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Factors influencing infection patterns of trophically transmitted parasites among a fish community: host diet, host–parasite compatibility or both?

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Parasite infection patterns were compared with the occurrence of their intermediate hosts in the diet of nine sympatric fish species in a New Zealand lake. Stomach contents and infection levels of three gastrointestinal helminth species were examined from the entire fish community. The results highlighted some links between fish host diet and the flow of trophically transmitted helminths. Stomach contents indicated that all but one fish species were exposed to these helminths through their diet. Host feeding behaviour best explained infection patterns of the trematode *Coitocaecum parvum* among the fish community. Infection levels of the nematode *Hedruris spinigera* and the acanthocephalan *Acanthocephalus galaxii*, however, were not correlated with host diets. Host specificity is thus likely to modulate parasite infection patterns. The data indicate that host diet and host–parasite compatibility both contribute to the distribution of helminths in the fish community. Furthermore, the relative influence of encounter (trophic interactions between prey and predator hosts) and compatibility (host suitability) filters on infection levels appeared to vary between host–parasite species associations. Therefore, understanding parasite infection patterns and their potential impacts on fish communities requires determining the relative roles of encounter and compatibility filters within and across all potential host–parasite associations.

Key words: fish diet; gastrointestinal helminths; host specificity; trophically transmitted parasites.

INTRODUCTION

Parasites are ubiquitous components of most ecosystems, occurring in virtually all food webs at all trophic levels, with most species serving as hosts for one or more parasite species. Parasitism is also increasingly recognized as playing an important role in structuring animal communities (Dobson & Hudson, 1986; Minchella & Scott, 1991; Mouritsen & Poulin, 2002; Marcogliese, 2004). By modifying host physiology, behaviour and survival, parasites can alter the influence of their host species on community functioning and structure (Holt & Lawton, 1994; Hudson & Greenman, 1998; Combes, 2001; Hudson *et al*., 2002; Wood *et al*., 2007).

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Fishes are hosts to taxonomically diverse parasites, and infections can significantly affect fish behaviour, metabolism, body condition, fecundity or survival (Barber *et al*., 2000; Dobson *et al*., 2008; Lafferty, 2008; Seppänen *et al*., 2009). Within a community, different fish species can exhibit broad variation in sensitivity to parasite infection, influencing interspecific competitive interactions and, ultimately, fish community dynamics and structure (Johnson & Hartson, 2009). For example, epizootics of the cestode *Ligula intestinalis* in its intermediate host, the roach *Rutilus rutilus* (L. 1758), can directly affect roach population structure *via* parasite-induced host mortality and sterility and indirectly that of sympatric fish species not infected by *L. intestinalis* (Kennedy, 1996; Marcogliese, 2004). By reversing the dominance of *R. rutilus* in interspecific competition, the parasite facilitates the expansion of a sympatric cyprinid, the rudd *Scardinius erythrophthalmus* (L. 1758) (Kennedy *et al*., 2001). Alternatively, sympatric hosts can harbour the same parasites but bear differential costs of infection (Hudson & Greenman, 1998; Johnson & Hartson, 2009). For instance, in a community consisting of three stickleback species, Poulin & Fitzgerald (1987) found that a shared parasite had very different infection levels and fitness impacts on different species, potentially influencing the fish community dynamics. Generally, sympatric fish species largely share the same parasites (Kennedy, 1990; Bergeron *et al*., 1997; Baldwin & Goater, 2003; Lymbery *et al*., 2010); yet, they are usually neglected in studies of fish communities (Marcogliese & Cone, 1997). Factors influencing fish species vulnerability to parasites and interspecific differences in infection levels, however, are often unknown.

Holmes (1987, 1990) suggested that three factors play essential roles in host vulnerability and infection levels among sympatric fish species: phylogenetic specificity (host–parasite co-evolution), exposure to parasites (encounter filter) and host suitability (compatibility filter). Where phylogenetic specificity is strong, parasites should preferentially or exclusively exploit host taxa with which they have co-evolved (Poulin, 1992, 1995, 2005; Blaylock *et al*., 1998; Lile, 1998; Marcogliese, 2002). Nevertheless, factors controlling parasite species composition and infection levels are often ecological, not physiological or phylogenetic (Holmes & Price, 1980; Kennedy, 1990; Marcogliese, 2002; Knudsen *et al*., 2004, 2008; Muñoz *et al*., 2007; MacColl, 2009). In parasites acquired by ingestion, host diet is the encounter filter and the main factor determining the number of parasite species and individuals to which a host is exposed (Poulin, 1995; Combes, 2001; Kuris *et al*., 2007).

Ingestion of larval helminth parasites by fishes is a frequent event due to the abundance and diversity of these trophically transmitted parasites in aquatic ecosystems (Marcogliese, 2002; Parker *et al*., 2003). Most helminths depend on the consumption of infected intermediate host prey by definitive hosts (Marcogliese, 1995, 2003; Marcogliese & Cone, 1997; Valtonen *et al*., 2010). Dietary preferences may thus predetermine trophic acquisition and infection levels of helminth parasites among sympatric fishes (Kennedy, 1990; Bell & Burt, 1991; Choudhury & Dick, 2000; Šimková *et al*., 2001; Knudsen *et al*., 2003, 2004). Host–parasite compatibility, however, may modulate encounter filter effects on parasite infection levels and must be accounted for to understand infections patterns among fish hosts (Holmes *et al*., 1977).

The relative roles of encounter and compatibility filters were assessed by quantifying host use by three gastrointestinal helminth parasites within the fish community of Lake Waihola, New Zealand. The nematode *Hedruris spinigera* has a two host

life cycle and uses the crustacean amphipod *Paracorophium excavatum* as its only intermediate host species (Luque *et al*., 2007, 2010). Adults are found in the pyloric region of the fish stomach where the larger female attaches deeply into the stomach wall using a recurved hook on its tail while the smaller male curls around the female (Hewitt & Hine, 1972; Hine, 1980; McDowall, 1990; Luque *et al*., 2010). *Acanthocephalus galaxii* (acanthocephalan), also possessing a two host cycle with only one intermediate host species, the amphipod *Paracalliope fluviatilis*, attaches in the duodenum of fishes using a hooked proboscis (Hewitt & Hine, 1972; Hine, 1977). Finally, the trematode *Coitocaecum parvum* has a three-host life cycle. Adults occur along the entire fish gut where, unlike the other two species, they can move freely by moving over the host epithelium using their oral and ventral suckers (MacFarlane, 1939; Holton, 1984). *Coitocaecum parvum* uses both *P. excavatum* and *P. fluviatilis* as its second intermediate hosts (Holton, 1984; Luque *et al*., 2007). In addition, the lake includes both native and introduced fish species. These introduced hosts are potentially important when assessing the role of host diet relative to host–parasite compatibility since they feed on native prey (*i.e.* intermediate host species) but are often incompatible with local parasites (Torchin *et al*., 2003; Byrne *et al*., 2004).

Four predictions were tested in relation to the main hypothesis: (1) gut contents directly reflect parasite infection levels (*i.e.* direct relationship between fish host diet and parasite acquisition); host diet thus determines the acquisition, accumulation and overall infection levels of helminth parasites in the fish community (Campbell *et al*., 1980; Martell & McClelland, 1995; Klimpel *et al*., 2003). (2) If some host specificity exists and varies among host–parasite associations, the degree of host–parasite compatibility should modulate parasite exposure effects on infection levels and result in lower than expected infection levels according to host diet. (3) Host–parasite incompatibility may influence parasite growth and fecundity and thus restrict parasite size and fecundity. These potential effects will be assessed for *C. parvum* using parasite size and fecundity data. (4) Interspecific differences in host–parasite compatibility may be particularly apparent between native and introduced fishes; introduced species tend to have lower infection burdens than native fishes and parasites often achieve higher growth and fecundity in their native hosts (Torchin *et al*., 2003).

MATERIALS AND METHODS

STUDY SITE

Samples were taken between November 2008 and February 2009 (Austral summer) in Lake Waihola (46° 01′ S; 170° 05′ E), near Dunedin, South Island, New Zealand. Lake Waihola is a shallow coastal lake, with an area of 6·35 km^2 and mean depth of 1·3 m, situated 10 km from the Pacific Ocean and influenced twice daily by a fresh to brackish tidal input, depending on tides and river flow (Hall & Burns, 2002; Wilhelm *et al*., 2007). Lake Waihola has a moderately diverse fish community that includes fishes from widely different taxa, of varying body sizes, status (native or introduced) and ecological traits (see Table I for details; Jeppesen *et al*., 2000; Kattel & Closs, 2007). In addition, the lake includes both native and introduced fish species, making it a good system in which to test the relative roles of diet (encounter filter) and host suitability (compatibility filter) as opposed to co-evolutionary history. As this lake is shallow and well-mixed all year round, due to regular winds and daily tides, it is often considered as a homogeneous functional unit. Accordingly, previous studies on the fish community, invertebrate fauna and flora collected at different sites in the lake did not detect any qualitative variation between sites (Wilhelm *et al*., 2007).

TABLE I. Details of name, status (native or introduced), size (mean ± S.E., minimum and maximum fork length, L_F) and gut length (L_G; mean ± S.E., minimum and maximum) of the fish species sampled in Lake Waihola with the number of individuals dissected (N) per species for the purpose of the study. Note that only one individual of *Leptoscopus macropygus* was captured and values that could not be calculated are indicated as not available (na)

Fish species				L_F (mm)		L_G (mm)	
Common name	Scientific name	Status	N	Mean ± S.E.	Minimum/maximum	Mean ± S.E.	Minimum/maximum
Common bully	*Gobiomorphus cotidianus*	Native	35	44·4 ± 1·5	32/72	20·9 ± 1·2	14/42
Black flounder	*Rhombosolea retiaria*	Native	46	90·5 ± 14·3	30/356	145·3 ± 29·6	19/650
Perch	*Perca fluviatilis*	Introduced	68	132·2 ± 10·1	36/360	99·5 ± 8·5	22/280
Yellow-eyed mullet	*Aldrichetta forsteri*	Native	29	185·5 ± 6·6	138/260	253·1 ± 11·3	150/380
Common smelt	*Retropinna retropinna*	Native	32	80·4 ± 1·9	65/104	49·5 ± 1·6	35/66
Inanga	*Galaxias maculatus*	Native	34	69·4 ± 2·3	45/105	349·1 ± 20·9	200/540
Brown trout	*Salmo trutta*	Introduced	23	397·8 ± 21·5	215/690	44·8 ± 1·8	20/70
Giant kokopu	*Galaxias argenteus*	Native	9	68·6 ± 10·3	39/125	60·4 ± 8·3	35/100
Estuary stargazer	*Leptoscopus macropygus*	Native	1	60·0 ± na	na	35 ± na	na

FISH COLLECTIONS

Fishes were collected weekly during the sampling period using gillnets (Oy Lindeman Ab;www.lindeman.fi) and a standard purse seine. For gillnetting, three 25 m long multi-mesh nets were used. These gillnets were benthic weighted sets with top floats, 1·5 m high and comprised five panels of 13, 25, 38, 56 and 70 mm meshes, each 5 m long. Gillnets were set randomly at different locations along the lake shore, covering the whole water column in all cases, and were checked every 15 min. Fishes caught in the nets were removed immediately to avoid excessive accumulation and the potential visual deterrence to incoming fishes. The seine was 20 m long and 1·5 m high, with a 5 mm mesh diameter, and dragged by two people along several stretches of the lake. All fishes set aside for later dissection were killed immediately to inhibit the digestion process and stored on ice to preserve internal tissues and parasites for future identification. Fishes captured in excess were immediately released. In the laboratory, fishes were identified to species, measured (fork length, L_F) to the nearest mm, weighed (mass, M) to the nearest 0·1 g and then dissected. Their gut was removed, from oesophagus to anus, for later stomach content and parasite analyses. Total gut length (L_G) was recorded to the nearest mm and differences in gastrointestinal morphology among fish species as well as parasite attachment sites were also noted since gut complexity can influence habitat availability for parasites (Campos & Carbonell, 1994).

STOMACH CONTENT ANALYSIS

Fish guts were preserved individually in buffered 10% formalin for at least 21 days and rinsed with tap water before dissection. The stomach contents of each fish were removed and examined stereomicroscopically, and prey items were counted and identified to species whenever their state of digestion allowed identification. Particular attention was given to the two amphipod species (*Paracalliope fluviatilis* and *Paracorophium excavatum*) as known intermediate hosts for the three helminth species considered in this study. To assess the dietary importance of particular prey items, diet composition as relative abundance of each prey item in the stomachs, the relative frequency of prey occurrence, and the per cent of stomachs in which prey species were found, were calculated for each fish species. For the two intermediate host species of parasites, the absolute abundance (*i.e.* mean number of the prey species per stomach) and intensity of predation (*i.e.* mean number of the prey items per stomach containing the prey) were also calculated.

PARASITE COLLECTION AND ANALYSIS

All fish guts were dissected and oesophagus, stomach, pyloric caeca, intestine and rectum examined for parasites. Particular attention was given to *C. parvum*, *H. spinigera* and *A. galaxii* although the presence of a few specimens of other species was observed. *Coitocaecum parvum*, *H. spinigera* and *A. galaxii* individuals were counted. Using a compound microscope with an ocular micrometer, *C. parvum* were also measured for total length and greatest width (at the level of the ventral sucker) to the nearest 0·025 mm. The body surface area of each *C. parvum* was then determined and used as a surrogate for body size (Lefebvre & Poulin, 2005; Lagrue & Poulin, 2007). This was done using the formula for an ellipsoid, 0·25 (πLW), where L and W are the total length and maximum width of the parasite. The reproductive status of each *C. parvum* was also estimated and recorded as immature (non-egg producing individuals) or mature (egg-producing individuals; Lefebvre & Poulin, 2005). These two developmental stages were distinguished according to the presence or absence of eggs *in utero* that can be seen through the translucent body; individuals without eggs were considered immature as egg production is continuous after maturation (Lefebvre & Poulin, 2005; Lagrue & Poulin, 2008). When present, eggs were counted as an estimate of egg production rate by mature *C. parvum*; there is a strong relationship between the number of eggs still *in utero* and individual egg production rate (Lefebvre & Poulin, 2005). Prevalence (per cent of host fish individuals infected; following Bush *et al.*, 1997) and mean abundances (mean number of parasite individuals per individual fish, with uninfected fishes included in the calculation; Bush *et al.*, 1997) were calculated for the three parasites species in each

fish host species to describe the parasite communities of all potential fish definitive hosts. Reference to *C. parvum* size hereafter refers to the parasite body surface.

DATA ANALYSIS

First, differences in parasite prevalence between fish species were tested using Fisher's exact tests; proportions of infected hosts were compared in a pair-wise manner between different fish species and for each of the three parasite species. Because all series of pair-wise comparisons consisted of multiple Fisher's exact tests, a sequential Bonferroni approach for multiple comparisons was used (Rice, 1989). The Bonferroni-adjusted α level consequently used for these P-values was $\alpha = 0{\cdot}00833$. Note that the standard $\alpha = 0{\cdot}05$ was used for all other analyses.

Fish mass and L_G were significantly correlated with fish L_F in all species ($0{\cdot}891 < r < 0{\cdot}990$ and $0{\cdot}815 < r < 0{\cdot}994$ for M and L_G, respectively, all $P < 0{\cdot}001$). When controlled for L_F, however, L_G was significantly different between fish species (ANCOVA, $F_{7,276} = 59{\cdot}210$, $P < 0{\cdot}001$). Consequently, L_G was used as a surrogate for host size since the length of a fish's gut corresponds to the effective habitat size. Although not quantifiable, interspecific differences in gastrointestinal morphology, that is habitat complexity, were considered and their potential implications for parasite infection patterns are discussed. The effects of L_G and intermediate host abundance in fish gut contents on parasite abundance were tested using general linear models (GLM) to determine whether these variables should be included as covariates in the following ANCOVA. Interspecific differences in parasite abundance among fish species were tested for the three parasite species using three ANCOVAs with parasite abundance as the dependent variable and L_G, intermediate host abundance and the abundances of co-occurring parasite species as potential covariates. Parasite abundances were $\log_{10}$ transformed before ANCOVA analyses to normalize the data, and *post hoc* tests (Tukey's HSD) were used when appropriate.

General liner models were used to test for negative or positive associations between the prevalences or mean abundances of the three parasite species across fish species. Where possible, correlations between parasite abundances were also tested at the level of the individual host within fish species. Finally, both the relation between parasite prevalence and occurrence of different intermediate hosts (*P. fluviatilis* and *P. excavatum*) in fish diet and the relation between mean intermediate host abundance in fish diet and mean parasite abundance were tested for the three parasite species using GLM.

Effects of fish host species and *C. parvum* reproductive status (egg or non-egg producing) on parasite size were tested using a two-way ANOVA with the body surface area of parasites used as the dependent variable. *Coitocaecum parvum* reproductive status and host species were defined as the main factors. A linear regression between *C. parvum* body size and the number of eggs counted *in utero* (egg production) was used to assess the effect of individual parasite size on egg production. Finally, an ANCOVA was used to test for fish-definitive host species effects on *C. parvum* egg production with fish host species as the main factor and *C. parvum* body size as a covariate to control for possible effects of parasite size on egg production. Only parasites that had produced at least one egg were included in this analysis and, as there is no relationship between fish L_F and *C. parvum* body size (Lefebvre & Poulin, 2005), L_F was not considered in these analyses. Parasite body surface area and egg production were $\log_{10}$ transformed before ANOVA and ANCOVA analyses to normalize the data, and *post hoc* tests (Tukey's HSD) were used when appropriate. All tests were performed using the STATISTICA software (Statsoft Inc., version 6, www.statsoft.com).

RESULTS

Specimens of nine different fish species, seven natives and two introduced, were captured in Lake Waihola and 277 were dissected for stomach contents and parasite examination (see Table I for details on specific fish status and sample sizes). All captured brown trout *Salmo trutta* L. 1758, giant kokopu *Galaxias argenteus*

(Gmelin 1789) and estuary stargazer *Leptoscopus macropygus* (Richardson 1846), and about a third of black flounder *Rhombosolea retiaria* Hutton 1873, perch *Perca fluviatilis* L. 1758 and yellow-eyed mullet *Aldrichetta forsteri* (Valenciennes 1836) individuals were dissected. These proportions were lower for the more abundant species like inanga *Galaxias maculatus* (Jenyns 1842; around 10% dissected), common bully *Gobiomorphus cotidianus* McDowall 1975 (*c*. 1%) and common smelt *Retropinna retropinna* (Richardson 1848; *c*. 1%). In species where only proportions of the fishes were dissected, these individuals were chosen haphazardly from the pool of captures and the proportion of fishes dissected was kept similar across sampling dates for all species. Furthermore, fishes were caught at similar rates and sampled evenly during the capture period. Because two different and non-exhaustive sampling methods were used, however, no accurate estimation of relative abundance could be calculated. *Perca fluviatilis* was the most abundant species in gillnet samples while *G. cotidianus* and *R. retropinna* were the most abundant species captured by seining.

Some individuals of *A. forsteri* were infected by a large (total length >5 mm) unidentified adult trematode (prevalence = 17·2%; mean ± S.E. abundance = 2·3 ± 1·6; site of infection = rectum) and some of the largest specimens of *R. retiaria* were infected with another unidentified trematode (prevalence = 6·5%; mean ± S.E. abundance = 0·7 ± 0·5; site of infection = rectum). Because these parasites were present in only one fish species, could not be identified and thus no information on their life cycles found, these two trematodes were not included in the analyses. Other fish species were infected only by the three species considered in this study. Note that two fish species, *G. argenteus* and *L. macropygus*, were excluded from the analyses because of the low number of individuals sampled. Also, *G. argenteus* was the only fish species in which none of the three parasite or two intermediate host species was found (0% prevalence; Tables II).

PARASITE PREVALENCE AND ABUNDANCE IN FISH HOSTS AND RELATION WITH FISH DIET

Prevalence patterns among fish species were widely different between the three parasite species (Table II). While there was no difference between *G. cotidianus* and *R. retiaria*, in prevalence of *C. parvum* (94·3 and 93·5%, respectively) the occurrence was significantly higher than in any other fish [Tables II and III(a)]. Prevalence of *C. parvum* in *P. fluviatilis* showed an intermediate value (67·6%), being lower than in the above two species but significantly higher than in the remaining fish species [Tables II and III(a)]. Finally, no other significant difference was detected under the Bonferroni-adjusted significance level [Tables II and III(a)]. The prevalences of *A. galaxii* and *H. spinigera* were significantly higher in *A. forsteri* (96·6 and 93·1%, respectively) than in any other fish species [Tables II and III(b), (c)]. *Acanthocephalus galaxii* prevalence ranged from 10·3% in *P. fluviatilis* to 53·1% in *R. retropinna* while prevalence of *H. spinigera* ranged from 0% in *G. cotidianus* to 46·9% in *R. retropinna*; all significant differences in pair-wise comparisons of parasite prevalence between fish species are given in Table III.

There was no significant correlation between prevalence of *C. parvum* and that of the two other parasite species among fish host species [$r = -0{\cdot}609$ and $-0{\cdot}432$, $n = 7$, both $P > 0{\cdot}05$ for *A. galaxii* and *H. spinigera*, respectively; Fig. 1(a), (b)]. In

TABLE II. Prevalence (proportion of infected individuals within sample size, n), and parasite abundances (mean number of parasites ± S.E. per individual) for the three parasite species in the nine fish species sampled in Lake Waihola. When prevalence was 0, parasite abundance could not be calculated and is shown as not available (na)

Parasite species		*Coitocaecum parvum*		*Acanthocephalus galaxii*		*Hedruris spinigera*	
Fish species	n	Prevalence (%)	Abundance	Prevalence (%)	Abundance	Prevalence (%)	Abundance
Gobiomorphus cotidianus	35	94·3	17·2 ± 3·0	11·4	0·2 ± 0·1	0·0	na
Rhombosolea retiaria	46	93·5	19·4 ± 6·6	34·8	4·4 ± 1·7	26·1	4·6 ± 2·2
Perca fluviatilis	68	67·6	2·1 ± 0·3	10·3	0·1 ± 0·0	14·7	0·2 ± 0·0
Aldrichetta forsteri	29	20·7	0·4 ± 0·2	96·6	40·1 ± 7·5	93·1	29·2 ± 8·7
Retropinna retropinna	32	6·3	0·1 ± 0·1	53·1	12·1 ± 3·5	46·9	12·1 ± 7·5
Galaxias maculatus	34	2·9	0·0 ± 0·0	38·2	0·7 ± 0·2	5·9	0·1 ± 0·1
Salmo trutta	23	0·0	na	52·2	3·5 ± 1·3	39·1	3·1 ± 1·4
Galaxias argenteus	9	0·0	na	0·0	na	0·0	na
Leptoscopus macropygus	1	100·0	2·0 ± 0·0	0·0	na	0·0	na

contrast, *A. galaxii* and *H. spinigera* prevalences were positively correlated among fish-definitive hosts [$r = 0{\cdot}934$, $n = 7$, $P < 0{\cdot}01$; Fig. 1(c)]. When considering mean parasite abundances among fish species, no significant correlation was observed between *C. parvum* and the two other parasite abundances ($r = -0{\cdot}312$ and $-0{\cdot}311$, $n = 7$, both $P > 0{\cdot}05$ for *A. galaxii* and *H. spinigera*, respectively) while *A. galaxii* and *H. spinigera* mean abundances were positively correlated ($r = 0{\cdot}993$, $n = 7$, $P < 0{\cdot}001$). Within fish host species, *C. parvum* abundance was positively correlated with that of *A. galaxii* in *G. cotidianus* and *R. retiaria* ($r = 0{\cdot}389$ and $0{\cdot}637$, $n = 35$ and 46, $P < 0{\cdot}05$ and $0{\cdot}001$, respectively) and with *H. spinigera* abundance in *R. retiaria* ($r = 0{\cdot}725$, $n = 46$, $P < 0{\cdot}001$). *Acanthocephalus galaxii* and *H. spinigera* abundances were positively correlated in *R. retiaria*, *A. forsteri* and *R. retropinna* ($r = 0{\cdot}792$, $0{\cdot}427$ and $0{\cdot}598$, $n = 46$, 29 and 32, $P < 0{\cdot}001$, $0{\cdot}05$ and $0{\cdot}001$, respectively). No other positive correlation was found and no negative relationship was detected between specific parasite abundances in any fish host species.

The occurrence and abundance of intermediate hosts (*P. fluviatilis* and *P. excavatum*) in stomach contents were highly variable between fish species (see Table IV). Prevalence of *C. parvum* in fish-definitive hosts was positively correlated with the occurrence of its intermediate hosts (*P. fluviatilis* and *P. excavatum*) in fish diet [$r = 0{\cdot}855$, $n = 7$, $P < 0{\cdot}05$; Fig. 2(a)]. In contrast, *A. galaxii* and *H. spinigera* prevalences were not correlated with the occurrence of their respective intermediate host (*P. fluviatilis* or *P. excavatum*) in fish stomach contents [$r = -0{\cdot}070$ and $0{\cdot}058$, $n = 7$, both $P > 0{\cdot}05$, respectively; Fig. 2(b), (c)]. Mean *C. parvum* and

TABLE III. Results of Fisher's exact tests for pair-wise comparisons of parasite prevalence between fish species for (a) *Coitocaecum parvum*, (b) *Acanthocephalus galaxii* and (c) *Hedruris spinigera*. *P*-values marked with an * are those significant after Bonferroni adjustment for multiple comparisons ($\alpha = 0{\cdot}00833$)

Fish species	*Gobiomorphus cotidianus*	*Rhombosolea retiaria*	*Perca fluviatilis*	*Aldrichetta forsteri*	*Retropinna retropinna*	*Galaxias maculatus*
			(a)			
R. retiaria	>0·05					
P. fluviatilis	<0·01*	<0·001*				
A. forsteri	<0·001*	<0·001*	<0·001*			
R. retropinna	<0·001*	<0·001*	<0·001*	>0·05		
G. maculatus	<0·001*	<0·001*	<0·001*	<0·05	>0·05	
Salmo trutta	<0·001*	<0·001*	<0·001*	<0·05	>0·05	>0·05
			(b)			
R. retiaria	<0·05					
P. fluviatilis	>0·05	<0·01*				
A. forsteri	<0·001*	<0·001*	<0·001*			
R. retropinna	<0·001*	>0·05	<0·001*	<0·001*		
G. maculatus	<0·01	>0·05	<0·01*	<0·001*	>0·05	
S. trutta	<0·01*	>0·05	<0·001*	<0·001*	>0·05	>0·05
			(c)			
R. retiaria	<0·001*					
P. fluviatilis	<0·05					
A. forsteri	<0·001*	<0·001*	<0·001*			
R. retropinna	<0·001*	<0·05	<0·001*	<0·001*		
G. maculates	>0·05	>0·05	>0·05	<0·001*	<0·001*	
S. trutta	<0·001*	<0·05	<0·05	<0·001*	>0·05	<0·01*

H. spinigera abundances were not correlated with the mean abundance of their respective intermediate hosts in fish stomach contents ($r = -0{\cdot}128$ and $-0{\cdot}211$, $n = 7$, both $P > 0{\cdot}05$, respectively). The significant correlation between *A. galaxii* abundance and the abundance of the crustacean *P. fluviatilis* (intermediate host for *A. galaxii*) in fish-definitive hosts ($r = 0{\cdot}910$, $n = 7$, $P < 0{\cdot}01$) was mostly due to the disproportionately high abundances of both the parasite and the prey intermediate host in *A. forsteri* compared to other fish species (Tables II and IV).

Positive correlations between host diet (intermediate host abundance) and parasite abundances within fish-definitive hosts were detected in only a few host–parasite species associations. Abundance of *A. galaxii* was weakly but significantly correlated with intermediate host (*P. fluviatilis*) abundance in the gut of *G. cotidianus* and *G. maculatus* ($r = 0{\cdot}422$ and $0{\cdot}395$, $n = 35$ and 34, respectively, both $P < 0{\cdot}05$). Abundance of *H. spinigera* was significantly correlated with intermediate host (*P. excavatum*) abundance only in *R. retiaria* ($r = 0{\cdot}408$, $n = 46$, $P < 0{\cdot}01$). Finally, *C. parvum* was the parasite species with an abundance most often correlated with the abundance of its intermediate hosts in fish definitive hosts: the correlation was significant in *R. retiaria* ($r = 0{\cdot}817$, $n = 46$, $P < 0{\cdot}001$), *A. forsteri*

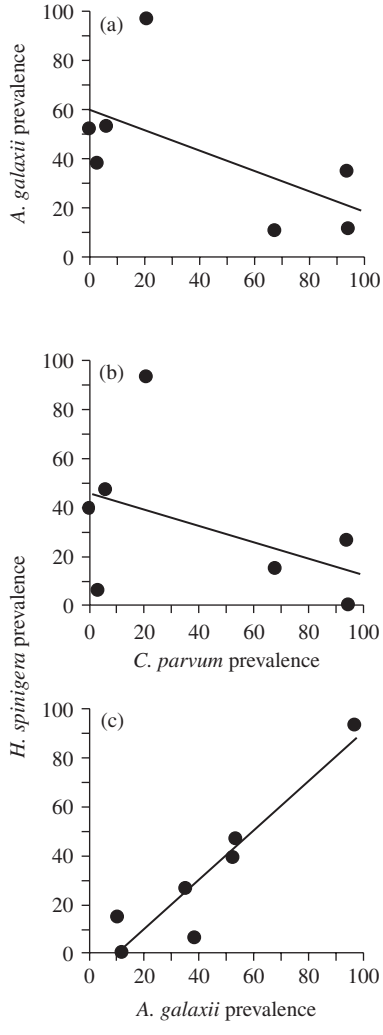

FIG. 1. Relationship between the prevalences (% of infected individuals) of (a) *Coitocaecum parvum* and *Acanthocephalus galaxii*, (b) *C. parvum* and *Hedruris spinigera*, and (c) *A. galaxii* and *H. spinigera*, across the nine fish host species. The curves were fitted by: (a) $y = -0{\cdot}4180x + 59{\cdot}408$ ($r^2 = 0{\cdot}371$), (b) $y = -0{\cdot}3196x + 45{\cdot}280$ ($r^2 = 0{\cdot}187$) and (c) $y = 1{\cdot}0057x - 10{\cdot}359$ ($r^2 = 0{\cdot}872$).

($r = 0{\cdot}692$, $n = 29$, $P < 0{\cdot}001$), *R. retropinna* ($r = 0{\cdot}515$, $n = 32$, $P < 0{\cdot}01$) and *G. maculatus* ($r = 0{\cdot}889$, $n = 34$, $P < 0{\cdot}001$). No negative relationship was found between intermediate host and parasite abundances in any host–parasite pairs.

Overall, within fish species, there was a general trend for an increase in parasite abundance with increasing L_G. Positive correlations between L_G and parasite abundance, however, were significant in only a small number of host–parasite pairs. The abundance of *C. parvum* was significantly correlated with L_G in *R. retiaria* only ($r = 0{\cdot}497$, $n = 46$, $P < 0{\cdot}001$). For *A. galaxii*, the trend was significant in *R. retiaria* and *R. retropinna* ($r = 0{\cdot}708$ and $0{\cdot}370$, $n = 46$ and 32, $P < 0{\cdot}001$

TABLE IV. Proportion of stomachs (% occurrence) in which the two intermediate host/prey species (*Paracalliope fluviatilis* and *Paracorophium excavatum*) were found and relative abundance (% abundance) among the total number of prey items of each intermediate hosts species in different fish species' stomach contents. Mean abundances (mean ± S.E. number of prey individuals per fish stomach) of both prey species are also given. Occurrence of *P. fluviatilis* + *P. excavatum* represents the percent of stomachs containing *P. fluviatilis* and *P. excavatum* as the parasite *C. parvum* can use both species for transmission

Prey species		*Paracalliope fluviatilis*			*Paracorophium excavatum*			*P. fluviatilis* + *P. excavatum*	
Fish species	*n*	Occurrence (%)	Abundance (%)	Mean abundance	Occurrence (%)	Abundance (%)	Mean abundance	Occurrence (%)	Mean abundance
Gobiomorphus cotidianus	35	82·9	63·0	6·4 ± 1·1	17·1	11·2	1·1 ± 0·6	85·7	7·5 ± 1·3
Rhombosolea retiaria	46	54·3	8·7	4·8 ± 1·9	78·3	36·0	20·0 ± 9·4	84·8	24·8 ± 9·9
Perca fluviatilis	68	51·5	13·0	2·9 ± 0·6	35·3	20·1	4·5 ± 1·3	64·7	7·4 ± 1·6
Aldrichetta forsteri	29	75·9	10·3	104·3 ± 38·4	34·5	0·3	3·4 ± 1·2	75·9	107·7 ± 38·0
Retropinna retropinna	32	9·4	20·0	1·1 ± 1·0	15·6	39·4	2·2 ± 1·1	25·0	3·3 ± 1·5
Galaxias maculatus	34	14·7	76·4	24·1 ± 16·2	2·9	0·1	0·0 ± 0·0	14·7	24·1 ± 16·0
Salmo trutta	23	8·7	0·3	0·2 ± 0·2	26·1	19·1	16·2 ± 13·0	26·1	16·4 ± 13·0
Galaxias argenteus	9	0·0	0·0	0·0 ± na	0·0	0·0	0·0 ± na	0·0	0·0 ± na
Leptoscopus macropygus	1	100·0	66·7	4·0 ± na	0·0	0·0	0·0 ± na	100·0	4·0 ± na

n, sample size.

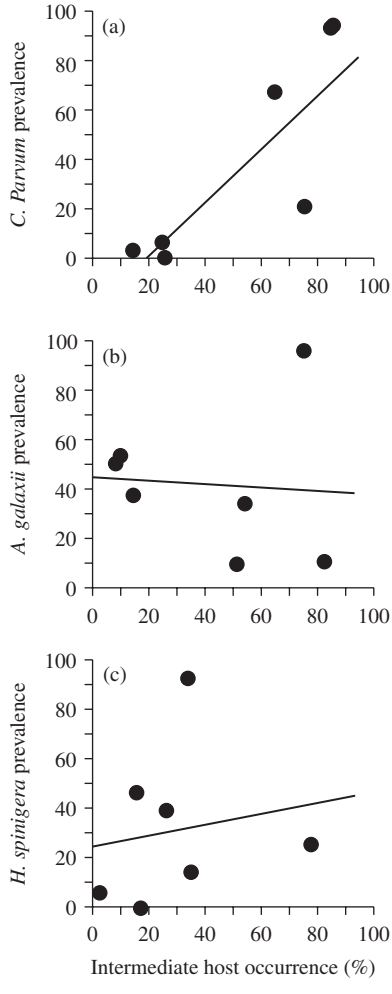

FIG. 2. Relationship between parasite prevalence (% of individuals infected) and the occurrence of amphipod intermediate host species in fish diet (percent of fish stomachs in which intermediate host prey were found) in (a) *Coitocaecum parvum*, (b) *Acanthocephalus galaxii* and (c) *Hedruris spinigera* among the nine fish host species. The curves were fitted by: (a) $y = 1{\cdot}1899x - 23{\cdot}302$ ($r^2 = 0{\cdot}731$), (b) $y = -0{\cdot}0655x + 45{\cdot}153$ ($r^2 = 0{\cdot}005$) and (c) $y = 0{\cdot}2212x + 25{\cdot}324$ ($r^2 = 0{\cdot}028$).

and $P < 0{\cdot}05$, respectively). Finally, abundance of *H. spinigera* was significantly correlated with L_G in *R. retiaria*, *P. fluviatilis*, *A. forsteri* and *R. retropinna* ($r = 0{\cdot}612$, $0{\cdot}277$, $0{\cdot}429$ and $0{\cdot}435$, $n = 46$, 68, 29 and 32, respectively, $P < 0{\cdot}001$ for *R. retiaria* and $P < 0{\cdot}05$ for the three other species). Again, no negative relationship was found between L_G and parasite abundance in any host–parasite pairs.

When controlling for L_G, intermediate host abundance in stomach contents and the abundances of co-occurring parasite species, fish species identity had significant effects on the abundance of different parasites (ANCOVA, $F_{6,256} = 83{\cdot}547$, $29{\cdot}746$ and $14{\cdot}267$, all $P < 0{\cdot}001$ for *C. parvum*, *A. galaxii* and *H. spinigera*, respectively).

Post hoc tests, however, detected contrasting patterns of specific parasite abundance between fish host species. In *C. parvum*, while there was no difference between *R. retiaria* and *G. cotidianus* (Tukey's HSD, d.f. = 256, $P > 0{\cdot}05$), the parasite abundance in these two species was higher than in any other fish species (Tukey's HSD, d.f. = 256, all $P < 0{\cdot}001$; Table II). Abundance of *C. parvum* was intermediate in *P. fluviatilis* (Table II), being lower than in *R. retiaria* and *G. cotidianus*, but higher than in all other fish species (Tukey's HSD, d.f. = 256, $P < 0{\cdot}001$; Table II). Patterns of parasite abundance were comparable in *A. galaxii* and *H. spinigera* but clearly different from those in *C. parvum* (Table II). *Acanthocephalus galaxii* and *H. spinigera* were more abundant in *A. forsteri* than in any other fish species (Tukey's HSD, d.f. = 256, all $P < 0{\cdot}001$). Both parasite species showed intermediate abundances in *R. retiaria*, *R. retropinna* and *S. trutta* (Table II). In these three fish species, the two parasites were significantly more abundant than in *G. cotidianus* (Tukey's HSD, d.f. = 256, all $P < 0{\cdot}05$; Table II) and *P. fluviatilis* (Tukey's HSD, d.f. = 256, all $P < 0{\cdot}05$; Table II). Abundances of *A. galaxii* and *H. spinigera* were also significantly higher in *R. retropinna* than in *G. maculatus* (Tukey's HSD, d.f. = 256, both $P < 0{\cdot}001$). No other significant difference was detected in specific parasite abundances between host species.

COITOCAECUM PARVUM BODY SIZE AND EGG PRODUCTION

Some fish species were never found infected with *C. parvum* or contained only egg-producing or only non-egg producing individuals and were consequently discarded from all or parts of the following analyses (see Table V for details on *C. parvum* infection). As observed in previous studies (Lefebvre & Poulin, 2005), egg-producing *C. parvum* individuals were significantly larger than immature (non-egg producing) specimens (mean ± S.E. body size = $0{\cdot}1345 \pm 0{\cdot}0013$ and $0{\cdot}0529 \pm 0{\cdot}0009$ mm^2, respectively; ANOVA, $F_{1,1641} = 302{\cdot}79$, $P < 0{\cdot}001$). Fish host species identity had a significant effect on *C. parvum* size (ANOVA, $F_{3,1641} = 29{\cdot}11$, $P < 0{\cdot}001$; Table V) and there was a significant interaction between the two factors (reproductive status × host species; ANOVA, $F_{3,1641} = 7{\cdot}02$, $P < 0{\cdot}001$). Egg-producing *C. parvum* individuals from *R. retiaria* were significantly larger than individuals from *G. cotidianus* and *P. fluviatilis* (Tukey's HSD, d.f. = 1641, $P < 0{\cdot}001$ and $P < 0{\cdot}01$, respectively; Table V). Similarly, immature (non-egg producing) parasites were slightly larger in *R. retiaria* although the difference was marginally significant only with individuals from *G. cotidianus* (Tukey's HSD, d.f. = 1641, $P < 0{\cdot}05$; Table V). No other significant difference was detected, possibly due to small sample size in the case of *A. forsteri* (Table V).

As found in previous studies on *C. parvum* (Lagrue & Poulin, 2007, 2008), egg production increased significantly with parasite size ($r = 0{\cdot}782$, $n = 1089$, $P < 0{\cdot}001$). Overall, when egg production was controlled for parasite body size, the mean number of eggs produced per mature *C. parvum* individual was significantly influenced by fish species identity (ANCOVA, $F_{5,1089} = 21{\cdot}879$, $P < 0{\cdot}001$). While parasite egg production was on average higher in *R. retiaria* when parasite body size is not considered (Table V), for a given size, *C. parvum* egg production was higher in *G. cotidianus* than in any other fish species (Tukey's HSD, d.f. = 1082, $P < 0{\cdot}001$ for *R. retiaria* and *P. fluviatilis*, $P < 0{\cdot}05$ for *A. forsteri*) although the difference was not significant when compared with *R. retropinna* or *G. maculatus* (Tukey's

TABLE V. Number (*n*) of *Coitocaecum parvum* individuals found in fish hosts with details on the proportion of egg-producing specimens, mean ± S.E. body size (body surface area) of each type of *C. parvum* and mean egg production (mean number of egg per egg-producing individual ± S.E.) for different fish species. Note that *G. argenteus* and *S. trutta* were not infected by *C. parvum* and were excluded from the table

			Egg-producing individuals		Non-egg producing individuals
Fish species	*n*	Proportion of egg-producing individuals (%)	Body size (mm^2)	Egg production	Body size (mm^2)
Gobiomorphus cotidianus	602	63·3	0·1150 ± 0·0015	3·8 ± 0·1	0·0497 ± 0·001
Rhombosolea retiaria	890	71·8	0·1472 ± 0·0017	4·6 ± 0·1	0·0561 ± 0·0017
Perca fluviatilis	127	44·1	0·1236 ± 0·0043	2·7 ± 0·3	0·0515 ± 0·0023
Aldrichetta forsteri	11	45·5	0·1055 ± 0·0080	1·6 ± 0·4	0·0541 ± 0·0076
Retropinna retropinna	3	100·0	0·1583 ± 0·0423	3·3 ± 1·9	na
Galaxias maculatus	1	100·0	0·1349 ± na	1·0 ± na	na
Leptoscopus macropygus	2	0·0	na	na	0·0329 ± 0·0150

HSD, d.f. = 1082, both $P > 0·05$), possibly due to the small sample size. *Coitocaecum parvum* egg production was also significantly higher in *R. retiaria* than in *P. fluviatilis* and *A. forsteri* (Tukey's HSD, d.f. = 1082, both $P < 0·001$). No other significant difference was found. Overall, both parasite body size and host species identity had an effect on *C. parvum* egg production.

DISCUSSION

The structure and dynamics of trophic interactions in food webs can be important determinants of helminth infections in fish-definitive hosts (Pérez-Ponce de León *et al*., 2000; Marcogliese, 2002), with parasite infection levels depending on the consumption of infected intermediate host prey. Here, of the three helminth species, only one showed an apparent correlation between infection level and fish host diet. *Coitocaecum parvum* prevalence was positively correlated with the occurrence and abundance of its crustacean intermediate hosts (*P. fluviatilis* and *P. excavatum*) in fish stomach contents. Differences in *C. parvum* infection levels observed among fish species in the Lake Waihola community can be explained largely by interspecific differences in host diets and thus specific encounter filters. In contrast, prevalence and abundance of *A. galaxii* and *H. spinigera* were not, or only weakly, correlated with fish host diets. Parasite life span, however, is unknown for these species and could potentially obscure any existing relationship between host diets and infection levels.

The data show that complete isolation between fish hosts and helminth parasites (closed encounter filter) is very rare in this ecosystem; only *G. argenteus* lacked dietary contacts with helminth larvae. Since the encounter filter is open in most fish species, compatibility filters are likely to modulate parasite infection patterns among these fish species (Holmes, 1987, 1990; Combes, 2001; Kuris *et al*., 2007). While *C. parvum* appears to be a true generalist, establishing, maturing and reproducing in any fish host once past the encounter filter, compatibility filters seem to modulate the two other helminth species infection levels. Indeed, lower than expected infection levels given host diet indicate some host–parasite incompatibility (Holmes, 1983; Poulin, 2005; Detwiler & Minchella, 2009).

Acanthocephalus galaxii and *H. spinigera* apparently fail to establish, develop and mature in a number of hosts. Abundance of *H. spinigera* was clearly higher in *A. forsteri* and *R. retropinna* and these two fish species were the only ones containing mature parasites, attached and in mating position. Since *H. spinigera* exclusively attaches and matures in the stomach of fish hosts, unattached larvae found beyond the host stomach in the other fish species are unlikely to establish and reach maturity (Luque *et al*., 2010). *Aldrichetta forsteri* and *R. retropinna* should thus be considered as suitable hosts for the parasite and the only two of 10 fish species maintaining the *H. spinigera* population (Holmes *et al*., 1977; Holmes, 1979). While *A. forsteri* and *R. retropinna* possess a well-defined pyloric stomach lined with a thick epithelium, other fishes display simpler guts with poorly defined pyloric stomachs where *H. spinigera* never attached. The compatibility filter may thus be primarily, though not exclusively, morphological in *H. spinigera* (Campos & Carbonell, 1994). Interestingly, *C. parvum*, which lives freely inside the fish gut, did not seem to be affected by host gut morphology unlike the more specialized *H. spinigera*.

Acanthocephalus galaxii seemed able to attach to any fish intestinal epithelium. Prevalence and abundance, however, were highly variable and parasites remained small and immature in all but two fish species, *A. forsteri* and *R. retropinna*, suggesting strong host–parasite compatibility filters (Holmes *et al*., 1977; Holmes, 1983). Lack of maturation is commonly observed in fish acanthocephalans and used to evaluate host status (Holmes, 1979; Rauque *et al*., 2003; Byrne *et al*., 2004). This suggests a physiological rather than morphological compatibility filter; *A. galaxii* can attach and establish but neither mature nor reproduce. Overall, helminth infection patterns observed here are due, at least partly, to morphological (*i.e.* appropriate attachment sites; Campos & Carbonell, 1994) or physiological or to both (gastrointestinal pH, digestive enzymes, available nutrients; Rogers, 1960; Irwin, 1997) compatibility filters.

Prevalences and mean abundances of *A. galaxii* and *H. spinigera* were positively correlated among fish-definitive host species even though they use different intermediate host species and attach to different sites in fish hosts. Encounter and compatibility filters are thus different for *A. galaxii* and *H. spinigera* but seem to result in the same infection patterns. In contrast, differences in encounter and compatibility filters between *C. parvum* and the other parasites are reflected by the lack of correlation between their prevalences and abundances. Unfortunately, the relative roles of these filters could not be determined and would require further investigation. Within host species, *A. galaxii* and *H. spinigera* abundances were either not or positively correlated. The positive association between the two parasites and attachment site specificity in their suitable hosts (*A. forsteri* and *R. retropinna*) indicated

that they were unlikely to compete (Poulin & Luque, 2003; Mideo, 2009). Again, absence of negative correlations between *C. parvum* abundance and that of the other two parasites suggested that, possibly because of its mobility and lack of site specificity in fish guts, *C. parvum* interactions with *A. galaxii* and *H. spinigera* were limited (Poulin, 2001). Interspecific competition was thus unlikely to influence parasite infection patterns in this particular fish community though this would require experimental confirmation.

The range of infected host species and parasite infection levels among different hosts may still underestimate the degree of host specificity (Holmes, 1979). Parasite growth and fecundity are also key variables of host–parasite compatibility that should be considered when determining host specificity (Holmes, 1983, 1987; Detwiler & Minchella, 2009). Physiological incompatibility could reduce parasite growth and fecundity after the parasite successfully established. Potential effects of host suitability on parasite growth and fecundity were assessed for *C. parvum*. Results showed that host identity influenced *C. parvum* maturity rates (*i.e.* proportion of egg-producing worms), growth and fecundity. *Coitocaecum parvum* achieved maximum size and fecundity in two host species, *R. retiaria* and *G. cotidianus*. Thus, these two hosts played the most important roles in the parasite's population dynamics and could be considered as main definitive hosts for *C. parvum* (Holmes, 1979; Olson & Nickol, 1996; Poulin, 2005).

What determines a parasite's host range and specificity in the wild has important implications in the context of biological invasions and the establishment of new host–parasite associations (Perlman & Jaenike, 2003). Helminths can colonize new hosts if these have diets similar to that of the original hosts and are thus exposed to similar parasites (Poulin, 2005). Native parasite-introduced host associations may subsequently amplify infections in native hosts ('spillback' effect; Kelly *et al*., 2009*a*). Introduced species tend to have lower infection burdens than native species and parasites often perform better, in terms of growth and fecundity, in their native hosts (Torchin *et al*., 2003; Byrne *et al*., 2004). Introduced species may act as sinks of parasite infection, potentially reducing infection levels in the native host fauna ('dilution' effect; Kelly *et al*., 2009*b*). Results suggest the possibility of a 'dilution' effect. Both *S. trutta* and *P. fluviatilis*, introduced from Europe (Thomson, 1922), were infected by the native parasites but were clearly less favourable hosts in terms of parasite prevalence, abundance, maturity and fecundity. Only immature *A. galaxii* and *H. spinigera* were found in introduced fish species and at low infection levels, indicating low host–parasite compatibility. *Salmo trutta* was also the only fish feeding on *P. fluviatilis* that was totally lacking *C. parvum*. In contrast, *C. parvum* prevalence was high in *P. fluviatilis* but the parasite's abundance and maturity rate (% of egg-producing individuals) were among the lowest of infected fish species, indicating host–parasite incompatibility in the *C. parvum* and *P. fluviatilis* association. Unsuitability of introduced fish species as hosts to native parasites probably arises from post-infection incompatibility rather than limited exposure to infection.

As hypothesized, host feeding behaviour contributed to some extent to helminth infection patterns in natural fish populations. While parasites infect a wide variety of fish hosts they often reach maturity in only a sub-set of hosts. These results suggest patterns of host specificity and interspecific differences in host–parasite compatibility. Thus, both fish host diet and host–parasite compatibility contribute to the distribution of helminths in the fish community. The relative weight of each factor

varied between host–parasite associations and is likely to be both host and parasite specific. The present results show that quantifying trophically transmitted helminth infection dynamics requires a precise understanding of the relative roles of both encounter (trophic interactions between prey and predator hosts) and compatibility (host suitability) filters.

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