through the addition of the predator–parasite web). A high number of parasite–parasite links was furthermore documented in the salt marsh system, mainly among trematodes (Lafferty *et al.* 2006a,b), whereas no similar trophic interactions were observed between the parasites in the Takvatn web.

An analytical approach comparable to the Takvatn and Carpinteria food-web studies was applied for the trophic web of Muskingum Brook in the Mullica river watershed, New Jersey (Hernandez & Sukhdeo 2008), except for the principal difference that predator–parasite and parasite–parasite links were not explored and quantified in the latter study. A comparison of results reveals that the three food webs responded similarly to the inclusion of parasites, despite the fact that a species-poor subarctic lake system is contrasted with a temperate riverine and a species-rich marine system. In particular, similar conclusions as for the Takvatn and Carpinteria webs were reached for the Muskingum Brook web with respect increased linkage density and connectance after the inclusion of parasites. The relative nestedness in contrast decreased in the Muskingum web (Hernandez & Sukhdeo 2008), but an inclusion of predator–parasite and parasite–parasite links in the matrix may potentially have resulted in an analogous increase as seen with the Takvatn and Carpinteria webs. All other important food-web metrics responded similarly in these three systems. The increases were, however, more pronounced for the Carpinteria food web than the Takvatn and Muskingum webs, both with respect to linkage density and connectance (predator–parasite and parasite–parasite links not included). The more dramatic effect of parasites in the salt marsh web may partly be related to a broader parasite census that included some viruses and protozoans. Furthermore, the salt marsh web included several parasites groups, in particular trematodes, which require benthic hosts, whereas the benthic food web compartment was not included in the Takvatn study.

The higher connectance due to parasite–hosts relationships observed in the present and other related studies does not necessarily imply reduced food web stability, as suggested by early theory (May 1974). Weak trophic interactions have for instance been shown to promote the stability of food webs (McCann, Hastings & Huxel 1998; Berlow 1999). Recent theoretical developments furthermore stress that the number of consumer-resource interactions can be high and still lead to stable food webs, as long as the structure rather than the strength of interactions promotes the stability of the community modules composing the food web (Allesina & Pascual 2008). Indeed, food transmitted parasites may help stabilize predator–prey modules composing a food web by changing the demographic and interaction parameters of predator and prey populations. In particular, the dynamics of predator–prey populations tend to be destabilized by high intrinsic growth rates of prey relative to predator, and by low efficiency and rapid saturation of the predator's functional responses (Begon, Townsend & Harper 2006). Food-transmitted parasites reduce the intrinsic growth rate of prey hosts via sublethal effects, and improve the hunting efficiency of predators by impairing prey host escape ability or otherwise changing prey behaviour so as to increase its vulnerability. Both nonlethal effects on intermediate hosts and increased vulnerability of intermediate hosts to their predators are adaptive to food transmitted parasites, but not to parasites that are directly transmitted, an important distinction between these two classes of natural enemies.

The predator–prey web in Takvatn constitutes a typical pelagic food web with energy transfer from phytoplankton, via rotifers, cladocerans and copepods to fish and birds. The web also represents a typical size hierarchy with a general increase in body size of more than one order of magnitude between consecutive trophic levels, the size differences being particularly large in the lower parts of the web. For parasite–host links, this size hierarchy is reversed, as parasites in general are much smaller than their definitive hosts. The incorporation of parasites in food webs is thus at variance with the typically anticipated role of body size in food-web structure as assumed by for example the cascade model (Cohen *et al.* 1990, 1993). Another emergent intricacy relates to the possibility of a combined ingestion of both a free-living prey and its potential parasites by the predator. When consumed by a suitable host, the ingestion of the parasite will usually lead to trophic transmission of the parasite from one host to the next (i.e. a parasite–host link). If the predator is not a suitable host, the ingestion will in contrast lead to the death of the parasite. If, for example, a three-spined stickleback parasitized by e.g. *D. dendriticum*, *S. solidus* and *Gyrodactylus arcuatus* Bychowsky is consumed by an Arctic charr, the *D. dendriticum* plerocercoids can transmit to the charr whereas the charr will digest the *S. solidus* and *G. arcuatus*. Predator–parasite links were highly prevalent in the Takvatn food web, and their inclusion in the food-web analysis allows consideration of mortality and transmission for parasite populations.

A few free-living species (in particular *C. scutifer*, *E. graciloides*, three-spined sticklebacks and Arctic charr) were highly connected nodes in the predator–prey network in Takvatn. These species fed on many prey species and were exploited by many predators, and thus had a central role in

the free-living trophic web. Interestingly, these species were also the most common hosts for trophically transmitted parasites. More than half of the parasite taxa in the pelagic food web in Takvatn were trophically transmitted, proceeding along the food chains from one host to the next during the completion of their life cycles. As a consequence, these parasites exploit hosts at multiple trophic levels, and their presence increases the degree of omnivory in the food web. The strong positive relationship between the diversity of trophically transmitted parasites in a host and the number of predator–prey links around a host suggests that the linkage density of potential host species may affect their exposure to trophically transmitted parasites. These findings may also relate to the evolution of complex life cycles in parasites as the use of highly connected species as hosts may enhance transmission. However, a strategy involving many and highly connected host species enhances the likelihood of trophic transmission at the potential cost of an increased hazard of accidental consumption by an unsuitable host. In contrast, specialization on a single host with low linkage density will reduce the probability of accidental predation by a nonhost, but may also severely reduce the possibilities for trophic transmission and subject such a parasite to population fluctuations based on changes in abundance of a single host species. In the Takvatn pelagic web, most trophically transmitted parasites like the two *Diphyllobothrium* species use a generalist strategy, parasitizing highly connected host species and having several alternative hosts at each life stage. Given the high fecundity of these common parasites, an adaptation towards increased transmission possibilities at the risk of accidental predation appears to be a reasonable and selectively advantageous strategy. It is also likely that parasites alter some of the predator–prey links. Behavioural modifications that increase the trophic transmission of parasites (Kuris 1997; Lafferty 1999) might attract more predators to an infected prey species (Mouritsen & Poulin 2003). Such a positive feedback between hosts and parasites may drive important aspects of food-web complexity, including interaction strength and nestedness.

In conclusion, parasites play a prominent role in the trophic network in Takvatn, resulting in distinct alterations in the topology of the food web. The parasite-associated changes in web structure seen in Takvatn and also shown by Lafferty *et al.* (2006a) and Hernandez & Sukhdeo (2008), indicate that common web assumptions such as those concerning complexity, stability, vulnerability to consumers and the role of body size should be revaluated in the context of a parasitized world. The dual roles of consumption and transmission by parasites hint that they may significantly and selectively alter interaction strength of web links. Furthermore, our findings suggest that parasites may be more likely to adopt highly-connected hosts during the evolution of complex life cycles. It is understandable that Linnaeus chiefly ignored parasite species in his epochal taxonomic and systematic works. 300 years later, it seems appropriate to fully integrate parasites into community ecology and to accentuate their potential roles in food web structure and dynamics.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Table S1. List of basal food items

Table S2. List of invertebrates

Table S3. List of fishes and birds

Table S4. List of parasites

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