

Body size, trophic level, and the use of fish as transmission routes by parasites

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Abstract Within food webs, trophically transmitted helminth parasites use predator–prey links for their own transfer from intermediate prey hosts, in which they occur as larval or juvenile stages, to predatory definitive hosts, in which they reach maturity. In large taxa that can be used as intermediate and/or definitive hosts, such as fish, a host species' position within a trophic network should determine whether its parasite fauna consists mostly of adult or larval helminths, since vulnerability to predation determines an animal's role in predator–prey links. Using a large database on the helminth parasites of 303 fish species, we tested whether the proportion of parasite species in a host that occur as larval or juvenile stages is best explained by their trophic level or by their body size. Independent of fish phylogeny or habitat, only fish body length emerged as a significant predictor of the proportion of parasites in a host that occur as larval stages from our multivariate analyses. On average, the proportion of larval helminth taxa in fish shorter than 20 cm was twice as high as that for fish over 100 cm in length. This is consistent with the prediction that small fishes, being more vulnerable to

predation, make better hosts for larval parasites. However, trophic level and body length are strongly correlated among fish species, and they may have separate though confounded effects on the parasite fauna exploiting a given species. Helminths show varying levels of host specificity toward their intermediate host when the latter is the downstream host involved in trophic transmission toward an upstream definitive host. Given this broad physiological compatibility of many helminths with fish hosts, our results indicate that fish body length, as a proxy for vulnerability to predators, is a better predictor of their use by helminth larvae than their trophic level based on diet content.

Keywords Food webs · Helminths · Complex life cycle · Trophic link · Intermediate hosts · Predation

Introduction

Parasites have long been neglected in studies of food webs and ecological networks (Marcogliese and Cone 1997; Morand and Arias-Gonzalez 1997). Today, however, integrating parasites and infectious diseases into trophic networks is at the center of current research into food web structure and dynamics (Lafferty et al. 2008; Poulin 2010). The inclusion of parasites as full participants in food webs can change key network metrics such as connectance, food chain length or linkage density (Huxham et al. 1995; Thompson et al. 2005; Hernandez and Sukhdeo 2008; Amundsen et al. 2009). In addition, parasite transmission routes can be mapped onto food webs, since trophically transmitted helminth parasites follow trophic links within food web networks (Sukhdeo and Hernandez 2005; Sukhdeo 2010; Poulin 2010). This allows a comparison between the actual transmission routes used by parasites and those

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that are not used but that would nevertheless be possible, i.e., all other trophic connections between prey and predators.

Parasitic worms transmitted by predation from an intermediate host, in which they occur as larval or juvenile stages, to a definitive host in which they will mature into adults, move up the food web in the process of completing their life cycles. Definitive hosts are predators, and thus should occur mostly at middle to high trophic levels; a herbivore toward the bottom of food chains does not ingest animals, and thus is unlikely to serve as definitive host for a trophically transmitted parasite. Although there are exceptions (i.e., fasciolid trematodes are acquired by grazing mammals that ingest cysts attached to vegetation), these are relatively few. In contrast, intermediate hosts are prey; a top predator that does not serve as prey to any other animal could not act as intermediate host, though it may still acquire some larval helminths as a dead-end host. Prey with many predators (i.e., having high vulnerability, where vulnerability is a measure of the number of predator species that eat a prey species) should support a greater diversity of larval parasites. Such highly vulnerable prey tend to be small-bodied species, positioned at low trophic levels. The diversity of adult parasites using a particular host species should increase with its trophic level, whereas the diversity of larval parasites may or may not decrease with increasing host trophic level (i.e., with decreasing vulnerability), resulting in a proportional decrease of larval helminth taxa in the parasite communities of hosts of increasing trophic level. An animal's position within a trophic network, therefore, should determine to a large extent whether its parasite fauna consists mostly of adult helminths (using it as definitive host) or larval helminths (using it as intermediate host).

Earlier reviews have suggested that fish species in the middle of food webs, feeding on both invertebrates and small fish, should harbor the greatest number of enteric parasite species (George-Nascimento 1987; Marcogliese 2002). In a comparative analysis among fish species, trophic level has been shown to correlate positively with the taxonomic diversity of parasites harbored by a fish, but not with how many species are harbored (Luque and Poulin 2008). These findings show that a host's trophic level can affect its parasite fauna, but do not address fish use by larval versus adult stages of trophically transmitted parasites. However, an analysis of the network position of species (mostly invertebrates) used as intermediate hosts by helminths within three aquatic food webs shows that they have more predators (mostly birds in these webs) and are involved in more food chains than other species not used as intermediate hosts (Chen et al. 2008). Thus, there is evidence from these few webs to suggest that the trophic level and vulnerability of a potential host can determine

what proportion of its parasites will use it as an intermediate rather than definitive host.

One property of host species, i.e., their body size, is associated with their trophic level and vulnerability, and possibly also with how many parasites they harbour. Since predators are larger than their prey, body sizes of species within a food web tend to increase with increasing trophic level (Cohen et al. 1993). Host body size has also long been considered a determinant of parasite species richness, although it generally explains only a small portion of the interspecific variance in the numbers of parasite species infecting different host species (Poulin 1997, 2004). Any relationship between an animal's body size and the proportion of parasites using it as an intermediate host should be negative, however, since large hosts are unlikely to serve as prey. Among 50 fish species from coastal Brazil, host body size did not covary with either the number of larval helminth taxa per fish species, or with their relative contribution to the total parasite species richness (Luque and Poulin 2004). Therefore, although host body size generally covaries with trophic level and vulnerability, it may not be the main factor determining host usage by larval parasites. Other factors may obscure any relationships between host body size, host trophic level, vulnerability and host use by larval helminths. For instance, in aquatic food webs, food chain lengths and several other properties of trophic networks have long been known to differ between freshwater and marine webs (Schoener 1989; Link 2002), imposing different constraints on what trophic levels are possible, and habitat would therefore also need to be taken into account.

Here, we investigate how the network position of a fish host affects the proportion of its parasite species that occur as larval or juvenile stages. The existing evidence is limited to three local food webs, and mostly to parasites using predator–prey links between birds and invertebrates for their transmission (Chen et al. 2008). We did not have measures of actual networks, so we estimated trophic level from FishBase (Froese and Pauly 2010) and used body size as a proxy for vulnerability. To do so, we analyze the occurrence of larval stages of helminth endoparasites (e.g., metacercariae of trematodes, plerocercoids of cestodes, juvenile nematodes, or cystacanths of acanthocephalans) in a large number of fish species from various freshwater and marine locations. Specifically, (1) we test the hypothesis that the proportion of parasites occurring as larvae, among all of the endohelminth species exploiting a fish, will decrease as a function of the trophic level of that fish, and increase with vulnerability as measured by body size, and (2) we determine if habitat and the total number of endohelminth parasite species (whether occurring as adults or larvae) infecting the fish also influence its relative use as an intermediate host by parasites. Our analyses take advantage

of a very large data set, covering broad taxonomic and geographic spectra, to detect general patterns regarding how host–parasite associations have adjusted over evolutionary timescales to exploit locally available transmission routes.

Materials and methods

We used a subset of the database compiled by Poulin and Leung (2010) from published surveys of endohelminth communities in vertebrates. In the present study, we only use surveys involving fish hosts, both marine and freshwater; these provide a large, representative and unbiased sample derived from 169 studies (many of which contributed more than one survey) published between 1952 and 2009. The dataset only includes studies that provided a list of all species of trematodes, cestodes, nematodes and acanthocephalans found in one sample of individual hosts from the same species, and that allowed the determination of which parasite species occurred at larval or juvenile stages. The methods used in each survey to recover and identify parasites follow standard parasitological procedures, though there was no way to control for variance in data quality among studies. For instance, methods and sampling were not systematically similar with respect to attention to larval and adult helminths. It is not uncommon for investigators to exclude mention of larval parasites in their surveys (a potential problem if larval stages are more commonly ignored in dissections of large-bodied fish due to the difficulty of processing the flesh of large individuals). Each entry in the dataset corresponds to one parasite survey for one host species from one study, i.e., one local parasite community; when there were two or more entries in the dataset for the same host species, we only retained the one including the most parasite species as the most representative of the whole parasite fauna of that host species. Also, we excluded surveys in which only one parasite species was found. For each entry, the following information was recorded: (1) the name of the host species; (2) the order to which the host species belonged; (3) whether the fish were from marine or freshwater habitats; (4) the total number of endoparasitic helminth species recorded; and (5) the number of these that occurred at larval or juvenile stages. From the latter two values, we computed the proportion of larval helminth species in each parasite community. In addition, we also obtained the following information for each host species from Fishbase (Froese and Pauly 2010): (6) their maximum recorded body length, and (7) their trophic level, defined as the number of energy-transfer steps between basal resources and the fish's position in the trophic web, as determined from available diet data. The mean body length and actual trophic position

of the fish specimens examined for parasites would have been preferable as measures of body size (or vulnerability to predation) and trophic level, respectively, but were not available for many surveys; for comparative purposes, maximum length and species-typical trophic level are appropriate measures to distinguish among fish species. Fish species for which information on either maximum body length or trophic level was unavailable were excluded from the analyses.

Studies of parasite species richness generally correct for sampling effort, since the more hosts that are examined in a particular survey, the more parasite species are found (Walther et al. 1995). However, here sampling effort was not treated as a confounding variable, since the analyses did not focus on how many species were found but on the proportion of these that occurred as larval stages. This proportion is not expected to covary with sampling effort, and preliminary analyses confirmed that it did not (see also Luque and Poulin 2004).

The proportion of parasite species in a fish that occur as larvae may be constrained to some extent by the host's phylogenetic affinities, because of host–parasite co-evolutionary history. Therefore, in the absence of a comprehensive species-level phylogeny of all fish species, we included host taxonomic order as a variable in the analyses to account for possible higher-order phylogenetic influences.

To investigate the determinants of the proportion of larval taxa making up the helminth communities of fish hosts, we used a generalized linear model (GLM) implemented with the statistical software JMP 7.0. Since the response variable was a proportion, i.e., the proportion of species occurring as larvae, which could not be normalized by arcsine transformation (too many 0s and 1s), the model had a binomial error structure and logit link function. The explanatory variables were transformed, when necessary, to meet the assumptions of normality. They were: host order, habitat (freshwater or marine), parasite species richness (or the \log_{10} -transformed total number of helminth taxa in the community), host body length (also \log_{10} -transformed), host trophic level, and all two-way interactions between the last four factors. After starting with a full model including all of the above, significance levels were based on the deviance explained by each factor, based on χ^2 statistics, following the backward stepwise elimination of unimportant ($P > 0.10$) terms. Preliminary analyses were also performed that consisted of various other starting models, but these always reduced to the same final model, and only that final model is presented in the results. Additionally, to disentangle the relative contributions of host body length and host trophic level to the variance in the proportion of helminth species occurring as larvae in a fish host, we estimated coefficients of determination (r^2) from simple/multiple regressions.

Results

The dataset used here included a total of 303 helminth communities, each from a different fish species (see the Electronic supplementary material, ESM). The 303 fish species represented 32 taxonomic orders, and consisted of 146 freshwater and 157 marine species, the latter including several brackish water species. The parasite species richness in the surveys ranged from 2 to 45 helminth species per community, with a median of nine species. Host body length (range 3.2–610 cm, median 45 cm) and trophic level (range 2–4.53, median 3.32) also showed considerable variability among fish species. Although there were many helminth communities in which no species occurred as larvae, and many in which all species were larval stages, the majority consisted of a mixture of species occurring as adults and others occurring as larvae (Fig. 1). There is thus considerable variation among fish species in the extent to which they are used as intermediate hosts.

Marine fish species included here tended to be a little longer (mean \pm SE; marine: 68.0 ± 5.5 , vs. freshwater: 66.7 ± 6.4 cm), positioned at a slightly higher trophic level (3.51 ± 0.04 vs. 3.27 ± 0.05), and harbored slightly more helminth species (11.2 ± 0.6 vs. 8.8 ± 0.5) than freshwater species (*t* tests, all $P < 0.03$). More importantly, we found significant positive correlations between the three predictors that were continuous variables (host length versus parasite species richness: $r = 0.245$, $P = 0.0001$; host trophic level vs. parasite species richness: $r = 0.241$, $P = 0.0001$; host length vs. host trophic level: $r = 0.510$, $P = 0.0001$). The strongest of these correlations was between host body length and host trophic level, but only

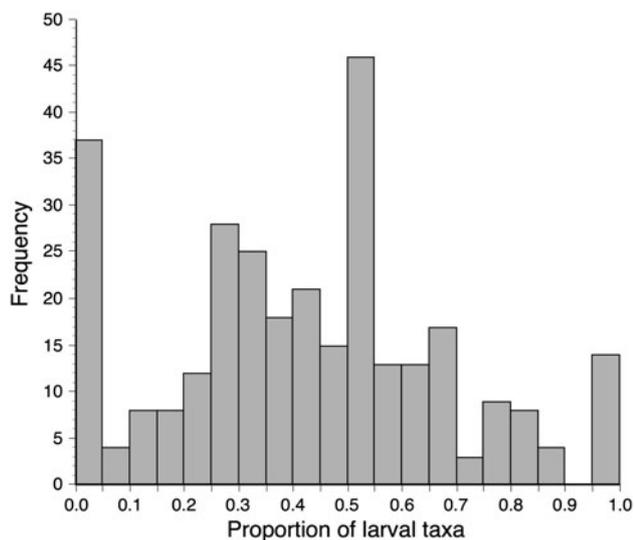


Fig. 1 Frequency distribution of the proportion of larval taxa out of all helminth taxa in a parasite community, among 303 surveys in different species of fish hosts

about 25% of the variance in trophic level is explained by fish length (Fig. 2). Collinearity between these variables is therefore unlikely to create problems, and they were allowed to “compete” in the same model to determine which of these two fish properties is the strongest predictor of the proportion of larval taxa within helminth communities.

Whatever the starting model in the GLMs testing for the determinants of the proportion of larval taxa in helminth communities, the same end result was obtained. There were no significant two-way interactions between the main factors. There was also no significant effect of four of these factors: host taxonomic order, habitat (freshwater or marine), parasite species richness, and host trophic level; in fact, none of these approached statistical significance (P always >0.4) in any model that included host body length. The model was reduced to a very parsimonious, single-factor version in which only host body length affects the proportion of helminth taxa occurring as larvae ($\chi^2 = 9.38$, $df = 1$, $P = 0.0022$). There was a negative relationship between these variables (Fig. 3): small fish species tended to harbor a greater proportion of larval helminth taxa than large-bodied fish species. The proportion of larval helminth taxa in fish shorter than 20 cm was twice as high as that for fish greater than 100 cm in length (Fig. 3). The proportion of larval helminth taxa in a fish also decreased with increasing trophic level (Fig. 3), though the drop was only noticeable among the lowest trophic levels. Regression analyses indicated that the variance in the proportion of helminths occurring as larvae in a fish explained by host body length alone (10.6%) was

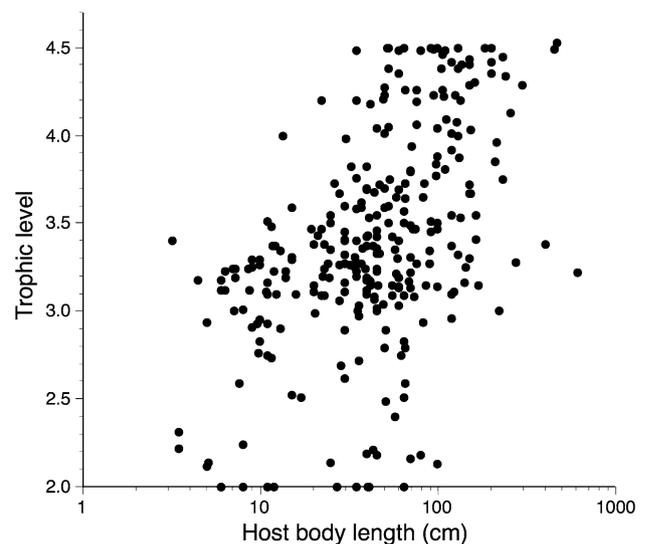


Fig. 2 Trophic level (i.e., number of energy-transfer steps between basal resources and the fish’s position in the trophic web) plotted as a function of total body length of hosts among the 303 fish species for which helminth communities were surveyed

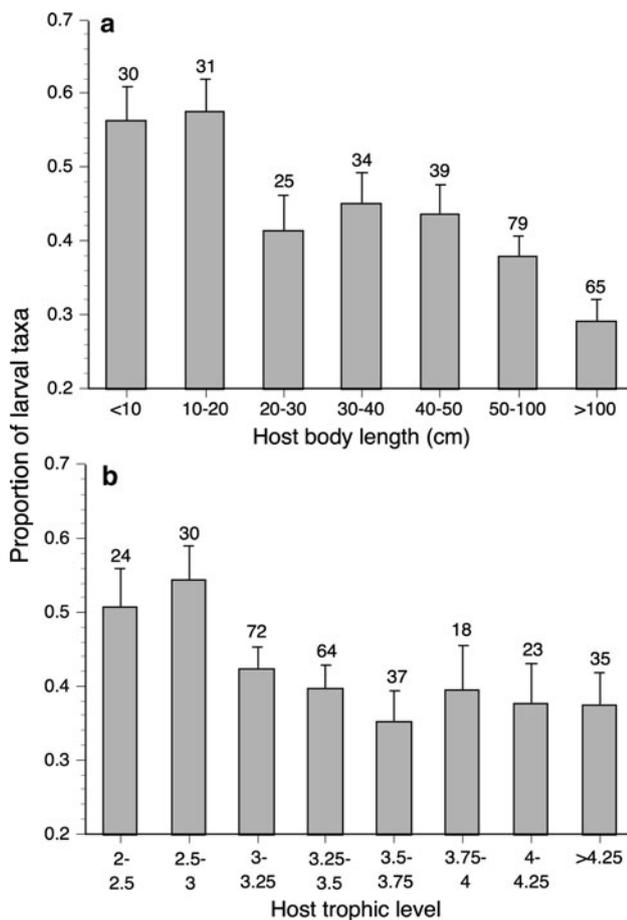


Fig. 3 Proportion of larval helminths in parasite communities of fish hosts as a function of **a** total fish body length and **b** fish trophic level, mean \pm SE. Fish species were grouped into arbitrary classes instead of plotted individually in order to better illustrate the general trends. Numbers above the bars indicate the number of communities surveyed in each class

greater than that explained by host trophic level (1.7%); combining both explanatory variables barely improved the total variance explained compared to what was explained by host body length alone (10.7 vs. 10.6%).

Discussion

The close coupling between parasite transmission and trophic links, i.e., predator–prey interactions, within food webs has several implications. For example, from a practical point of view, the presence of adult helminths in the gut contents of predators provides strong evidence of an existing trophic link with the animal serving as intermediate host (Sukhdeo 2010; Valtonen et al. 2010). From an evolutionary perspective, a close match between the use of animals as intermediate hosts and their position within trophic chains can indicate whether ecological conditions

played a role in the evolution of parasite transmission routes. Here, we found that the relative role played by a fish as the intermediate host of helminths, as opposed to being their definitive host, is more strongly related to its body size than its trophic level, in a statistical sense. Trophic level and body size tend to covary strongly among fish species (Jennings et al. 2001); however, in our analyses body size outcompeted trophic level as a predictor of the relative contribution of larval helminths to a fish's parasite fauna.

Intermediate hosts provide nutrients for developing parasites, but also serve as conduits for transmission to the definitive host where helminth parasites reach sexual maturity and reproduce. There is evidence that some helminths show very little specificity toward their intermediate hosts when the latter is the downstream host involved in trophic transmission toward an upstream definitive host. For instance, among parasites of Canadian freshwater fishes, the larval or juvenile stages of helminths such as the plerocercoids of the cestodes *Diphyllbothrium* spp. or *Triaenophorus* spp., or the larvae of nematodes like *Eustrongylides* spp., are found in numerous fish species belonging to several different families (Margolis and Arthur 1979; McDonald and Margolis 1995). Recent studies, however, used molecular tools to reveal high cryptic specificity among widespread taxa of larval trematodes (Diplostomidae) and cestodes (Tetraphyllidea), with individuals from different host species often belonging to distinct species (Jensen and Bullard 2010; Locke et al. 2010). These taxa are only identified to genus level in the vast majority of surveys in our dataset, and cryptic species are therefore unlikely to affect our estimates of the proportion of larval helminths per fish species. At the genus level, these taxa remain generalist parasites for their intermediate hosts. Given these widespread taxa's physiological compatibility with numerous potential intermediate hosts, one might expect natural selection to favor those parasites showing biased infection of intermediate hosts that facilitate transfer to a predatory definitive host. Over evolutionary time, this would result in a gradually improving fit between the relative use of animals as intermediate hosts by parasites (whether or not accompanied by cryptic parasite speciation) and these animals' positions within trophic networks. In three intertidal or estuarine food webs, Chen et al. (2008) found that animals used as intermediate hosts by helminths tend to have more predators (mostly birds) and participate in more food chains than those not used as intermediate hosts. Although we did not measure vulnerability directly, we arrived at a similar result assuming that smaller fish have higher vulnerability to predation.

This cannot merely be explained by coevolutionary history, because we found no effect of host taxonomy on

the proportion of helminth species occurring as larvae in a fish. The greater use of small fish as intermediate hosts is also not an artefact of differences in overall parasite species richness as a function of fish body size, since this variable had no effect on the results and was not retained in our model, and our measure of relative use of fish as intermediate hosts (i.e., number of larval helminth taxa divided by total number of helminth taxa) controls for parasite species richness. Also, among fish species, parasite species richness generally correlates positively, and not negatively, with fish body size (Poulin 1995; Gregory et al. 1996; but see Sasal et al. 1997). Finally, an environmental influence due to habitat differences between freshwater and marine fish can also be ruled out. Among other differences, trophic chains are generally slightly longer in marine systems, with more trophic levels, than in freshwater ones (Link 2002), but habitat had no effect in our analyses on the relative use of fish as intermediate hosts. It must be pointed out, however, that although statistically significant following data transformation, the differences between marine and freshwater fish in “raw” values of body sizes and trophic levels (see the “Results” section) are very small. It is still too early to conclude whether host-level properties, such as body size and diet (a key determinant of trophic level) are more important than system-level properties in determining host use by larval helminths (Lafferty et al. 2008).

Other aspects of body size besides vulnerability to predators could predispose fishes to differential acquisition of larval and adult helminths as a consequence of size-dependent infection processes. Both within and among fish species, feeding is generally gape-limited, with the diversity and size range of potential prey increasing with gape size, which is itself a function of body size (Gerking 1994; Wainwright and Richard 1995; Hyndes et al. 1997; see also Marcogliese 2002). This is relevant for several cestode taxa that have a first intermediate host in their life cycle before infecting a fish as a second intermediate host, thus requiring two trophic transmission events to complete their cycle. Genera like *Diphyllbothrium* or *Triaenophorus* that infect freshwater fish provide good examples. These cestodes use a copepod as first intermediate host, from where they must be ingested by fish as second intermediate hosts (Pasternak et al. 1995; Pulkkinen et al. 2000). Clearly, small fish species are much more likely to be involved in the copepod-to-fish phase of the life cycle than large fish, since the latter feed on prey much larger than copepods. This would restrict the use of fish as intermediate hosts by these cestodes to small-bodied fish species only, whatever their average trophic level. Infection by other larval helminths is not so clearly biased toward small-sized fish, however. For instance, fish used as intermediate hosts by trematodes are infected by skin-penetrating infective stages, and larger fish are generally more vulnerable

because of a larger external surface area (Poulin 2000). It may be that beyond a certain body size, skin or scale thickness protects larger fish from infection by these parasites. Alternatively, large-bodied fish species may occur less frequently in shallow inshore areas close to snail populations, which serve as trematode first intermediate hosts and from which infective stages are released.

The surveys from which the data were derived indicate whether or not helminths are found as larvae, but without confirming the role of the fish in the parasite’s life cycle. Fish harboring larval helminths may not necessarily act as intermediate hosts for these parasites. Firstly, these fish may be paratenic hosts, inside which the parasites survive but achieve no development. Paratenic hosts either bridge a gap in trophic transmission, when they prey on intermediate hosts and are themselves eaten by suitable definitive hosts, or they provide alternative paths toward the definitive host. Second, fish harboring larval parasites may be dead-end hosts (sensu Leung and Poulin 2008): although the parasites survive in these fish, there is no trophic link connecting the fish to a suitable predatory definitive host. For instance, juvenile stages of the nematodes *Pseudoterranova* spp. show very little host specificity, and they are found in numerous species of coastal marine fish (Margolis and Arthur 1979; McDonald and Margolis 1995; McClelland 2002). Some of these are intermediate hosts in the strict sense, others are paratenic hosts, and the rest are dead-end hosts. Whether the fish is a true intermediate host or not, its likelihood of acquiring larval helminths should remain tied to its ecological properties, and it is therefore very unlikely that the way the data were compiled has biased our assessment of the influence of fish trophic position.

Our measure of trophic level may also have influenced the results. We used the index provided in Fishbase (Froese and Pauly 2010), corresponding to the number of energy-transfer steps between basal resources and the fish’s position in the trophic web, derived from available diet data. Index values may, in some cases, slightly over- or underestimate the true trophic level of a species, as they are based on gut content data that do not always capture a fish’s entire diet (e.g., because of the rapid digestion of soft-bodied prey; Arai et al. 2003). Also, with energy flowing upward through a web, this measure focuses on the number of upstream links separating a fish from the base of the web, whereas from the parasite’s perspective, it is the number of links above the fish in the web, i.e., the downstream links, that should determine its probability of reaching a definitive host. However, for any given food chain length, the number of links separating a species from the base is exactly inversely proportional to the number of links separating it from the top (Chen et al. 2008). Therefore, the measure we used still captures well the number of

predatory links above a given species in a food web; if a host's trophic level affects its use as an intermediate host by parasites, this measure should be appropriate to detect it. Finally, since most diet studies are based on adult fish, the trophic level information in Fishbase mostly captures the food web position of adult fish. Early in their ontogeny, practically all fish are small-bodied and occupy low trophic levels; long-lived helminth larvae acquired early in life may persist until the fish has grown large and moved up the food chain. Not only can this explain why large fish species that are top predators still harbor relatively many larval helminths (see Fig. 3), but it also indicates why trophic level as measured here did not prove a reliable predictor of the proportion of helminth species occurring as larvae in a fish.

In conclusion, our analyses indicate that when host body size and host trophic level compete, in a statistical sense, as determinants of the proportion of helminth taxa that occur as larvae in a fish, host body size emerges as the better predictor. This does not mean that trophic level has no influence, since the greater interspecific variability among fish in body length (about 200-fold) than in trophic level (about twofold) may account in part for the former being a stronger predictor than the latter. The trophic positions of hosts within a food web were found to be important for taxonomically different host taxa (i.e., mostly invertebrates, and not fish) in a small number of aquatic webs (Chen et al. 2008). One possible direction for future research could be to determine whether the influence of trophic position is restricted to certain host taxa or to certain parasite taxa, possibly using more detailed within-web comparisons.

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