COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Vulnerability and diet breadth predict larval and adult parasite diversity in fish of the Bothnian Bay

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Abstract Recent studies of aquatic food webs show that parasite diversity is concentrated in nodes that likely favour transmission. Various aspects of parasite diversity have been observed to be correlated with the trophic level, size, diet breadth, and vulnerability to predation of hosts. However, no study has attempted to distinguish among all four correlates, which may have differential importance for trophically transmitted parasites occurring as larvae or adults. We searched for factors that best predict the diversity of larval and adult endoparasites in 4105 fish in 25 species studied over a three-year period in the Bothnian Bay, Finland. Local predator–prey relationships were determined from stomach contents, parasites, and published data in 8,229 fish in 31 species and in seals and piscivorous birds. Fish that consumed more species of prey had more diverse trophically transmitted adult parasites. Larval parasite diversity increased with the diversity of both prey and predators, but increases in predator diversity had a greater effect. Prey diversity was more strongly associated with the diversity of adult parasites than with that of larvae. The proportion of parasite species present as larvae in a host species was correlated with the diversity of its predators. There was a notable lack of association with the diversity of any parasite guild and fish length, trophic level, or trophic category. Thus, diversity is associated with different nodal properties in larval and adult parasites, and association strengths also differ, strongly reflecting the life cycles of parasites and the food chains they follow to complete transmission.

Keywords Species richness · Helminths · Trophic transmission · Food webs · Predator–prey

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Introduction

Parasites are cryptically embedded within food webs. Many helminths, in particular, rely on trophic interactions for transmission and are both intimately entwined in and logically constrained by the food-web structure (Marcogliese and Cone 1997; Lafferty et al. 2008; Sukhdeo 2010). As a result, George-Nascimento (1987) and Marcogliese (2002) suggested that overall parasite diversity should be highest in fish in the middle of the food web because they function as both intermediate and definitive hosts. To some extent, this prediction was recently supported by Anderson and Sukhdeo (2011), who found total parasite species richness in *Fundulus heteroclitus* was best explained by the centrality and connectedness of these fish within local food webs in four brackish marshes in New Jersey sampled over a

3-year period. However, Lafferty et al. (2006a, b) observed greater parasite diversity in hosts at higher trophic levels in a Californian salt marsh. Chen et al. (2008) re-analyzed this Californian system along with two other previously published aquatic food webs and also found that hosts higher in food chains tended to have more species of parasites, and this was also a characteristic of hosts with broad diets and access to more diverse prey.

Taken together, these studies show total parasite diversity is concentrated in nodes that favour transmission, rather than randomly distributed in food webs, although which nodal properties are most important is not yet clear. Following this logic, a given food-web position is likely to have different effects on larval and adult parasites, as these are at different points in transmission cycles. Wiśniewski (1958) and Esch (1971) were among the first to suggest that larval stages should be the dominant developmental stages in fish in aquatic food webs that include higher predators such as birds and mammals. Stated more generally, fish with more predators should function more as intermediate hosts than as definitive hosts and, by extension, predatory fish should function more as definitive hosts. In testing these ideas, the effects of trophic attributes of hosts should be distinguished from those of their body size, which may be related to both trophic linkages (Woodward and Hildrew 2002) and parasite species richness (Poulin 1995; Luque et al. 2004; Luque and Poulin 2008). In an early analysis of parasite records in 34 freshwater fish species in the British Isles, Price and Clancy (1983) found that trophic categories predicted species richness in adult trematodes better than those of all or only larval trematodes, and none of these endpoints were strongly related to fish size. Similarly, Timi et al. (2011) found that trophic level, and not fish size, best explained the resemblance of generalist larval parasite communities in 16 fish species in the Argentine Sea, and that larval parasite diversity increased with both the size and trophic level of the host.

Several studies have employed the proportion of parasite species present as larvae to indicate the extent to which a fish serves as an intermediate host. In 50 species of marine fish off Brazil, Luque and Poulin (2004) found that the larval proportion of parasite richness was unrelated to a variety of variables, including trophic category and host size. However, in the three food webs studied by Chen et al. (2008), this proportion was higher in hosts with more diverse predators and in those that were implicated in more food chains. In contrast, in a dataset compiled from studies of 303 fish hosts, Poulin and Leung (2011) found that while smaller fish and those at lower trophic levels tended to have more species of larval parasites, only body length explained the proportion of parasite species that occur as larvae, which was two times higher in small (<20 cm) fish compared to large (>100 cm) hosts.

In the work described herein, we used an extensive database on parasites and stomach contents in 31 species of brackish-water fishes studied over a three-year period in the Bothnian Bay, Finland, to follow up the works of Lafferty et al. (2006b), Chen et al. (2008) and Poulin and Leung (2011). Our study was strengthened by the use of empirical measures of parasitism and of the size, trophic level, local abundance, diet breadth, and vulnerability to predation of fish, with minimal data obtained from the literature or other systems. In addition to proportions of total parasite richness (Chen et al. 2008; Poulin and Leung 2011), we also analyzed the absolute species richnesses of larval and adult parasites separately to test for differences in the effects of fish size and trophic position. While previous analyses have used trophic levels, we also used categories reflecting both diet and habitat (Valtonen et al. 2010). In addition, because closely related hosts have similar richnesses in parasites due to their shared evolutionary history (Poulin 1995), some of the association of parasite diversity with host trophic level (Lafferty et al. 2006b; Chen et al. 2008) could be an artefact of the dominance of certain host taxa at different trophic levels (see also Luque and Poulin 2004); we therefore controlled for host phylogeny. We analysed not only the diversity of larval and adult parasites, but also the total numbers of individual larvae and adults (abundance). Such a measure can be considered an approximation of parasite flow through a particular group of fish (Valtonen et al. 2010). Using this approach, our principal goal was to determine whether the numbers of larval and adult parasite species in fish and their respective abundances are better predicted by (1) fish size or trophic level (or category), (2) vulnerability to predation, or (3) diet breadth.

Materials and methods

The study area was a low-salinity (0.2–0.3 %) portion of the Bothnian Bay, at the northeastern extremity of the Baltic Sea. Most of the 52 fish species recorded in the region are of freshwater origin (Andreasson and Petersson 1982), but some marine species, such as *Zoarches viviparus*, *Clupea harengus*, *Myoxocephalus scorpius*, *Ammodytes tobianus*, and *Pomatoschistus minutus* complete their life cycles in the bay, which is also inhabited by ringed (*Phoca hispida*) and grey (*Halichoerus crypus*) seals.

In 1977–1979, stomach contents and metazoan parasites were examined in 8,229 adult fish belonging to 31 species collected from the Bothnian Bay (N 65.183, W 24.653), as described by Valtonen et al. (2001, 2010). For the present study, 4,105 of these fish, representing 25 fish species, were selected based on necropsy completeness and the availability of data for ≥15 fish per species (Table 1). For each of these species, the total diversity (species richness) and total

Table 1 Species and sample sizes of 4105 fish in 25 species in which trophically transmitted larval and adult parasites were studied in the Bothnian Bay (Baltic Sea), 1977–1979

	Total N	Local abundance (0 = accidental, 3 = common)
Freshwater		
Cypriniformes		
Alburnus alburnus (L.)	42	1
Leuciscus idus (L.)	28	2
Leuciscus leuciscus L.	67	3
Phoxinus phoxinus (L.)	122	3
Rutilus rutilus (L.)	255	3
Esociformes		
Esox lucius L.	84	2
Gadiformes		
Lota lota (L.)	104	2
Gasterosteiformes		
Gasterosteus aculeatus L.	424	3
Pungitius pungitius (L.)	266	3
Osmeriformes		
Osmerus eperlanus (L.)	332	3
Perciformes		
Gymnocephalus cernuus (L.)	382	3
Perca fluviatilis (L.)	289	3
Petromyzontiformes		
Lampetra fluviatilis (L.)	50	3
Salmoniformes		
Coregonus albula L.	312	3
Coregonus lavaretus lavaretus (L.)	147	3
Coregonus lavaretus widegreni (Malmgren)	180	3
Salmo trutta L.	54	2
Scorpaeniformes		
Myoxocephalus quadricornis L.	275	3
Marine		
Clupeiformes		
Clupea harengus L.	361	3
Gadiformes		
Gadus morhua L.	15	0
Perciformes		
Ammodytes tobianus L.	172	3
Pomatoschistus minutus (Pallas)	28	3
Zoarces viviparus L.	65	2
Salmoniformes		
Salmo salar L.	21	2
Scorpaeniformes		
Myoxocephalus scorpius (L.)	30	2

mean abundance (number of parasites per host) were calculated for two guilds of endoparasites. The diversity and abundance of trophically transmitted adult endoparasites were analyzed in 3,775 fish in which complete necropsies for all adult parasites were performed. The diversity and abundance of larval endoparasites were analyzed in 1,637 fish in which all larval parasites were enumerated, and in 3932 fish in which most larval parasites were enumerated (the difference being mainly attributable to 2286 fish in which the eyes were not examined; however, eyes were examined in at least 8 individual fish, or 12 % of the total sample, in each of the 25 species).

Nine factors were assessed for their ability to predict the diversity and abundance of adult or larval endoparasites in the 25 fish species: mean fish length, number of fish examined, host origin (marine/freshwater), local host abundance, host trophic level determined empirically and from the literature, trophic category, diet breadth (number of prey species in fish diets), and vulnerability to predation (number of species of predators in a food web; Lafferty et al. 2006b; Chen et al. 2008; Poulin and Leung 2011). Mean fish length and number of fish examined were calculated from original samples. Fish were classified as primarily marine or freshwater and local abundance was rated 0–3, according to Valtonen et al. (2010) (Table 1). Trophic level (position in an energetic hierarchy between a fish species and primary producers, typically given position 1) was obtained from FishBase (Froese and Pauly 2000) and also calculated empirically from the diet data (see below). In the latter case, trophic level was made equal to 1 + mean trophic level of food items. Invertebrate food items were assigned trophic levels of 2.0–2.5 and fish species occurring as prey were initially assigned values from FishBase. The resulting trophic levels for consumer fish species were then substituted where they occurred as prey, and this was carried out iteratively until the mean change in trophic level was <5 %. On average, empirical trophic levels were 0.21 (range −1.38 to 0.60) lower than, and not strongly correlated ($R = 0.41$, $P = 0.025$) with values obtained from FishBase. Trophic categories were assigned as benthivore (given a value of 1 in multiple regressions, see below), planktivore (2), omnivore (3), and piscivore (4), as in Valtonen et al. (2010).

The number of prey species in the diets of the 25 fish species was inferred from stomach contents (all 4105 fish) in which prey were identified to species, genus, or in some cases higher taxa (see Appendix S2 in Valtonen et al. 2010). Additional prey species were inferred from the life cycles of trophically transmitted parasites. Still others were obtained from studies conducted in the same region on the stomach contents of *Osmerus eperlanus* (1968–1969), *Coregonus albula* (1978–1981), *Phoxinus phoxinus* (1982), *Clupea harengus* (1978–1979), and *Salmo trutta* (1971–1974) from Timola (1980), Hyvärinen and Valtonen (1983), Myllylä et al. (1983), Harju (1983), and Kantola (1975), respectively. Fish species composition is considered stable over this interval (e.g. Lehtonen et al. 1993; Valtonen et al. 2004). In total, 93 species of prey were recorded.

The number of predator species feeding on the 25 fish species was inferred from the stomach contents and trophically transmitted parasites of all 8,229 fish in 31 species, as well as 109 ringed and 49 grey seals examined between 1977 and 1999 in the Bothnian Bay (Appendix S2, Valtonen et al. 2004, 2010). This was supplemented with data from other studies of the diets of seals in the Baltic Sea

(Söderberg 1975; Tormosov and Rezvov 1978; Stenman and Pöyhönen 2005). Because dietary data from birds in the Bothnian Bay are scarce, prey of 19 local avian piscivorous species were extrapolated from studies of the same species occurring elsewhere, including North America (Feltham 1990; Fox et al. 1990; Kubetzki and Garthe 2003; Gilliland et al. 2004; Poole 2005; Ross et al. 2005; Santoul 2005), and local experts and unpublished reports were also consulted. In total, predation by up to 53 species was possible.

Initial general linear models showed that host order explained significant variation in the abundance and total and proportionate diversities of larval and adult parasites. To better control for the tendency of related fish species to have similar abundances and richnesses in parasites (Poulin 1995; Locke et al. 2013b), standardized phylogenetically independent contrasts between the 25 species were obtained using Felsenstein's (1985) method with the PDAP module of Mesquite 2.6 (Midford et al. 2005). Evolutionary relationships were estimated using maximum likelihood analysis of a 599-base-pair alignment of previously published sequences of cytochrome *c* oxidase 1 conducted in Mega 5.10 (Tamura et al. 2011; see the Electronic supplementary material, ESM). In multiple regressions of independent contrasts obtained from this phylogeny, all possible combinations of up to eight predictors were compared and, to avoid over-fitting, models within up to two units of the lowest Akaike information criterion corrected for small sample sizes (AICc) were considered equally parsimonious (Burnham and Anderson 2002). Scatterplots were inspected for influential points and outliers.

Results

Fish and parasite community description

In the 25 fish species considered here, the mean number of parasite species was 9.9 (range 0–21), of which a mean of 4.6 (range 0–9) were present as larvae and 5.2 (range 0–12) were adults. No parasites were observed in *Ammodytes tobianus*, while *Lota lota* had the most diverse parasites (9 larval and 12 adult species). All 34,415 adult helminths (encompassing 35 species) were acquired in prey, of which cestodes accounted for 50 %, digeneans 25 %, acanthocephalans 14 %, and nematodes 11 %. Five of the 22 species of larval helminths observed were digeneans that penetrate their hosts and mature in piscivorous birds, and the remainder were members of other taxa and acquired in food. Host-penetrating digeneans accounted for 19,785 (73 %) of the 26,824 individual larval helminths. The average mean abundance of trophically transmitted adult parasites was 15.8 (range 0–80.9) and that of larval parasites

was 17.7 (range 0–115.1), with the highest numbers of both guilds occurring in *Salmo salar*.

Vulnerability to predation was lowest in cod and lamprey (each consumed by five species of predators), highest in three-spined stickleback (28 species of predators), and decreased with increasing fish size ($R = -0.45$, $P = 0.025$). Overall, there was a mean of 17.1 species of predators per fish species. Diets included a mean of 29 species of prey, ranging from 5 in *A. tobianus* to 45 in *L. lota*. Fish with more diverse diets had more species of predators ($R = 0.54$, $P = 0.005$) and higher empirically measured trophic levels ($R = 0.49$, $P = 0.013$). Neither estimate of trophic level was related to vulnerability to predation ($P \geq 0.09$).

Parasite richness

The results of multiple regressions are summarized in Table 2. In three equally parsimonious models, 66 % of the variance in the number of trophically transmitted parasite species present as adults was explained by diet breadth and sampling effort (Table 3a; Fig. 1). Fish that consume more species of prey have more diverse adult trophically transmitted parasites; this factor alone explains 53 % of the variance in adult parasite species richness. There was also a significant and negative relationship between adult parasite species richness and the number of fish examined. This negative effect of sampling effort is puzzling and could be an artefact caused by our examination of fewer numbers of larger fish ($R = -0.49$, $P = 0.030$). In models consisting of diet breadth, sampling effort, and fish length, the latter was always nonsignificant and "out-competed" by sampling effort. In a model restricted to length and diet breadth ($R^2 = 0.57$, $P < 0.0001$; ΔAICc = 6.94), length had a positive, marginally significant effect ($P = 0.084$). Empirical trophic level and trophic category each appeared once in two other models within two AICc units of that presented in Table 3a, with positive but nonsignificant coefficients ($P \geq 0.22$).

Variation in larval parasite richness was explained with equal parsimony by 12 models containing between two and five factors ($0.76 \leq R^2 \leq 0.80$). In all of these models, larval parasite richness was positively and significantly associated with both diet breadth and vulnerability to predation. Other factors retained were trophic category (higher larval parasite diversity in benthic fishes in 6 models, $P \geq 0.053$), habitat (higher diversity in fish of freshwater origin in 5 models, $P \geq 0.08$), fish abundance (lower diversity in abundant fishes in 4 models, $P \geq 0.08$), and empirical trophic level (higher diversity at higher trophic levels in 3 models, $P \geq 0.14$). No predictors other than diet breadth and vulnerability to predation appeared in more than half of the other models, and none made a significant contribution in any particular model; these two factors are thus the only predictors with consistent and meaningful biological relevance. Because they are measured in the same units (number of species of prey or predators), they are directly comparable. Considered in isolation, slightly less variance is explained by vulnerability ($R^2 = 0.60$) than diet breadth ($R^2 = 0.65$). However, the slopes of the individual regression lines differ ($t_{20(2\text{-tail},\alpha=0.05)} = 6.254$, $P < 0.0005$) and the coefficients indicate that an increase in the number of species of predators is associated with twice as great an increase in larval parasite diversity as an equivalent increase in prey species (Fig. 2).

Diet breadth positively affected the diversity of both adult and larval parasites (Tables 2, 3a, b). However the slope is significantly higher ($t_{20(2\text{-tail},\alpha=0.05)} = 2.681$, $P = 0.007$) in adult parasites than in larval parasites, i.e. an increase in diet diversity is associated with a greater increase in the diversity of adult than larval parasites.

Vulnerability to predation explained 25 % of the variance in the proportion of species that are larval (or, conversely, adults) (Table 3c; Fig. 3). In an equally parsimonious model that also included a significant effect of vulnerability, there was a nonsignificant tendency ($P = 0.44$) for the proportion of larval parasites to be higher in freshwater fish.

Table 2 Summary of factors explaining variations in the diversity and abundance of trophically transmitted adult and larval parasites in 25 fish species in the Bothnian Bay

	Richness		Proportion	Abundance	
	Adult	Larvae		Adult	Larvae
Diet breadth	+	+			+[b]
Vulnerability to predation		+	+		−[b]
Mean length				+	+[a]
Trophic level (FishBase)					−[b]
Trophic level (empirical)					
Trophic category					
Sampling effort	−				
Origin (marine/freshwater)				+ (Marine)	+[a] (Marine)
Fish abundance					+[a]

Positive effects are indicated by +; negative effects by −

[a] Including all fishes

[b] Excluding *Salmo salar*

Table 3 Multiple regressions of standardized phylogenetically independent contrasts of predictors of the diversity, abundance, and richness ratios of larval and adult parasites in 25 fish species in the Bothnian Bay

Model	Sum of squares	df	Mean square	F	P	Adjusted R^2
(a) Adult parasite diversity						
Regression	45.23	2	22.61	28.65	<0.0001	0.664
Residual	17.36	22	0.79			
Total	62.59	24				
(b) Larval parasite diversity						
Regression	61.43	2	30.72	48.39	<0.0001	0.761
Residual	13.97	22	0.63			
Total	75.40	24				
(c) Proportion of parasite species that are larval						
Regression	0.0409	1	0.0409	7.0753	0.0147	0.252
Residual	0.1211	21	0.0058			
Total	0.1623	22				
(d) Adult parasite abundance						
Regression	1388.74	2	694.37	12.18	0.0003	0.460
Residual	1253.76	22	56.10			
Total	2642.49	24				
(e) Larval parasite abundance						
Regression	3556.828	3	1185.609	9.713538	0.0004	0.494
Residual	2563.206	21	122.0574			
Total	6120.034	24				

Coefficients	Slope (SE)	t	P
Model (a)			
Diet breadth	0.179 (0.024)	7.57	<0.0001
Sampling effort	−0.001 (0.003)	−3.43	0.0024
Model (b)			
Diet breadth	0.115 (0.023)	5.05	<0.0001
Vulnerability	0.215 (0.050)	4.33	0.0003
Model (c)			
Vulnerability	0.001 (0.004)	2.66	0.0147
Model (d)			
Habitat	12.670 (5.485)	2.31	0.0307
Mean length	0.0560 (0.017)	3.33	0.0030
Model (e)			
Fish abundance	19.338 (5.816)	3.33	0.003
Habitat	22.227 (8.677)	2.56	0.018
Length	0.116 (0.027)	4.34	0.0002

The predictors shown occurred and contributed significantly to all of the most parsimonious models (lowest AIC and ΔAICc < 2)

Parasite abundance

Trophically transmitted adult parasites were significantly more abundant in larger fish and in those of marine origin (Table 3d; Fig. 4). These factors were also included in two equally parsimonious models in which fish species with adult parasites had nonsignificant tendencies ($P \geq 0.32$) to have either higher vulnerability or local abundance.

In five equally parsimonious models, larval parasites were significantly more abundant in larger fishes of marine origin that were locally abundant (Table 3e). In some of these models, larval parasites were more abundant in fish with broader

diets, lower trophic levels from FishBase, and higher empirical trophic levels, but in all the latter cases, not significantly so. The relationship with fish size appears to be driven largely by *S. salar* (Fig. 4), which were heavily infected (see above) and larger than other fish sampled (mean length = 741 mm versus average mean length = 232 mm [range 42–523 mm] for other species); the same patterns emerged in plots of non-contrasted data (not shown). When *S. salar* was excluded from the analysis, other factors (diet diversity, vulnerability, trophic level from FishBase) made significant contributions to the top four equally parsimonious models (Table 2). Two of these models also include positive but nonsignificant
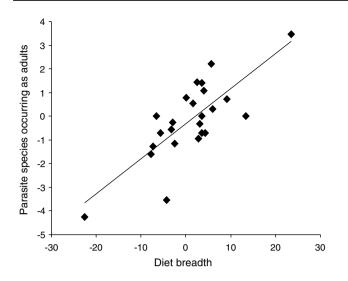
Fig. 1 Standardized phylogenetically independent contrasts in the richness of trophically transmitted adult parasites plotted against contrasts in diet breadth (i.e. number of species of prey) in 25 fish species in the Bothnian Bay
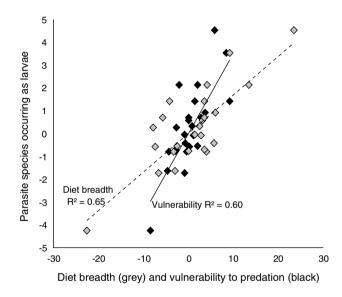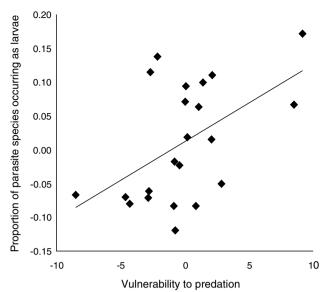

Fig. 3 Standardized phylogenetically independent contrasts in the proportion of parasite species that are larval plotted against contrasts in vulnerability to predation (i.e. number of species of predators) in 25 fish species in the Bothnian Bay
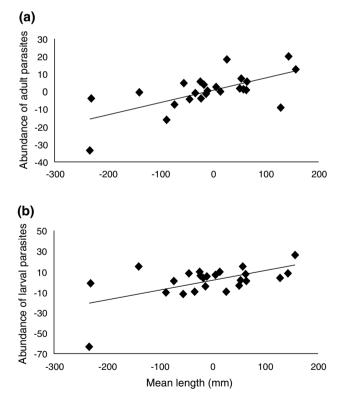

Fig. 2 Standardized phylogenetically independent contrasts in the richness of larval parasites plotted as a function of contrasts in diet breadth (i.e. number of species of prey, *dashed line*) and vulnerability to predation (i.e. number of species of predators, *solid line*) in 25 fish species in the Bothnian Bay

associations with length ($P > 0.06$) and a tendency for higher abundance in fishes of marine origin ($P > 0.08$).

Discussion

In 25 fish species in the Bothnian Bay, we observed connections between parasite diversity and food web structure

Fig. 4 Standardized phylogenetically independent contrasts in the abundance of **a** trophically transmitted adult parasites and **b** larval parasites plotted against contrasts in mean length in 25 fish species in the Bothnian Bay. *Lower left points* in **a** and **b** are contrasts between *Salmo salar* and *Salmo trutta*

that follow logically from parasite life cycles. Larval parasite species were more numerous in hosts with more diverse prey and predators, but predator diversity had a larger effect. The diversity of prey was correlated with that of both larval and adult parasites, but its effect was stronger on adult parasites. In contrast, the diversity of adult parasites was unrelated to the diversity of predators. In other words, the diversity of different subsets of parasites was associated only with hosts with which parasites were trophically linked. Neither the trophic level nor host size drives the diversity of larval or adult parasites; instead, what a fish eats and what eats it are the most important factors contributing to parasite diversity in this system. Smaller fish did tend to have more predators, which has been observed previously (Woodward and Hildrew 2002; Lafferty et al. 2006a), but fish size does not seem useful as a proxy for measuring how vulnerability to predation affects parasite diversity. Thus, our results do not support the findings of Poulin and Leung (2011) on the importance of fish size for larval parasite diversity (proportionate or total richness). However, the data are broadly consistent with other work indicating that trophic interactions are important correlates of endoparasite richness (Lafferty et al. 2006b; Chen et al. 2008) and that the diversity of parasites reflects that of hosts in other parts of the food web (Hechinger and Lafferty 2005). In contrast to these studies, however, we show that different aspects of fish trophic ecology affect larval and adult parasites in distinct ways, and that these differences strongly reflect parasite transmission patterns.

The total and proportionate richnesses of parasites were not associated with the same factors for adult and larval worms (Table 2). Moreover, increases in prey diversity had a greater effect on the diversity of adult parasites than on larvae. This is logical because all adult parasite species encountered are acquired in prey, but nearly one-quarter of larval parasite species penetrate their hosts. In addition, some larval helminths acquired in food may have relatively low specificity in their invertebrate hosts (e.g. Wisniewski 1958), which could reduce the effect of diet breadth on the diversity of ingested larval parasites. Furthermore, the diversity of adult parasites was largely driven by the diversity of the prey which transmit them, whereas the diversity of larval parasites was more strongly affected by that of the predators in which they eventually mature. While we did not analyze total parasite diversity, the importance of vulnerability to predation and diet breadth for adult and larval parasite species richness suggests that being located in the middle of a fish subweb (where both vulnerability and diet breadth would be greatest) should promote overall parasite species richness, as suggested by George-Nascimento (1987) and Marcogliese (2002), and supported by Chen et al. (2008) and Anderson and Sukhdeo (2011).

Vulnerability to predation was associated with twice the increase in larval parasite diversity as prey diversity. This may also be a reflection of host penetration by some larval species, and low specificity among those that are ingested. The strong effect of predator diversity on larval parasites plausibly reflects convergent adaptation by distantly related parasites to use species as intermediate hosts that are likely to be consumed by definitive hosts (Benesh et al. 2011).

In the Bothnian Bay, the proportion of parasite species present as larvae was related to vulnerability to predation. Fish with more species of predators thus seem to serve mainly as intermediate hosts. Again, this could be explained by convergence of life cycle patterns among phylogenetically distinct parasites (Benesh et al. 2011). However, the corresponding adult proportion of total parasite richness did not vary with diet breadth (i.e. fish with more species of prey did not serve mainly as definitive hosts). This might be because prey diversity affects the absolute diversity of both larval and adult parasites, thus evening out its effects on the proportionate richness of either group. In addition, this relationship might have emerged had we measured parasite richness in nodes such as top predators (e.g. seals and piscivorous birds, which have no larval parasites and may have broad diets reflecting locally abundant taxa: Fox et al. 1990; Sinisalo et al. 2006) and primary consumers (in which all trophically transmitted parasites are larval, and diet consists of vegetation).

There was a notable lack of association between any aspect of the diversities of the two parasite guilds and trophic level, which echoes what was observed by Poulin and Leung (2011) in fish, but is quite distinct from analyses by Lafferty et al. (2006a, b) and Chen et al. (2008) of well-characterized food webs. Trophic level may have been unimportant in our study because it varies relatively little in the limited context of a fish community. On the other hand, the lack of an effect of trophic level may result from partitioning of parasites into separate developmental guilds. Even in the analysis by Chen et al. (2008) of webs including top terrestrial predators and primary consumers, the effects of trophic level were difficult to distinguish from those of being either a predator or prey of many species. It seems plausible that a host's position in an energetic hierarchy will have smaller effects (if any) on its parasite diversity compared to the diversity of its prey or predators, as indicated by our results. Associations between parasite diversity and trophic level or body size (Chen et al. 2008; Poulin and Leung 2011) may reflect their correlation with the diversities of prey and predators, which we suggest may be the underlying predictors of primary importance.

The tendency for both larval and adult parasites to be more abundant in larger fishes of the Bothnian Bay echoes the results of other studies. Host size was also correlated with variation in larval parasite abundance among 50

species of marine fish studied by Luque and Poulin (2004). In our samples, adult parasites were dominated by cestodes, and larval parasites were mostly skin-penetrating digeneans, both of which tend to be more abundant in larger fish in the same species (Poulin 2000). Larger fish may have more abundant parasites because they present larger targets for penetrating larval stages and because they consume more infected prey. Larval stages are also likely to accumulate in hosts over time (unlike adults in the intestine, which may be shorter-lived). When one outlier was removed, larval parasites were found to be more abundant in fish at lower trophic levels. Fish feeding at lower trophic levels may tend to have broadly similar patterns of habitat use (e.g. Livingstone 1982; Garrison and Link 2000) and, as a group, be more exposed to penetrating parasites, which constitute nearly three quarters of the larval helminths in this system (Valtonen et al. 2003). In addition, parasites in general may be more abundant at low trophic levels (Hechinger et al. 2011). The surprising decrease in the abundance of larval parasites with predator diversity may reflect the tendency for larger hosts to have fewer predators. However, because completely different correlates of larval abundance emerged depending on the inclusion of a possible outlier, these trends should be interpreted with caution. In general, the abundance of parasites may be more likely to fluctuate with local and stochastic factors than species composition (Timi et al. 2010; Locke et al. 2013b; Timi and Lanfranchi 2012).

There have been a number of calls to include parasites alongside other data in studies of aquatic food webs and fish trophic ecology (Marcogliese and Cone 1997; Lafferty et al. 2008; Sukhdeo 2010; Locke et al. 2013a). Our results suggest that studies of parasite richness should take food web structure into account, and that the metrics of primary importance relate directly to parasite transmission patterns rather than other food-web attributes. The diversities of larval and adult trophically transmitted parasites (and, we suspect, those with direct life cycles) are not associated with the same factors, and predator and prey diversities (as opposed to fish size or trophic position) appear to be important but distinct correlates of parasite richness in these guilds. Future comparative studies of parasite abundance could be greatly advanced by including food webs with quantitative estimates of prey and predator importance (linkage strength; Marcogliese 2003), in addition to their diversities. Prey and predator abundances may prove to be better predictors of the abundances of larval and adult parasites.

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