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Endoparasites of European perch *Perca fluviatilis* fry: role of spatial segregation

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ABSTRACT: A total of 246 perch *Perca fluviatilis* L. fry, 20 to 106 d old from 3 different reservoir subpopulations (epipelagic perch fry, EPF; bathypelagic perch fry, BPF; littoral perch fry, LPF), were examined for parasites. Six species of endoparasites were found: the nematode *Camallanus lacustris* was the most common, followed by the cestodes *Proteocephalus percae*, *Bothriocephalus claviceps*, *Glanitaenia osculata* and the acanthocephalan *Acanthocephalus lucii*. All worms were juvenile or immature and were recovered from the intestinal lumen, with the exception of plerocercoids of *Triaenophorus nodulosus*, which were found in the body cavity or already encysted in the liver (the final site of infection of metacestodes). A marked difference was found in infection rates in the 3 spatially segregated subpopulations of perch fry. Parasites were found almost exclusively in LPF, which were heavily infected (overall prevalence = 30%) compared with the other studied subpopulations. Two species (*C. lacustris* and *T. nodulosus*) were found in 1 fish each (prevalence = 3%) in BPF, whereas EPF were uninfected. The species richness and prevalence of parasites in LPF increased from 20–24 d old fry (2 species of parasites; prevalence = 13%) to 106 d old fry (5 species of parasites; prevalence = 80%).

KEY WORDS: Acanthocephala · Age dynamics · Cestoda · Helminths · Nematoda · Recruitment · Freshwater · Parasite

INTRODUCTION

European perch *Perca fluviatilis* L. is a common freshwater fish widely distributed in the Palaearctic Region that hosts a large number of parasites, especially endoparasites, such as trematodes, cestodes and nematodes (Bauer 1987, Carney & Dick 1999, Wierzbicka et al. 2005). The parasite fauna of perch in Europe is relatively well studied, but little is known about the age dynamics of infections with endoparasites and almost no information exists on parasitism in the early ontogenetic stages (i.e. larvae and early juveniles).

In deep canyon-shaped reservoirs, perch fry occur as 3 different subpopulations: epipelagic, bathypelagic and littoral (Čech et al. 2005). Epipelagic perch fry (EPF) spend all their time in the upper 4 m of the water column (i.e. above the thermocline). Bathypelagic perch fry (BPF) exhibit regular diurnal vertical migrations staying in dark conditions in deep cold water during daylight hours (Čech & Kubečka 2006, Čech et al. 2007a,b) and spending the night in relatively warm surface water (Čech et al. 2005). The temperature difference between epipelagic and bathypelagic habitats, the habitats where the EPF and the BPF subpopulations occur, respectively, during daylight hours is usu-

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ally 5–10°C (Čech et al. 2005, Čech & Kubečka 2006). At least part of the littoral perch fry (LPF) subpopulation has diurnal horizontal migrations, and is present in shallow littoral habitat during the daylight and found in the epilimnion during the night (Gliwicz & Jachner 1992, Vašek et al. 2006). However, most of the LPF subpopulation is present in a warm littoral habitat 24 h d^{-1} (Čech et al. 2005). It is unknown whether this unique spatial and behavioural segregation of these 3 perch fry subpopulations is reflected in their recruitment of parasites and parasite richness.

Parasites are useful indicators of the biology of their hosts including diet, migration and population differentiation (Williams et al. 1992, MacKenzie et al. 1995) as well as food-web structure (Marcogliese et al. 2006). On the other hand, parasitism may influence the behaviour of fish (or hosts), which results in differential habitat use and an increase in vulnerability to predators by infected individuals (Seppälä et al. 2005). Here we address questions of whether (1) there are differences in the prevalence of parasites among 3 different subpopulations of perch fry (EPF, BPF, LPF) and (2) parasite prevalence and their numbers increased with the age of fry.

MATERIALS AND METHODS

The study was carried out in the deep, canyon-shaped Římov Reservoir, Czech Republic, 170 km south of Prague (48° 50′ N, 14° 30′ E) in 2006 to 2008. The reservoir has a surface area of 2.1 km^2 and a maximum depth of 45 m. Fish were sampled during mid-day (10:00 to 14:00 h) on 6 sampling dates (see Table 1). The EPF were caught at a depth of 0 to 2 m below the water surface using the multifunctional RV 'Ota Oliva' and an ichthyoplankton frame trawl (2 × 2 m mouth opening, 1 × 1.35 mm mesh size). The BPF were caught using the same equipment at a depth of 11 to 13 m (2006 and 2008) and 7 to 9 m (2007) below the water surface, i.e. in all cases well below the thermocline (ca. 4 m deep). The depth of the BPF subpopulation was continually checked with a split-beam scientific echosounder (either SIMRAD EY 500 or SIMRAD EK 60); the accuracy of the depth of the towed net for sampling the BPF was checked by a commercial echosounder (Eagle Ultra Classic; for details of pelagic sampling see Čech et al. 2005, 2007b). By performing several vertical tows of the net, Čech et al. (2005) verified that contamination of ichthyoplankton catches of the BPF by the EPF when pulling the net from the deeper layers to the surface is negligible. Moreover, the BPF lifted from depths of 7 to 9 or 11 to 13 m always had overfilled swim bladders and were easily distinguishable from the EPF. Both EPF and BPF were caught at least 100 m from the shore in an area where both epipelagic and bathypelagic habitats were well developed. The LPF were caught using a short-handled dip net (0.5 m in diameter, 0.2 ×0.2 mm mesh size), fry beach seine net (2 × 10 m, mesh size 1 × 1.35 mm) and later in the season using an electrofishing boat in a shallow littoral area of the reservoir (maximum distance from the shore = 5 m, maximum depth = 1 m).

Perch fry were transported to the laboratory alive in plastic containers and immediately pressed individually between glass plates and screened for parasites with the aid of a high magnification stereomicroscope or light microscope. Parasites were further examined *in vitro* using an Olympus BX 51 microscope with Nomarski interference contrast (NIC) and identified on the basis of relevant literature (Ergens & Lom 1970, Kuperman 1973, Scholz 1989, Moravec 1994, Scholz & Hanzelová 1998). The age of perch fry was estimated using otoliths, i.e. daily increments in the sagittae (Campana 1992). The total length (TL in mm) of each fish was measured from the tip of the mouth to the end of the caudal fin with a plastic ruler.

The morphometric data (TL) were analyzed using the software package Statistica 6.0 (1997) (StatSoft). To improve the fit of the normal distribution, a $\log_{10}$ transformation was performed on the prevalence of parasites. Univariate comparisons of parasite species present for each variable were performed separately using 1-way ANOVA. If this test indicated significant differences between the subpopulations, post-hoc Tukey's Honestly Significant Difference (HSD) test with unequal sample sizes was used.

RESULTS

A total of 246 perch fry from 20 to 106 d old were examined for parasites (Table 1). The mean, maximum

Table 1. *Perca fluviatilis.* Age, sampling date (d/mo/yr) and numbers of examined and infected epipelagic (EPF), bathypelagic (BPF) and littoral (LPF) perch fry from the 3 habitats. The number of age-stratified samples containing infected fish is shown in **bold** text

Age (d)	Date	Total	EPF	BPF	LPF
20	7/6/06	30	10	10	10/**3**
24	24/5/07	60	20	20/**1**	20/**1**
24	29/5/08	45	15	15/**1**	15/**2**
44	13/6/07	71	20	20	31/**5**
72	11/7/07	20	0	0	20/**8**
106	14/8/07	20	0	0	20/**16**
Total		246	65	65/**2**	116/**35**

Table 2. *Perca fluviatilis*. Mean, SD, minimum (min.) and maximum (max.) size (total length, TL) of epipelagic (EPF), bathypelagic (BPF) and littoral (LPF) perch fry examined for parasites in 2006 to 2008. EPF and BPF subpopulations were not present in the reservoir during mid-July and mid-August sampling. Sample dates are given as d/mo/yr; p-value determined from ANOVA and Tukey's HSD test; ns: not significant

Date	Sub-population	n	TL (mm) Mean	SD	Min.	Max.	p-value
7/6/06	EPF	10	17	1.8	14	19	<0.05
	BPF	10	19	1.2	16	20	<0.05
	LPF	10	22	1.8	20	26	<0.001
24/5/07	EPF	20	20	0.8	18	22	ns
	BPF	20	16	1.0	15	18	<0.001
	LPF	20	20	1.6	17	24	ns
13/6/07	EPF	20	18	1.4	16	21	<0.001
	BPF	20	26	2.4	20	29	<0.001
	LPF	31	33	3.4	26	40	<0.001
11/7/07	LPF	19	56	3.4	47	61	
14/8/07	LPF	20	71	8.5	62	95	
29/5/08	EPF	15	17	1.7	15	21	ns
	BPF	15	16	1.2	14	18	<0.001
	LPF	15	18	1.9	15	21	ns

and minimum sizes of fish as well as their numbers for each sampling date and each perch fry subpopulation are given in Table 2.

In total 6 species of endoparasites were found in the EPF, BPF and LPF examined: 4 cestodes, *Bothriocephalus claviceps* (Goeze, 1782), *Glanitaenia osculata* (Goeze, 1782), *Proteocephalus percae* (Müller, 1780) and *Triaenophorus nodulosus* (Pallas, 1781); 1 nematode, *Camallanus lacustris* (Zoega, 1776); and 1 acanthocephalan, *Acanthocephalus lucii* (Müller, 1776). All endohelminths were juvenile or immature. Perch fry were also infected with 2 ectoparasites: *Argulus* sp. (~20 and ~5% prevalence in EPF and LPF, respectively) and the ciliate *Trichodina* sp. (~1% prevalence in EPF and LPF), but these data are not well supported, because ectoparasites may have been lost during collection. No monogeneans were found.

In general, the nematode *Camallanus lacustris* was the most common parasite (46 specimens in 18 fish), followed by juveniles of the cestode *Proteocephalus percae* (15 worms corresponding to the stage of plerocercoid, i.e. without segmentation, in 9 fish) (Fig. 1). With the exception of *Triaenophorus nodulosus* found in the body cavity or already encysted in the liver, all endohelminths were recovered from the intestinal lumen.

A marked difference was found in infection rates in the 3 spatially segregated subpopulations of perch fry (Table 1). Endohelminths were found almost exclusively in LPF, which were heavily infected (overall prevalence of 30%). Two species (*Camallanus lacustris* and *Triaenophorus nodulosus*) were found in 1 fish each (3% prevalence) in BPF, whereas EPF were uninfected (Table 1). The 1-way ANOVA demonstrated a difference between the prevalence of infection in 3 subpopulations (F = 9.07, $p < 0.05$). The post-hoc Tukey's HSD test showed significant differences between EPF and LPF ($p = 0.0045$) and between BPF and LPF ($p = 0.0081$).

Species richness and prevalence of parasites in LPF increased from 20–24 d old perch fry (1 species of parasite per sample, prevalence of 5 to 30%) to 106 d old fry (5 species of parasites, prevalence of 80%) (Fig. 1).

DISCUSSION

In all but one case (24 May 2007) the LPF were always the largest fry in the sample, which corresponds with the previous results of Čech et al. (2005) and Vašek et al. (2006). On 2 sampling dates (7 June 2006 and 13 June 2007), the EPF were significantly smaller than BPF, in contrast to the other 2 sampling dates (24 May 2007 and 29 May 2008) when the situation was completely opposite (Table 2). The subpopulations of EPF and BPF were neither detected using echosounders nor caught using the trawl on the 2 latest sampling dates (11 July and 14 August 2007), which is

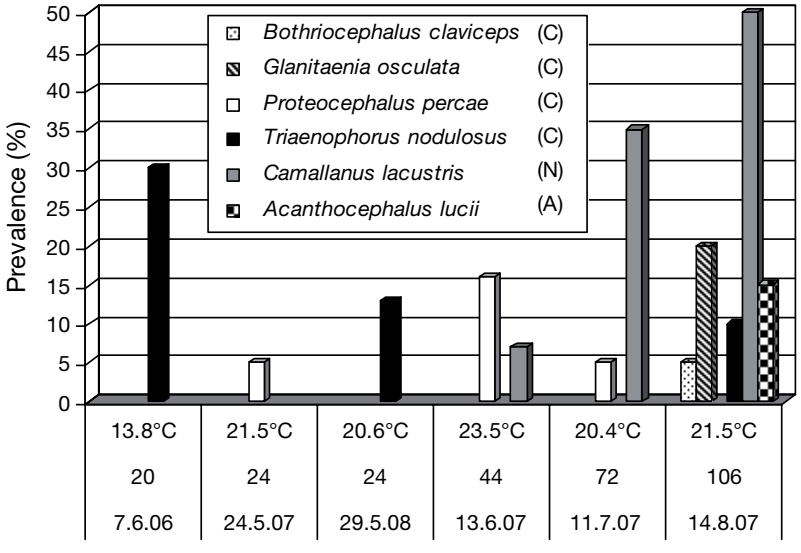

Fig. 1. *Perca fluviatilis*. Prevalence of endohelminth parasites (A: Acanthocephala; C: Cestoda; N: Nematoda) in the littoral perch fry (LPF) subpopulation with data on water temperature (°C), fry age (d) and sampling date (d/mo/yr)

why they were not included in the parasitological analysis. Most probably a continuous summer shift of perch fry occurred from the pelagic into the littoral habitat of the reservoir (Coles 1981, Wang & Eckmann 1994, Čech & Kubečka 2006).

A marked difference in the parasite fauna of perch fry from different subpopulations was found in the present study. These differences may reflect different ecological conditions and availability of intermediate hosts, as well as a different mode of perch feeding in each of the lacustrine zones (see Wierzbicki 1971). Our data indicate that different feeding behaviour occurs early in life and perch from littoral zones are the most heavily infected. A similar observation was reported for adult fish by Wierzbicki (1971).

All but one of the helminth parasites found in perch fry use planktonic copepods as intermediate hosts, which can be correlated with planktonic feeding. The first colonizers of perch fry populations were the tapeworm *Triaenophorus nodulosus*, which has a 3-host life cycle (definitive hosts are pike *Esox lucius* L., whereas planktonic fishes such as perch serve as the second intermediate hosts with larvae—plerocercoids—encysted within the liver, Kuperman 1973), and *Proteocephalus percae*, a specific parasite of perch, rarely found in other percid fishes (Scholz & Hanzelová 1998). Finding of the acanthocephalan *Acanthocephalus lucii* in a 106 d old perch confirms that fry feed upon benthic isopods because this acanthocephalan uses the isopod *Asellus aquaticus* L. as its intermediate host (Andryuk 1974, Brattey 1988).

The present study also has shown a pronounced spatial structure of parasite communities in perch fry, with considerable difference in the infection rate of littoral versus epipelagic and bathypelagic subpopulations of fish. Similar data are not available for cestodes, but a marked spatiotemporal pattern in communities of larval trematode parasites was recently reported in close (distance of about 50 m) littoral and benthic populations of the snail *Valvata macrostoma* Mörch from Lake Konnevesi in Finland (Faltýnková et al. 2008).

Perch fry in the littoral zone of the Římov Reservoir became infected as early as 20 to 24 d after hatching by the cestodes *Triaenophorus nodulosus* and *Proteocephalus percae*. Bykhovskaya-Pavlovskaya (1940) also reported early infections of perch fry with *P. percae*. Kuperman (1963) experimentally infected perch fry with *T. nodulosus*. He observed that the tapeworm infected perch only in the first months of the host life and noted that this endoparasite does not have a significant effect on the fitness of young perch.

The prevalence of *Proteocephalus percae* was highest in 44 d old LPF (15%), but the parasite was not found in 106 d old fry (Fig. 1). The absence of tapeworms at the beginning of autumn may be related to seasonality in the occurrence and maturation of most freshwater fish cestodes in temperate zones (see Chubb 1982, Scholz 1986). Tapeworms, especially proteocephalideans, mature at the end of spring when eggs are laid and specimens of the old generation disappear. Recruitment of the new generation takes place in autumn, usually in October.

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