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esa ECOSPHERE

Indirect effects of invasive crayfish on native fish parasites

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Abstract. Interactions between invasive and native species are often modified by parasites. One little-studied scenario is that invasive species affect parasite transmission to native hosts by altering the relative abundance of hosts needed in parasite life cycles, for example by predation on these hosts. Here we show that presence of an invasive crayfish species, *Pacifastacus leniusculus*, decreases the mean abundance of native parasites transmitted from snails and aquatic isopods to perch, *Perca fluviatilis*, in two large boreal lakes in Finland. In contrast, parasites transmitted to the fish from planktonic copepods or mussels, hosts not readily preyed on by crayfish, were not affected by crayfish presence. We suggest that the effect of crayfish on native parasite fauna of fish is mediated via complex effects on invertebrate populations. Hence, our study provides an example of how the indirect ecological effects of species introductions can extend beyond the generally anticipated direct effects, predation and competition.

Key words: benthic invertebrates; concomitant predation; ecosystem effects; intermediate host; invasive species; *Pacifastacus leniusculus*; parasite transmission; *Perca fluviatilis*; perch; signal crayfish.

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Introduction

Introduced and invasive species are recognized as threats to native biodiversity worldwide (Sala et al. 2000, Clavero and García-Berthou 2005, Snyder and Evans 2006). One important category of interaction between introduced and native species is the role of invasive species in transmission of parasites among native species. In this regard, several alternative scenarios have been brought forward (e.g., Prenter et al. 2004, Hatcher and Dunn 2011, Britton 2012). The most obvious risk is the introduction of novel diseases to natives by invasive species (Prenter et al. 2004, Crowl et al. 2008). Alternatively, invasive species could act as alternative or even preferred hosts for the parasites of native species, thus amplifying the parasite burden on native species ('spill-back' effect) (Kelly et al. 2009, Poulin et al. 2010). Competition or habitat alteration imposed by the invasive species could also lead to changes in behavior or physiology in native species increasing either their exposure or susceptibility to parasites (Poulin et al. 2010).

An alternative, but little studied, scenario is that by altering the relative abundance of hosts needed in parasite life cycles, invasive species could either decrease or increase parasite transmission to the native hosts (Holmes 1979, Poulin et al. 2010). For example, the digenean trematode, *Ichthyocotylurus pileatus*, has a complex three-host life cycle involving the adult worm maturing in the gut of a fish-eating bird, asexually multiplying cercarial stages in the aquatic snail, *Valvata macrostoma*, and encysted metacercarial stages attached to internal organs

of the fish host, *Perca fluviatilis* L. (Faltýnková et al. 2009). If any of the hosts—the bird, the snail or the fish—should either increase or decrease in abundance due to environmental changes, this would impinge on the transmission of the parasite and consequently on its abundance in the hosts.

The simplest way in which invasive predatory species can affect parasites is by consuming the parasite's host. This has a two-fold impact on the parasite. It decreases the abundance of the hosts, thus decreasing transmission potential for the parasite. In addition, it may decrease the abundance of the parasite directly when infected hosts are consumed by an unsuitable host (Poulin et al. 2010). This kind of concomitant consumption is likely to be common in nature (Johnson et al. 2011), although its significance might only be revealed after changes in the ecosystem.

The effect of invasive predatory species on parasite transmission was studied previously in Kenya, where incidence of human schistosomiasis, a severe disease caused by invading cercarial stages of the trematode *Schistosoma haematobium*, was suggested to decrease in school children after introduction of crayfish, *Procambarus clarkii* into adjacent aquatic habitats (Mkoji et al. 1999). A clear effect was detected at one of three control-impact pairs, where crayfish were shown to consume the snail host of the parasite.

In this paper we show that invasive predators can have profound effects on the composition and abundance of the parasite communities of native species by interfering with the pathway from intermediate hosts to the main host. We demonstrate that the native parasite fauna of the European perch, *Perca fluviatilis*, is affected by the presence of the invasive predatory crayfish species, *Pacifastacus leniusculus* (Dana), in two large boreal lakes in Finland. Parasites transmitted from benthic invertebrates, especially snails, the preferred prey of crayfish, were markedly less abundant at sites impacted by crayfish than at sites free from crayfish. Our results from spatially and temporally realistic natural settings thus demonstrate more far-reaching indirect ecological effects of species introductions than generally anticipated.

Materials and Methods

The study was conducted in Lake Päijänne (61°31′ N, 25°24′ E) in August 2008 and in Lake Saimaa (61°15′N, 25°13′ E) in August 2009. Päijänne is an oligotrophic lake with a surface area of 1 118 km^2, and maximum and mean depths of 95.3 m and 16.2 m. Saimaa (1377 km^2) is classified as oligo-mesotrophic and has a maximum depth of 85.8 m and mean depth of 10.8 m. Both lakes were originally inhabited by only very scarce native crayfish (*Astacus astacus* L.) populations and introductions of signal crayfish (*Pacifastacus leniusculus*) of North American origin started in the early 1990s. The distribution of signal crayfish in the study lakes is still patchy due to the different introduction policies of water owners. Signal crayfish disperse naturally within the lakes, but all inhabitable shores are not yet colonized due to the complex shore structure and large size of the lakes (Ruokonen et al. 2012).

In both lakes, five sites with well-established signal crayfish populations and five sites without crayfish were chosen for the study. The selected sites were similar in the main environmental factors (e.g., slope, substrate particle size, fetch) which are known to shape the structure of littoral communities (see Ruokonen et al. 2012). To avoid spatial bias, the crayfish and non-crayfish sites were both selected equally around the lakes in longitudinal and latitudinal directions (Fig. 1 in Ruokonen et al. 2012). All sites were trapped for crayfish to estimate their abundance (catch per unit effort, CPUE) and to ensure the absence of crayfish at control sites. At each site, 25 cylindrical funnel traps baited with fresh fish flesh were set along the shore during the evening and collected the following morning. At the crayfish sites of Päijänne and Saimaa the mean CPUE was 3.71 (range 1.5 to 8.6), and 2.88 (0.8 to 6.4) crayfish per trap per night, respectively (Ruokonen et al. 2012). At the control sites, no crayfish were caught, and the absence of crayfish was also confirmed visually by a scuba diver.

Benthic multi-mesh (from 6 to 55 mm) gillnets (length 30 m, height 1.5 m) were used to catch perch in the littoral area. Four nets were set during the evening at each site at an angle of ca. 45 degrees angle to the shoreline and starting at 1 m depth. After 12 h, the nets were lifted and fish

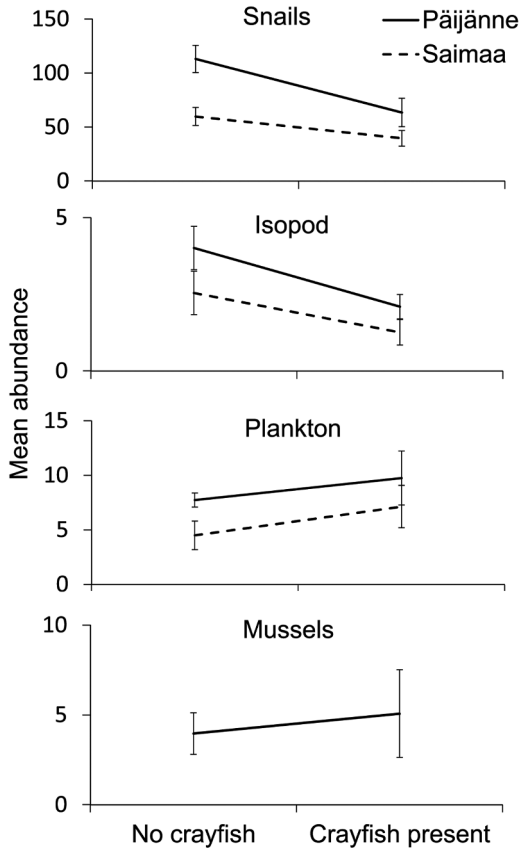

Fig. 1. The mean abundances (mean number of parasites per fish ± SE) of parasites transmitted from different groups of intermediate hosts (snails, isopods, copepods or mussels) in crayfish and non-crayfish sites in lakes Päijänne and Saimaa. Note that the scale on y-axis differs between the groups and that parasites transmitted from mussels were not detected from Lake Saimaa in this study.

were collected. Fish were packed individually in randomly pre-coded plastic bags and frozen. In the laboratory, fish were measured, weighed and examined for parasites. The digestive tract cut open, organs (heart, liver, spleen, swim bladder) and left eye were removed from fish, pressed separately between glass plates and examined under a microscope with 400 x magnification using transmitted light. During parasite investigation, examiners were unaware of the origin of fish to eliminate subjective bias in the results.

For each parasite species and site, prevalence of infection was calculated as percentage of fish infected and mean abundance as the mean number of parasites per fish. Parasites were grouped into four categories according to their intermediate hosts: parasites transmitted to perch from either snails, mussels, planktonic copepods or isopods, each forming one group (see Appendix: Table A1).

Generalized linear mixed models (GLMM) (Zuur et al. 2009) were used to examine the effect of crayfish presence or absence on the prevalence and abundance of perch parasite groups. Models with a binomial error distribution for parasite prevalence and with a Poisson error distribution for parasite abundance were determined including all first-order interactions in initial models. Significance of individual variables/interactions was used as guidance in model selection. Initial models included crayfish status (two levels: crayfish and non-crayfish), lake (two levels: lakes Saimaa and Päijänne) and centered fish length (continuous) as fixed variables. Random intercept and slope (length × site) were added to the models to determine possible site (20 sites) variation and a length-site interaction. The test statistics (Z-values) and significance levels for each model are presented for all main effects under interest regardless of statistical significance. Analyses were conducted using the lme4 library (Bates et al. 2008) within R 2.15.0 (R Development Core Team 2008).

The patterns of variation in the parasite community composition of perch among crayfish and non-crayfish sites were explored by Non-metric Multidimensional Scaling (NMS) ordination (e.g., McCune and Grace 2002). Bray-Curtis distance measure and transformed ($\log(x + 1)$) mean parasite abundance data were used for the ordination of averaged samples from each site. In addition, differences in parasite community composition were tested with two-factor (lake and crayfish status) non-parametric multivariate analysis of variance (perMANOVA) (Anderson 2001). Analysis was done for transformed ($\log(x + 1)$) mean parasite data for each site using Bray-Curtis measure of dissimilarity with 4999 permutations. NMS-ordination and perMANOVA were conducted with PC-ORD 5.0 software (McCune and Mefford 1999).

Results

In both lakes, nearly all studied fish were

Table 1. Prevalences (mean ± SE) and abundances (mean number of parasites per studied fish ± SE) of parasite species found from perch at crayfish and non-crayfish sites in lakes Päijänne and Saimaa. The number of fish studied per site varied from 6 to 21 in Lake Päijänne and from 6 to 25 in Lake Saimaa.

Parasite species	Host group	Prevalence infected (%)		Abundance	
		Crayfish	No crayfish	Crayfish	No crayfish
Lake Päijänne					
Diplostomum spp.	snails	94 ± 0.04	100	17.7 ± 3.0	24.9 ± 3.6
Tylodelphys spp.	snails	94 ± 0.05	98 ± 0.01	31.5 ± 10.9	48.0 ± 6.2
Ichthyocotylurus spp.	snails	90 ± 0.02	97 ± 0.02	14.0 ± 3.6	40.0 ± 8.2
Azygia sp.	snails	16 ± 0.03	11 ± 0.02	0.3 ± 0.1	0.2 ± 0.05
Bunodera lucioperca	mussels	10 ± 0.03	3 ± 0.02	0.8 ± 0.3	0.03 ± 0.02
Rhipidocotyle campanula	mussels	32 ± 0.13	27 ± 0.07	4.3 ± 2.2	3.9 ± 1.2
Camallanus lacustris	copepods	81 ± 0.04	79 ± 0.02	9.3 ± 2.5	7.4 ± 0.6
Proteocephalus percae	copepods	6 ± 0.04	2 ± 0.01	0.1 ± 0.1	0.02 ± 0.01
Triaenophorus nodulosus	copepods	30 ± 0.06	28 ± 0.03	0.4 ± 0.1	0.3 ± 0.04
Acanthocephalus lucii	isopod	56 ± 0.03	57 ± 0.03	2.1 ± 0.4	4.0 ± 0.7
Lake Saimaa					
Diplostomum spp.	snails	53 ± 0.11	85 ± 0.10	6.9 ± 1.9	12.9 ± 3.7
Tylodelphys spp.	snails	61 ± 0.13	80 ± 0.08	18.5 ± 7.7	30.5 ± 6.4
Ichthyocotylurus spp.	snails	86 ± 0.05	82 ± 0.04	14.0 ± 1.9	16.3 ± 4.0
Camallanus lacustris	copepods	63 ± 0.08	73 ± 0.07	6.8 ± 1.9	4.2 ± 1.3
Triaenophorus nodulosus	copepods	27 ± 0.07	23 ± 0.07	0.3 ± 0.08	0.3 ± 0.11
Acanthocephalus lucii	isopod	40 ± 0.08	60 ± 0.09	1.3 ± 0.4	2.5 ± 0.7

infected with parasites transmitted from snails (Table 1) and no differences in the prevalence between crayfish and non-crayfish sites or lakes were detected (Table 2). Nor was any effect detected of crayfish presence on an acanthocephalan transmitted from isopods *Asellus aquaticus* L or on the parasites transmitted from planktonic copepods (Table 2). The prevalence of the acanthocephalan did not differ between lakes, but parasites transmitted from copepods had lower prevalence in Lake Saimaa than in Lake Päijänne (Table 2; $P = 0.003$). Parasites with mussel intermediate hosts were found only from fish collected from Päijänne, and no significant

Table 2. Results of the GLMM-models on the effect of crayfish presence or absence on the prevalence and abundance of perch parasite groups.

Characteristic	Response	Model terms	*Z*	*P*
Prevalence	Snail	Crayfish status	−0.015	0.988
		Lake	−0.666	0.505
		Fish length	2.192	0.028
	Isopod	Crayfish status	−1.062	0.288
		Lake	−1.77	0.076
		Fish length	4.912	<0.001
	Plankton	Crayfish status	−0.015	0.988
		Lake	2.591	0.003
		Fish length	5.786	<0.001
	Mussels	Crayfish status	0.379	0.705
		Fish length	−2.099	0.036
Abundance	Snail	Crayfish status	−3.077	0.002
		Lake	−3.63	<0.001
		Fish length	8.075	<0.001
	Isopod	Crayfish status	−2.499	0.012
		Lake	−1.916	0.055
		Fish length	6.804	<0.001
		Lake × Fish length	−3.317	<0.001
	Plankton	Crayfish status	0.206	0.837
		Lake	−0.304	0.761
		Fish length	6.355	<0.001
	Mussels	Crayfish status	0.54	0.589
		Fish length	3.537	<0.001
		Crayfish status × length	2.029	0.043

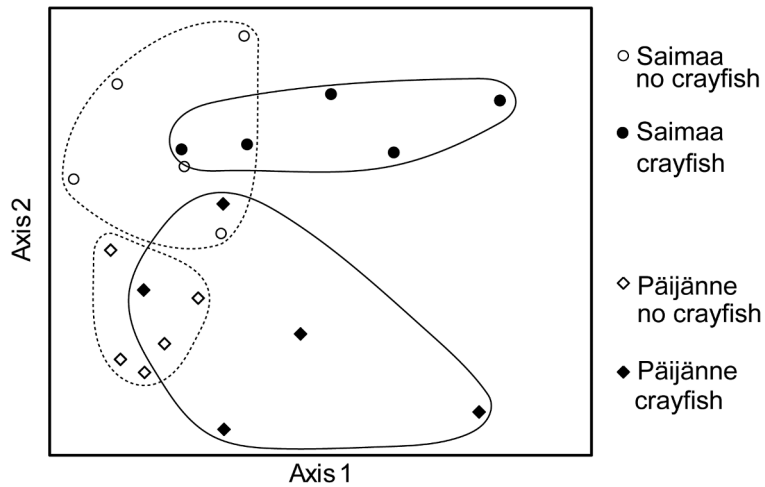

Fig. 2. NMS-ordination of sampling sites in parasite space (10 species). The crayfish and non-crayfish sites are delineated by solid and dashed lines, respectively. Sites without crayfish were grouped more tightly than sites with crayfish on Axis 1.

effect of crayfish on parasite prevalence was found. Fish length had a significant effect on prevalence in all parasite groups, i.e., parasites transmitted from snails, isopods, copepods and mussels (Table 2).

The abundance of parasites transmitted from snails as well as from isopods was significantly affected by crayfish presence (Table 2; $P = 0.002$ and $P = 0.012$, respectively), being lower at crayfish sites (Table 1; Fig. 1). Fish in Saimaa had fewer snail-transmitted parasites than those in Päijänne ($P < 0.001$) and for the isopod-transmitted parasite the difference between lakes was nearly significant ($P = 0.055$). The abundance of parasites transmitted from planktonic copepods was not significantly affected by crayfish presence or lake (Table 2; Fig. 1). In Päijänne, crayfish presence did not significantly affect the abundance of parasites having mussels as intermediate host (Table 2; Fig. 1). As for prevalence, fish length had a significant effect on abundance in all parasite groups (Table 2; $P < 0.001$ for parasites transmitted from snails, isopods, copepods and mussels). In addition, for parasites transmitted from isopods, the model revealed a significant interaction between fish length and lake (Table 2; $P < 0.001$). For parasites transmitted from mussels in Päijänne, the model suggested interaction between fish length and crayfish status of the site (Table 2; $P = 0.043$).

The NMS-ordination of sites using abundance data for the 10 parasite species converged on a stable, 2-dimensional solution (final stress = 12.21, final instability < 0.001, iterations 36; Fig. 2). In the ordination, the community compositions of perch parasites differentiated between crayfish and non-crayfish sites in both study lakes along the first axis, whereas lakes differed along the second dimension. Generally parasite assemblages among sites without crayfish were more similar to each other than assemblages among the sites with crayfish. Visual interpretation of differences in community compositions were confirmed by PerMANOVA results. Community compositions differed significantly between crayfish and non-crayfish sites ($P = 0.010$) and between lakes ($P < 0.001$). Furthermore, there was no significant interaction between the crayfish status and lake ($P = 0.589$).

Discussion

Our results provide a novel demonstration that the ecological effects of invasive species can extend beyond the most obvious direct effects of competition with and predation on native species. An omnivorous predatory invasive crayfish species, *Pacifastacus leniusculus*, clearly affected the parasite fauna of the native fish species, *Perca fluviatilis*. Perch from crayfish areas

had significantly fewer parasites transmitted from snails and from the benthic isopod *Asellus aquaticus* than perch from non-crayfish areas, while parasites transmitted via planktonic copepods or mussels were not affected by crayfish presence.

We argue that this pattern was mediated indirectly via changes in the composition of benthic invertebrate fauna acting as intermediate hosts for parasites with complex life-cycles and infecting perch either as the final host or as the second intermediate host (see Appendix: Table A1). Signal crayfish has been shown to decrease the total abundance and species richness of benthic invertebrates (Nyström et al. 1996, Nyström et al. 1999, Bjurström et al. 2010), especially snails and macrophyte-associated invertebrates such as *A. aquaticus*. At our study sites, the most marked change in benthic invertebrate fauna was a decrease in snail abundance and diversity at crayfish impacted sites on the stony shores favored by signal crayfish (Ruokonen et al., *submitted*), although total benthic invertebrate abundances did not differ between crayfish and non-crayfish sites. However, the associations between parasite abundance and abundance of snails or isopods were not linear or positive for most of the sites (data not shown), indicating that the effect is not directly density-dependent. In addition to a decrease in the abundance of invertebrates, either via direct predation or by indirect effects of habitat alteration, crayfish could also change the population structure of an invertebrate species towards the smaller end of the size distribution. Such a change could affect, for example, the transmission of *Acanthocephalus lucii* from the isopod *A. aquaticus*, in populations of which large isopods are more likely to be infected (Hasu et al. 2007). Furthermore, parasite-induced behavioural changes could make infected isopods more vulnerable to predation (Seppälä et al. 2008).

As a benthic feeder, signal crayfish do not consume plankton directly. However, functional changes imposed by the presence of crayfish could lead to changes in the consumption of plankton by fish and consequently to changes in the abundance of parasites transmitted from plankton. Perch feed on zooplankton mainly as fry, but larger fish are also exposed to some parasites via prey fish having either infected copepods in their stomachs, or parasites in their intestines. According to our results for prevalence and abundance of parasites transmitted from planktonic copepods, no such functional changes were apparent in our study areas. Furthermore, Ruokonen et al. (2012) showed that the presence of signal crayfish did not affect the densities or diets of benthic fish at the same study sites. We found parasites transmitted via mussels only from Lake Päijänne, and no differences between crayfish and non-crayfish sites were detected. The densities of mussels did not differ between the study sites, either (Ruokonen et al., *submitted*). On the other hand, *Anodonta* spp., hosts for the most abundant mussel-transmitted parasite, might be too big to be consumed by signal crayfish.

When examining the individual parasite species, all those transmitted via snails, except one *Azygia* species, had lower abundance at crayfish sites than at non-crayfish sites (Tables 1 and 2), indicating that the crayfish had a similar impact on all species even when they have different snail species as hosts (Table 2). Snail-parasitizing trematodes multiply asexually within the host producing large numbers of free-swimming cercariae, which then penetrate fish hosts upon encounter. One infected snail host can produce tens of thousands of cercariae per day for several weeks (Karvonen et al. 2004). Although cercariae live less than two days (Karvonen et al. 2003), their vast numbers ensure encounter with fish hosts. Hence it is not surprising that no differences in the prevalence of snail-transmitted parasites were detected between crayfish and non-crayfish sites. In addition, some individual fish at crayfish sites may get high numbers of parasites, if they happen to swim by a cloud of cercariae produced by even a single infected snail remaining in the habitat.

Previously, Orlofske et al. (2012) showed that direct predation on infective free-swimming larval stages of parasites can reduce infection levels in subsequent hosts. However, for trematode parasites transmitted from a snail host, concomitant predation of their larval stages with the infected snails has a potential for higher and longer-lasting impacts on parasite prevalence and abundance. By cutting down the expected life-time reproduction of the parasite in snails, predation on infected snails has a more far-

reaching effect on parasite transmission than predation on single cercariae.

Although the complex shore structure within the large lakes we studied has so far prevented the signal crayfish from spreading evenly to all shore areas since their patchy introductions a couple of decades ago (Ruokonen et al. 2012), all crayfish and non-crayfish sites within a lake are interconnected and within a distance of tens of kilometers from each other. Therefore the clear impact of the presence of signal crayfish on the parasites of a fish species capable of moving between the sites is perhaps surprising. However, recent investigations have shown that perch may cluster into small patches even within a large open water area, and thus exhibit limited dispersal between sites (Bergek and Olsson 2009, Bertrand et al. 2011), which might explain the consistent differences in parasite fauna. Such an effect might be weaker for fish with stronger dispersal within the whole lake.

So far, the role of parasitism in animal invasions has been considered in cases where the invasive species has been capable of sharing parasites with the native species, either amplifying them or acting as a sink for the parasites (Prenter et al. 2004, Kopp and Jokela 2007, Thieltges et al. 2009, Paterson et al. 2011). There are also well-documented cases where parasites are used as weapons of competition (Prenter et al. 2004, Haddaway et al. 2012), whereby invasive species are either spreading a new parasite to the native species, or the invasive species benefit from being resistant to parasites debilitating the native species. Predator effects on restricting disease spread amongst prey species are well documented for various ecosystems (Ostfeld and Holt 2004, Hall et al. 2005, Hatcher et al. 2006). As described previously for the effect of introduced crayfish, *Procambarus clarkii*, on the incidence of schistosomiasis in school children in Kenya (Mkoji et al. 1999), predator effects on parasites can also extend to hosts other than the prey species. Here we have demonstrated that invasive predatory species can influence parasite occurrence and abundance in hosts other than the prey species indirectly by interfering with the pathway from intermediate hosts to the main host.

Our results provide an example of how indirect effects of invasive species on ecosystems can be more far-reaching than generally anticipated. Through effects on host demography and behavior, changes in parasite abundance and community composition may further impinge on other levels of an ecosystem, potentially leading to a cascade of unforeseen feedback effects. The net effect of the impact will depend on the balance between the negative (predation, competition for food, habitat alteration) and positive (decrease in parasite load) effects.

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Supplemental Material

Appendix

Table A1. Parasite species found from the perch studied at lakes Päijänne and Saimaa and their known life cycles including the first and second intermediate hosts and final host. Note that some parasites have only one intermediate host. The parasites were grouped according to the invertebrate hosts from which they are transmitted to perch. *Bunodera lucioperca* was grouped with parasites coming from mussels only, although it also has copepods as second intermediate hosts. All species transmitted via snails or mussels belong to Trematoda producing free swimming cercariae via asexual multiplication, which then infect the second intermediate host by penetration through skin or gills. Exceptions are *Azygia lucii* and *Bunodera lucioperca*, cercariae of which are large and eaten by the next host in the life cycle. All other species are transferred in the food chain.

Parasite species	Source	Host			Host group
		First intermediate	Second intermediate	Final	
Diplostomum spp.†,‡,§,¶	1	*Lymnea stagnalis*, *Radix balthica*, *Myxas glutinosa*	several fishes incl. perch	fish eating birds	snails
Tylodelphys spp.†,‡,§,#	2	*Radix* spp.	several fishes incl. perch	fish eating birds	snails
Ichthyocotylurus spp.†,‡,||,††	3,4	*Valvata* spp.	several fishes incl. perch	fish eating birds	snails
Azygia lucii†,‡‡	5,6	*Anisus vortex*, *Galba palustris*, *Planorbis planorbis*	. . .	pike, perch, burbot	snails
Bunodera lucioperca†,‡‡	7	*Pisidium amnicum*	copepod	perch, ruffe	mussels
Rhipidocotyle campanula†,‡‡	8	*Anodonta* spp.	roach	perch	mussels
Camallanus lacustris§§,‡‡	9	copepod	. . .	several fishes incl. perch	copepods
Proteocephalus percae¶¶,‡‡	9	copepod	. . .	perch	copepods
Triaenophorus nodulosus¶¶,‡,||	9	copepod	perch, burbot	pike	copepods
Acanthocephalus lucii##,‡‡	9	*Asellus aquaticus*	. . .	several fishes incl. perch	isopod

Note: Sources are: 1, Karvonen et al. (2006); 2, Faltýnková (2005); 3, Faltýnková et al. (2007); 4, Faltýnková et al. (2008); 5, Niewiadomska (2003); 6, Odening (1976); 7, Rantanen et al. (1998); 8 Taskinen et al. (1991); 9, Chubb (1982).

† Trematode, ‡ larval stage, § Site of infection: eye (lens or vitrous humor), ¶ includes metacercariae of several species, # includes two species, *T. clavata* and *T. podicipina*, || Site of infection: body cavity, †† includes two species, *I. erraticus* and *I. pileatus*, ‡‡ Site of infection: gut, §§ Nematode, ¶¶ Cestode, ## Acanthocephalan.