

Research note

Interspecific associations among larval helminths in fish

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Abstract

Various processes can generate associations between the larvae of different helminth species in their fish intermediate or paratenic host. We investigated the pairwise associations among larval helminth species in eight different fish populations, using two different coefficients of associations, in order to determine in what situations they are strongest. All helminth species included use the fish studied as either their second intermediate host or their paratenic host, and are acquired by the fish when it ingests an infected first intermediate host. The intensity of infection correlated positively with fish length for most helminth species. Pairs of species which both exhibited positive correlations with fish length tended to be more strongly associated with one another, although this tendency was not pronounced. Similarity in life cycle had a more important influence on pairwise associations. Among the 62 pairwise associations that could be computed, pairs of helminth species that shared both first intermediate hosts and definitive hosts were the most strongly associated, followed by pairs that shared only one other host, and finally by pairs that did not share other hosts. The results suggest that assemblages of larval helminth parasites in fish are not random collections of locally available species, but rather structured packets of larval parasites that travel together along common transmission routes. © 2001 Australian Society for Parasitology Inc. Published by Elsevier Science Ltd. All rights reserved.

Keywords: Intermediate host; Jaccard coefficient; Size versus intensity relationship; Sørensen coefficient; Transmission route

Many helminth parasites use fish either as their second intermediate host or as a paratenic (transport) host. These helminths complete their life cycle when their fish intermediate/paratenic host is ingested by their definitive host, which is either another fish or some other vertebrate. Despite the many studies on the community ecology of parasites in fish, there has been very little work done on larval helminths. Most investigators have focused on adult helminths in the gastrointestinal tract of fish (see Holmes, 1990; Kennedy, 1990; Poulin, 1998), or on the ectoparasites of fish (e.g. Rohde et al., 1995). Adult endohelminths and ectoparasites form two distinct guilds of parasites, which live in the same habitat and may compete for the same resources. Larval helminths, on the other hand, appear less likely to compete for resources because they occur in various organs and because many of them are not actively feeding on host nutrients or tissues. These features suggest that they do not form an interactive guild, and it is perhaps for this reason that their statistical associations among fish hosts have received little attention.

Are there reasons to expect interspecific associations among larval helminths in fish? The answer to this question

is yes, with at least two processes acting to generate associations between species of larval worms. First, since fish often acquire larval worms when they ingest infected prey, it is possible that the long-lived larval worms accumulate inside a fish as it grows. Indeed, there is much evidence that numbers of parasites per host increase with fish length, though this relationship is far from universal (Poulin, 2000). If two or more species of larval worms are simultaneously accumulating in fish over time, we might expect statistical associations to exist among these species: large fish likely to harbour one species would also be likely to harbour other species, whereas small fish would be unlikely to harbour any species.

The second process that may generate associations among larval helminths in fish is the possible transfer to the fish host of associations that existed in the previous intermediate host. There are many reports that larval worms tend to co-occur more or less than expected by chance in their intermediate hosts (see review in Lafferty et al., 2000). This can sometimes be explained by the patchy distribution of helminth infective stages, but it often appears to be an adaptive strategy of larval helminths that can lead to an increase in their probability of reaching their next host. For instance, if two helminth species share the same intermediate and definitive hosts, and if one of them is capable of

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altering the behaviour of the intermediate host in ways that enhance its chance of being ingested by the definitive host, then the second species would benefit by seeking intermediate hosts already harbouring the first parasite. Similarly, if they have different definitive hosts, the two species would benefit by avoiding sharing an intermediate host if one or both of them are capable of modifying its behaviour. These scenarios have been documented in some systems but have been recognised only recently (see Thomas et al., 1997, 1998; Dezfuli et al., 2000; Lafferty et al., 2000). The outcome is that fish hosts may contain several helminth larvae that are not merely random assemblages of the species locally available, but instead structured packets of larvae that are more likely to share the same definitive host than one would expect by chance alone. From the perspective of the definitive host, which is usually a predatory fish or a fish-eating bird or mammal, ingesting an infected fish could mean not only acquiring one parasite species, but a ready-made community of larval helminths ready to compete for attachment space in the host's gut (Bush et al., 1993; Lotz et al., 1995; Poulin, 1998). These ideas have not yet been tested rigorously, but their importance for transmission and life cycle studies should be clear.

The objectives of this study were to (1) test for interspecific associations among species of larval helminths in several populations of freshwater and brackish water fish belonging to different species, and (2) determine whether these associations are influenced by fish size and by whether the parasite species also share other hosts in their life cycle. All the helminth species considered here use the study fish as either their second intermediate host or their paratenic host; all species are acquired by the fish when it ingests an infected first intermediate host (or another paratenic host). We predicted that interspecific associations should be stronger between helminth species that also share first intermediate and definitive hosts than between helminth species that only have the fish species studied in common.

Fish were obtained from the north-eastern Bothnian Bay (65° 10'N, 24° 54'E) of the Baltic Sea, and from Lake Yli-Kitka (66° 07'N, 28° 38'E), in north-eastern Finland. The Bothnian Bay has a very low salinity, and both the bay and the lake are oligotrophic and share many fish species. Large numbers of fish were sampled monthly or bimonthly in 1978–1979 from the catches of commercial fishermen at both locations. The methods of capture remained the same throughout the study period at both locations, and involved trawl and fyke nets in summer and seine nets in winter in the Bay, and seine nets in the lake. All newly caught fish were measured, dissected, and searched for larval helminths. This consisted in the careful examination of the gut lumen, viscera, body cavity and muscles under a dissecting microscope (40× magnification); all cysts were opened and all individual parasites, within cysts or not, were identified. We only included helminth species that are acquired by fish through ingestion of infected prey, and excluded those which occurred in fewer than five individual hosts in a fish

sample. Only fish species with at least two helminth species meeting these criteria could be included in the analyses.

Two measures of pairwise associations between species were used. For many helminth species, infected fish harboured only a single worm; in many other species, even if numbers of worms per fish reached high values, the median number was usually low. Consequently, the first measure of interspecific association we chose is based on presence/absence data. We used the Jaccard coefficient of association to test for associations between all pairs of helminth species in each fish species. This coefficient, or r_j , does not take into account uninfected fish, and has been recommended by Janson and Vegelius (1981) as one of the best coefficients among the ones that have been proposed. It is computed as the proportion of fish that harbour both parasite species in a pair out of all the fish that harbour at least one of the two species. The coefficient equals zero when the two helminth species in a pair never co-occur, and one when they are always found together.

The second measure of association between pairs of helminth species that we used was a modification of Sørensen's coefficient, r_s , as described by Southwood and Henderon (2000) (p. 494):

$$r_s = 2 \left[\frac{J_T}{J_A + J_B} - 0.5 \right]$$

where J_T is the total number of individual helminths of species A and B in fish where both species are present, and J_A and J_B are the total number of individual helminths of each species found in all fish. The coefficient has the normal range of -1 (no association) to $+1$ (complete association); values less than zero simply mean that fewer than 50% of individual worms of both species co-occur together, and not that they are negatively associated. By focusing on the proportion of individuals occurring together, this index gives more weight to the fish that harbour large numbers of parasites than the previous measure.

Relationships between the numbers of worms per fish and fish length were assessed for each parasite species using Spearman's rank correlation coefficients, with correction for tied ranks. These coefficients were computed to provide an index of the association between fish size and intensity of infection; their statistical significance is not of primary importance here. The two measures of species associations described above were treated separately, and were log-transformed ($\log(x + 1)$ for r_j and $\log(x + 2)$ for r_s) to meet the requirements of a parametric two-way analysis of variance (ANOVA). Each pairwise association was treated as an independent observation in the analyses. The influence of two factors on the strength of species associations was assessed with the ANOVA: the fish length versus intensity of infection relationship, and whether helminth species share other hosts in their life cycle. Pairwise associations between helminth species in each fish species were first classified either as (1) pairs of helminths that both showed a significant positive relationship with fish length, or (2)

pairs of helminth species that did not. This procedure generated two classes for the first factor in the ANOVAs. Pairwise associations were also grouped into three categories: (1) those in which both species share the same first intermediate host and same definitive host; (2) those in which the two species share only one other host, either the first intermediate host or the definitive host; and (3) those in which the two helminth species do not share hosts other than the fish species studied. This created three classes for the second factor in the ANOVAs. The identity of intermediate and definitive hosts in the Bothnian Bay and Lake Yli-Kitka have been determined in many separate surveys, unpublished in many cases, not listed here. Separate two-factor ANOVAs were performed on the two dependent variables, i.e. r_j and r_s values.

The analyses that follow are based on a total of 3219 worms recovered from 1688 individual fish hosts. The helminths belong to 13 different species which utilise a range of first intermediate hosts and definitive hosts (Table 1). The fish represent seven species and eight populations (*Gymnocephalus cernuus* is represented by separate samples from the Bothnian Bay and Lake Yli-Kitka). Most larval helminth species occur at relatively low prevalences and low numbers per fish (Table 2). Fish length often correlates positively with the numbers of helminths per fish: 30 out of the 33 possible helminth-fish species combinations are characterised by a positive correlation coefficient between length and intensity of infection (Table 2). Only one of the negative correlation coefficients is statistically significant at $P \leq 0.05$, whereas 16 positive coefficients are significant.

Most of the pairwise associations among these helminths are rather weak. Using Jaccard's coefficient of association, 48 out of 62 possible pairwise combinations have a coefficient value lower than 0.2, suggesting the two species in a pair do not co-occur very often in the same fish individual (Table 3). Using Sørensen's coefficient, 57 out of the 62 pairs have negative coefficient values, meaning that usually less than half of the individuals from the two helminth species in a pair co-occur in the same fish (Table 4). Despite being computed differently, i.e. one focusing on number of co-occurrences in fish using presence/absence data and the other on the proportion of individuals that co-existed, values of the two coefficients were strongly positively correlated (product-moment correlation coefficient on log-transformed coefficients: $r = 0.945$, $P = 0.0001$). Despite the general weakness of these pairwise associations, their variability may be explained by the two factors considered here.

If helminths of different species accumulate in the same fish over time as the fish grows, pairwise associations may appear as a result. The ANOVAs suggest that pairs of helminths that both showed a significant positive relationship with fish length tend to display stronger interspecific associations than pairs of helminth species that did not, although this trend was not significant (Jaccard's coefficient: $F_{1,56} = 1.868$, $P = 0.1772$; Sørensen's coefficient: $F_{1,56} = 3.065$, $P = 0.0855$). Whether or not helminth species shared other hosts in their life cycles had a greater influence on the strength of interspecific associations (Jaccard's coefficient: $F_{2,56} = 3.158$, $P = 0.0502$; Sørensen's coefficient: $F_{2,56} = 3.289$, $P = 0.0446$). Pairs of helminth species that shared both first intermediate hosts

Table 1
First intermediate hosts and definitive hosts of the helminth parasites considered in this study^a

Helminth species	Abbrev.	First intermediate host	Definitive host
CESTODA			
<i>Diphyllobothrium dendriticum</i>	Dden	Cyclopoid copepod	Gulls, <i>Larus</i> spp.
<i>Diphyllobothrium ditremum</i>	Ddit	Cyclopoid copepod	Diving ducks
<i>Diphyllobothrium latum</i>	Dlat	Cyclopoid copepod	Terrestrial mammals
<i>Schistocephalus pungitii</i>	Spun	Cyclopoid copepod	Fish-eating birds
<i>Schistocephalus solidus</i>	Ssol	Cyclopoid copepod	Fish-eating birds
<i>Triaenophorus crassus</i>	Tera	Cyclopoid copepod	Pike, <i>Esox lucius</i>
<i>Triaenophorus nodulosus</i>	Tnod	Cyclopoid copepod	Pike, <i>Esox lucius</i>
<i>Eubothrium</i> sp.	Eubo	Cyclopoid copepod	Salmonid fish, or burbot <i>Lota lota</i>
NEMATODA			
<i>Contracaecum osculatatum</i>	Cosc	amphipod, <i>Monoporeia affinis</i> ^b	Grey seal, <i>Halichoerus crypus</i>
<i>Eustrongylides mergorum</i>	Emer	Oligochaetes ^b	Fish-eating birds
<i>Raphidascaris acus</i>	Racu	Chironomids + other insects ^b	Pike, <i>Esox lucius</i> , and burbot, <i>Lota lota</i>
ACANTHOCEPHALA			
<i>Corynosoma semerme</i>	Csem	amphipod, <i>Monoporeia affinis</i>	Ringed seal, <i>Phoca hispida</i> , and grey seal, <i>Halichoerus crypus</i>
<i>Corynosoma strumosum</i>	Cstr	amphipod, <i>Monoporeia affinis</i>	Ringed seal, <i>Phoca hispida</i> , and grey seal, <i>Halichoerus crypus</i>

^a Abbreviations of species names that are used in other tables are also shown.

^b These nematodes may also use other invertebrates and fish as paratenic hosts before infecting the fish species studied.

Table 2

Summary of infection parameters for the larval helminth species acquired via ingestion found in each of the fish species studied; species for which fewer than five fish in a sample were infected are not listed

Host species (no. examined)	Mean fish length (cm (range))	No. fish infected	Range of infection intensities	Total no. worms recovered	Correlation of intensity with fish length ^a
Helminth species					
<i>Coregonus albula</i> (Bothnian Bay, <i>n</i> = 164)	16.6 (11–23)				
<i>Diphyllbothrium ditremum</i>		20	1–3	28	0.367***
<i>Triaenophorus crassus</i>		18	1–2	21	0.080
<i>Osmerus eperlanus</i> (Bothnian Bay, <i>n</i> = 332)	15.6 (7–26)				
<i>Diphyllbothrium ditremum</i>		11	1	11	0.059
<i>Triaenophorus nodulosus</i>		6	1–2	7	0.099
<i>Contrac AECum osculatum</i>		9	1–2	10	0.172**
<i>Corynosoma semerme</i>		36	1–7	66	0.303***
<i>Corynosoma strumosum</i>		11	1–2	12	0.089
<i>Lota lota</i> (Bothnian Bay, <i>n</i> = 83)	47.0 (31–72)				
<i>Diphyllbothrium dendriticum</i>		21	1–12	73	-0.061
<i>Diphyllbothrium latum</i>		37	1–10	117	0.193
<i>Triaenophorus nodulosus</i>		49	1–16	152	-0.151
<i>Contrac AECum osculatum</i>		13	1–3	21	0.086
<i>Eustrongylides mergorum</i>		33	1–9	93	0.278*
<i>Corynosoma semerme</i>		11	1–18	46	0.054
<i>Corynosoma strumosum</i>		21	1–16	55	0.055
<i>Gasterosteus aculeatus</i> (Bothnian Bay, <i>n</i> = 360)	6.6 (3–9)				
<i>Diphyllbothrium dendriticum</i>		72	1–6	104	0.199***
<i>Diphyllbothrium ditremum</i>		229	1–9	529	0.350***
<i>Schistocephalus solidus</i>		159	1–8	283	0.529***
<i>Triaenophorus nodulosus</i>		31	1–3	34	0.163**
<i>Eustrongylides mergorum</i>		5	1	5	0.029
<i>Raphidascaris acus</i>		48	1–8	77	0.208***
<i>Pungitius pungitius</i> (Bothnian Bay, <i>n</i> = 328)	5.0 (1–7)				
<i>Diphyllbothrium ditremum</i>		50	1–6	71	0.083
<i>Schistocephalus pungitii</i>		10	1–3	16	-0.151**
<i>Triaenophorus nodulosus</i>		7	1	7	0.103
<i>Myoxocephalus scorpius</i> (Bothnian Bay, <i>n</i> = 30)	25.2 (18–33)				
<i>Contracaecum osculatum</i>		6	1–3	10	0.384*
<i>Corynosoma semerme</i>		29	1–158	795	0.584**
<i>Corynosoma strumosum</i>		28	1–32	162	0.598**
<i>Gymnocephalus cernuus</i> (Bothnian Bay, <i>n</i> = 163)	13.0 (5–20)				
<i>Triaenophorus nodulosus</i>		12	1–2	14	0.072
<i>Eubothrium</i> sp.		10	1–2	11	0.116
<i>Eustrongylides mergorum</i>		48	1–8	75	0.172*
<i>Corynosoma semerme</i>		13	1–12	30	0.241**
<i>Gymnocephalus cernuus</i> (Lake Yli-Kitka, <i>n</i> = 228)	8.8 (6–18)				
<i>Triaenophorus nodulosus</i>		84	1–22	265	0.421***
<i>Eustrongylides mergorum</i>		5	1–3	7	0.122
<i>Raphidascaris acus</i>		8	1–4	12	0.157*

^a Spearman's rank correlation coefficient: **P* < 0.05; ***P* < 0.01; ****P* < 0.001.

and definitive hosts were the most strongly associated, followed by pairs that shared only one other host, and by pairs that did not share other hosts (Fig. 1). A back-calculation using the Sørensen coefficient formula indicates that in pairs of helminth species that share both first intermediate hosts and definitive hosts, on average 36% of individual worms co-occur with the other species; this number is only about 15% for pairs of helminth species that do not share other hosts. The interaction terms in the ANOVAs were not significant (Jaccard's coefficient: $F_{2,56} = 1.794$, $P = 0.1757$; Sørensen's coefficient: $F_{2,56} = 0.818$, $P = 0.4463$).

Within an ecosystem, the complex life cycles of helminth parasites involve many transmission events among many host species within the food web. Two different helminth species may travel completely separate routes (i.e. they have no host species in common), or they may share one, two or even three host species. The life cycles of such parasites can therefore overlap one another, even to the point of being identical. In the host-parasite systems we studied, the last host used by all helminth species before reaching the definitive host was a fish. We showed that helminth species with similar life cycles are more likely to co-occur in the fish host than helminth species that share no other hosts between

Table 3

Matrix of pairwise associations between larval helminth species, using Jaccard's coefficient, r_j (species names are abbreviated as in Table 1); each fish sample is treated separately

Host species	Ddit	Dlat	Spun	Ssol	Tcra	Tnod	Eubo	Cosc	Emer	Racu	Csem	Cstr
<i>C. albula</i> (Bothnian Bay)												
Ddit					0.056							
<i>O. eperlanus</i> (Bothnian Bay)												
Ddit						0.000		0.000			0.022	0.000
Tnod								0.000			0.050	0.063
Cosc											0.023	0.053
Csem												0.119
<i>L. lota</i> (Bothnian Bay)												
Dden		0.261				0.273		0.097	0.286		0.107	0.077
Dlat						0.387		0.220	0.458		0.143	0.184
Tnod								0.148	0.519		0.111	0.186
Cosc									0.150		0.091	0.172
Emer											0.073	0.174
Csem												0.308
<i>G. aculeatus</i> (Bothnian Bay)												
Dden	0.249			0.229		0.096			0.027	0.043		
Ddit				0.453		0.092			0.017	0.126		
Ssol						0.105			0.025	0.150		
Tnod									0.000	0.126		
Emer										0.019		
<i>P. pungitius</i> (Bothnian Bay)												
Ddit			0.091			0.018						
Spun						0.063						
<i>M. scorpius</i> (Bothnian Bay)												
Cosc											0.207	0.214
Csem												0.966
<i>G. cernuus</i> (Bothnian Bay)												
Tnod							0.100		0.091		0.000	
Eubo									0.055		0.000	
Emer											0.070	
<i>G. cernuus</i> (Lake Yli-Kitka)												
Tnod									0.047	0.070		
Emer										0.000		

them. The trend is not very strong, but it is there. This means that assemblages of larval helminth parasites in fish are not random selections of locally available species, but rather non-random packets of larval parasites that travel together along common transmission routes.

Our analysis ruled out the possible effect of host size as the sole factor leading to the formation of interspecific associations among helminth species. Larger fish have had longer to accumulate helminths than smaller fish, and may also have a greater exposure to helminths because of the greater diversity of prey on which they feed. Here, pairs of helminth species that both accumulate as their fish host grows (i.e. species for which intensity of infection correlates significantly with fish size) do tend to be more strongly associated with one another than other pairs of species. However, our analysis factored out this small effect to reveal that stronger associations are not merely the outcome of the simultaneous and passive accumulation of larvae in fish, but a reflection of other ecological processes.

What other forces could generate these stronger-than-expected associations? Recent discussions of the evolution of parasite transmission along food chains have emphasised

the possibility that parasites that have similar life cycles could benefit by associating within the same intermediate of paratenic host individuals (Thomas et al., 1998; Lafferty, 1999; Lafferty et al., 2000). Studies on invertebrate intermediate hosts have shown that two different helminth species may be selected to associate more often than expected by chance in this intermediate host, if one of the two can alter host behaviour in a way that enhances the probability of transmission to the next host for both parasites (Thomas et al., 1997; Dezfuli et al., 2000). This phenomenon is referred to as hitch-hiking (Thomas et al., 1998). Associations established early in the life cycle can then be transferred to subsequent hosts in the shared life cycle of the two parasites (Lotz et al., 1995). The hitch-hiking process can be repeated in the second intermediate host or a paratenic host, if one parasite can again modify host behaviour in a way that benefits both parasite species. This is certainly possible for some of the helminth species included in our analysis. For instance, the cestodes *Schistocephalus* spp. are capable of manipulating the behaviour of their copepod first intermediate host (Wedekind and Miliński, 1996) as well as that of the sticklebacks *Gasterosteus*

Table 4

Matrix of pairwise associations between larval helminth species, using the modified Sørensen's coefficient, r_s (species names are abbreviated as in Table 1); each fish sample is treated separately

Host species	Ddit	Dlat	Spun	Ssol	Tcra	Tnod	Eubo	Cosc	Emer	Racu	Csem	Cstr
<i>C. albula</i> (Bothnian Bay)												
Ddit					-0.755							
<i>O. eperlanus</i> (Bothnian Bay)												
Ddit						-1.000		-1.000			-0.948	-1.000
Tnod								-1.000			-0.836	-0.684
Cosc											-0.921	-0.818
Csem												-0.615
<i>L. lota</i> (Bothnian Bay)												
Dden		-0.105				-0.040		-0.596	-0.133		-0.798	-0.813
Dlat						-0.100		-0.246	0.410		-0.742	-0.488
Tnod								-0.630	0.404		-0.798	-0.527
Cosc									-0.439		-0.791	-0.474
Emer											-0.856	-0.392
Csem												0.069
<i>G. aculeatus</i> (Bothnian Bay)												
Dden	-0.182			-0.209		-0.667			-0.927	-0.845		
Ddit				0.286		-0.723			-0.944	-0.528		
Ssol						-0.640			-0.938	-0.494		
Tnod									-1.000	-0.459		
Emer										-0.951		
<i>P. pungitius</i> (Bothnian Bay)												
Ddit			-0.563			-0.923						
Spun						-0.826						
<i>M. scorpius</i> (Bothnian Bay)												
Cosc											-0.123	-0.116
Csem												0.994
<i>G. cermuus</i> (Bothnian Bay)												
Tnod							-0.600		-0.753		-1.000	
Eubo									-0.837		-1.000	
Emer											-0.752	
<i>G. cermuus</i> (Lake Yli-Kitka)												
Tnod									-0.890	-0.625		
Emer										-1.000		

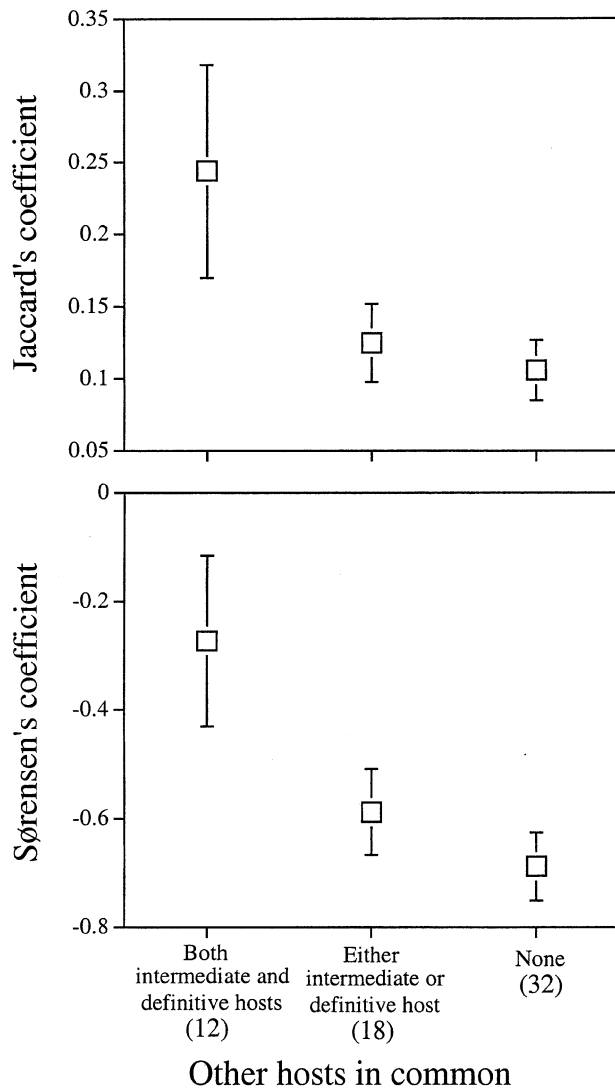


Fig. 1. Mean (and SE) values of pairwise coefficients of association among larval helminths in fish, depending on whether the two species in a pair also share both first intermediate hosts and definitive hosts, only one of those other hosts, or no other hosts. Values for the Jaccard and Sørensen coefficients are shown separately; numbers of pairwise associations in each category are indicated below the bottom graph.

aculeatus and *Pungitius pungitius* that serve as their second intermediate host (Smith and Kramer, 1987; LoBue and Bell, 1993). Any other helminth also maturing in fish-eating birds could benefit by associating with these cestodes, and the association would be passed on along their trophic transmission route. The other cestodes included in our analyses are also capable of manipulating the behaviour of their copepod first intermediate hosts in ways that may enhance transmission to their next host (Poulin et al., 1992; Pasternak et al., 1995; Pulkkinen et al., 2000), and the acanthocephalans might be capable of it as well (Moore, 1984). These effects in first intermediate hosts could favour the establishment of other associations among helminths.

Other factors can serve to maintain interspecific associations throughout the shared life cycle once they are estab-

lished. For instance, if two helminth species with identical life cycles co-occur in the definitive host, their eggs will be released in the host's faeces at the same place and time. A first intermediate host feeding nearby and ingesting eggs of one helminth species would be more likely to also ingest eggs of the second species than a conspecific host foraging some distance away. This can facilitate the establishment of a positive association between larvae of these species in their first intermediate host, on which the local fish will then feed. The association will thus be transferred up the food chain and further down the life cycles of both parasites. We might therefore expect associations between helminth species with shared interests to exist at all stages of the life cycle.

From the perspective of the definitive hosts that feed on fish, the results of this study mean that not all prey fish present equal risks of acquiring parasites. Some fish are likely to contain ready-made packets of helminth larvae of different species, all capable of infecting the same definitive host species, whereas other fish may contain other helminth larvae that present no risk for that particular definitive host. Few food web studies have considered parasites (see Marcolli and Cone, 1997) and it may be too early to speculate on how associations between helminth species might fit in a food web. It is possible, however, that different groups of parasites use host populations in non-random ways that reflect both the similarity of their life cycles and the different links connecting the host population to higher levels in a complex food web. The trends we found in fishes from Finland are clear-cut (e.g. Fig. 1) though not very strong; it would now be interesting to see whether they also occur in other ecosystems.

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References

- Bush, A.O., Heard, R.W., Overstreet, R.M., 1993. Intermediate hosts as source communities. *Can. J. Zool.* 71, 1358–63.
- Dezfuli, B.S., Giari, L., Poulin, R., 2000. Species associations among larval helminths in an amphipod intermediate host. *Int. J. Parasitol.* 30, 1143–6.
- Holmes, J.C., 1990. Helminth communities in marine fishes. In: Esch, G.W., Bush, A.O., Aho, J.M. (Eds.). *Parasite Communities: Patterns and Processes*. Chapman and Hall, London, pp. 101–30.
- Janson, S., Vegelius, J., 1981. Measures of ecological association. *Oecologia* 49, 371–6.
- Kennedy, C.R., 1990. Helminth communities in freshwater fish: structured communities or stochastic assemblages? In: Esch, G.W., Bush, A.O., Aho, J.M. (Eds.). *Parasite Communities: Patterns and Processes*. Chapman and Hall, London, pp. 131–56.
- Lafferty, K.D., 1999. The evolution of trophic transmission. *Parasitol. Today* 15, 111–5.
- Lafferty, K.D., Thomas, F., Poulin, R., 2000. Evolution of host phenotype manipulation by parasites and its consequences. In: Poulin, R., Morand, J.

- S., Skorping, A. (Eds.). Evolutionary Biology of Host–Parasite Relationships: Theory Meets Reality, Elsevier Science, Amsterdam, pp. 117–27.
- Lobue, C.P., Bell, M.A., 1993. Phenotypic manipulation by the cestode parasite *Schistocephalus solidus* of its intermediate host, *Gasterosteus aculeatus*, the threespine stickleback. *Am. Nat.* 142, 725–35.
- Lotz, J.M., Bush, A.O., Font, W.F., 1995. Recruitment-driven, spatially discontinuous communities: a null model for transferred patterns in target communities of intestinal helminths. *J. Parasitol.* 81, 12–24.
- Marcogliese, D.J., Cone, D.K., 1997. Food webs: a plea for parasites. *Trends Ecol. Evol.* 12, 320–5.
- Moore, J., 1984. Altered behavioral responses in intermediate hosts: an acanthocephalan parasite strategy. *Am. Nat.* 123, 572–7.
- Pasternak, A.F., Huntingford, F.A., Crompton, D.W.T., 1995. Changes in metabolism and behaviour of the freshwater copepod *Cyclops strenuus abyssorum* infected with *Diphyllbothrium* spp. *Parasitology* 110, 395–9.
- Poulin, R., 1998. Evolutionary Ecology of Parasites: From Individuals to Communities, Chapman and Hall, London.
- Poulin, R., 2000. Variation in the intraspecific relationship between fish length and intensity of parasitic infection: biological and statistical causes. *J. Fish Biol.* 56, 123–37.
- Poulin, R., Curtis, M.A., Rau, M.E., 1992. Effects of *Eubothrium salvelini* (Cestoda) on the behaviour of *Cyclops vernalis* (Copepoda) and its susceptibility to fish predators. *Parasitology* 105, 265–71.
- Pulkkinen, K., Pasternak, A.F., Hasu, T., Valtonen, E.T., 2000. Effect of *Triaenophorus crassus* (Cestoda) infection on behavior and susceptibility to predation of the first intermediate host *Cyclops strenuus* (Copepoda). *J. Parasitol.* 86, 664–70.
- Rohde, K., Hayward, C., Heap, M., 1995. Aspects of the ecology of metazoan ectoparasites of marine fishes. *Int. J. Parasitol.* 25, 945–70.
- Smith, R.L., Kramer, D.L., 1987. Effects of a cestode (*Schistocephalus* sp.) on the response of ninespine sticklebacks (*Pungitius pungitius*) to aquatic hypoxia. *Can. J. Zool.* 65, 1862–5.
- Southwood, T.R.E., Henderson, P.A., 2000. Ecological Methods, 3rd Edition Blackwell Science, Oxford.
- Thomas, F., Mete, K., Helluy, S., Santalla, F., Verneau, O., De Meeus, T., Cézilly, F., Renaud, F., 1997. Hitch-hiker parasites or how to benefit from the strategy of another parasite. *Evolution* 51, 1316–8.
- Thomas, F., Renaud, F., Poulin, R., 1998. Exploitation of manipulators: ‘hitch-hiking’ as a parasite transmission strategy. *Anim. Behav.* 56, 199–206.
- Wedekind, C., Milinski, M., 1996. Do three-spined sticklebacks avoid consuming copepods, the first intermediate host of *Schistocephalus solidus*? An experimental analysis of behavioural resistance. *Parasitology* 112, 371–83.