INFESTATION OF YOUNG NORTHERN PIKE *ESOX LUCIUS* (ESOCIDAE) WITH MACROPARASITES IN DIFFERENT REACHES OF THE RIVER CONTINUUM

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The composition of infracommunities and quantitative characteristics of infestation of underyearlings of northern pike *Esox lucius* with macroparasites have been studied in the small Ild River (a second-order tributary of the Rybinsk Reservoir) from different reaches of the river continuum (from the upper reaches to the mouth). The number of parasite species, mean abundance, and prevalence were significantly higher in the lower reaches than in the upper reaches of the river. Pike samples from different reaches significantly differed in the infection variability between the individuals. The highest coefficient of variation in the number of parasites in one fish individual was observed in the sample from the upper reaches (162%), while it was significantly lower in individuals from the middle and lower reaches (89 and 57%, respectively). Among various parasites from the lower part of the river, we have recorded manipulators of host behavior, which increase the fish availability for predators. These include several trematode species (Trematoda) of the family Diplostomidae. Underyearlings from the sample from the upper reaches were most variable in size, dominated by small individuals. The specimens from the lower reaches were characterized by a minimum variability in body length. The largest (on average) individuals were recorded in the sample from the middle reaches. Parasites are presumably a significant factor influencing the pike population structure and migratory activity, which is usually considered a sedentary species.

Keywords: macroparasites, underyearlings of northern pike *Esox lucius*, river continuum, heterogeneity of the environment, intrapopulation polymorphism.

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INTRODUCTION

Predator pressure and food availability are considered to be the main factors determining fish fitness, population size, and migration activity (Northcote, 1978; Pavlov, 1979; Gliwicz et al., 2006; Giam and Olden, 2016). Relatively recently, such factors have been attributed to parasite infestation, considering them along with predators as influential natural enemies (Poulin and FitzGerald, 1989; Raffel et al., 2008; Hulthén et al., 2015; Koprivnikar and Penalva, 2015). The methods of protecting fish from predators, both individual and group, are quite well studied, which cannot be said about the methods of protection from parasites (Mikheev, Pasternak, 2006). The main protection against them is provided by innate and acquired immunity, as well as local adaptations (Ebert, 1994; Kalbe and Kurtz, 2006). However, immune protection does not guarantee complete safety, especially in those biotopes in which the productivity and diversity of both parasites and intermediate hosts, which also serve as fish food sources, are high.

Balancing between resource availability and threats, fish can choose different tactics: 1) stay in a highly productive biotope, investing many resources in protection; 2) move in search of a safer but less nutritious biotope. The main research within this dilemma has been conducted considering predator-prey interactions (Brabrand, Faafeng, 1993; Skov et al., 2011; Muška et al., 2013). For fish-parasite systems, such studies are few and predominantly descriptive in nature. To better understand the role of parasites as an ecological factor affecting fish population characteristics and their spatial distribution, it is necessary to investigate not only the quantitative parameters of their infestation and the structure of parasite communities, but also to identify categories of parasites that are most influential in terms of their impact on host fitness. For comparative research in this direction, heterogeneous environmental areas with a wide range of

resource and risk variability are best suited. Such an area may be a river continuum/gradient, in which different zones differ significantly in basic abiotic and biotic parameters, while maintaining connectivity, providing hydrobionts with the possibility of migrations and movements (Vannote et al., 1980; Rosi-Marshall, Wallace, 2002; Statzner, Higler, 2011; Humphries et al., 2014; Curtis et al., 2018).

High-productivity biotopes (environmental areas) providing fish with intensive feeding and growth are often associated with a high level of threats: death from predators and risk of parasite infection. In the river continuum, these can be the lower reaches of rivers with diverse biotopes, high abundance and diversity of invertebrates and vertebrates (Krylov et al., 2007; Mikheev et al., 2013). Ecologically plastic fish species, such as roach *Rutilus rutilus* and perch *Perca fluviatilis* , which have a wide feeding spectrum, phenotypic variability (polymorphism), high migratory activity, can avoid dangerous areas, sacrificing intensive feeding and growth (Brabrand, Faafeng, 1993; Muška et al., 2013). This is achieved through horizontal migrations from the coastal zone to open areas (Bohl, 1980; Brodersen et al., 2011), vertical migrations (Zaret, Suffern, 1976; Mehner, Kasprzak, 2011) or movement along the river continuum (Skov et al., 2013). Unlike these relatively small omnivorous fish, large predators such as pike *Esox lucius* , are much more strongly tied to biotopes that provide them with abundant food necessary for rapid growth in the early stages of development, as well as shelter from predators (Miller et al., 2001). At the same time, pike may be at high risk of infection by parasites that can reduce fitness – deplete resources, impair hunting efficiency, and manipulate host behavior, making it more accessible to predators (Moore, 1995; Barber et al., 2000; Poulin, 2010).

Adaptations related to protection from parasites largely depend on the harm caused by parasites. This harm is determined not only by quantitative parameters of infection but also by the

nature of the impact on the host. In juvenile perch, it was shown that the most influential are few and far from the most numerous macroparasites (Slivko et al., 2021).

The purpose of our study is to investigate the parasite load (intensity and extensiveness of infection) on pike fingerlings and their size composition in different biotopes of the river continuum from the headwaters to the river mouth, as well as to identify parasites with the highest virulence, i.e., those having the maximum negative impact on host fitness.

MATERIAL AND METHODOLOGY

The material was collected on the small River Ild (length 46 km) - a second-order tributary of the Rybinsk Reservoir. Pike fingerlings were caught on July 15-30, 2020 using a fry drag net at three river sections: in the upper (57°90′ N, 38°05′ E - 57°89′ N, 38°05′ E), middle (57°95′ N, 38°06′ E - 57°96′ N, 38°07′ E) and lower (58°02′ N, 38°24′ E - 58°01′ N, 38°25′ E - at the confluence of the Ild River into the Sutka River) reaches. The lower course of the Ild River is a rather extensive, ~5 km, backwater zone of the reservoir. The distance along the riverbed between sampling sites in the upper and middle reaches is ~11 km, in the middle and lower reaches - 28 km. In the upper reaches, the river consists of alternating narrow channels and stretches densely overgrown with aquatic vegetation with heavily silted bottom, ranging from 3 to 10 m wide in the stretches. In the middle reaches, stretches alternated with extended rocky riffles, heavily overgrown with aquatic vegetation; the river width ranged from 5 to 13 m in the stretches. In the lower reaches with vegetation along the banks at the sampling site, the river width reaches 150-400 m. In the upper and middle reaches of the river, due to the presence of springs, the water temperature was lower (16-18°C) than in the reservoir's backwater zone (21-24°C). Standard body length (*SL*) was measured in fish. A total of 49 pike fingerlings were studied: 15 specimens *SL* 92.5 mm from the

upper reaches, 14 specimens *SL* 167 mm from the middle reaches, and 20 specimens *SL* 107.8 mm from the lower reaches.

Captured fingerlings were subjected to complete parasitological analysis for macroparasites (Bykhovskaya-Pavlovskaya, 1985; Identification guide..., 1987). The following parameters were used to characterize fish infestation: prevalence - the proportion of infected individuals in the sample, %; mean abundance (MA) - the average number of parasites per host individual in the entire sample (including uninfected fish), specimens; intensity of infection (II) - the number of parasites (minimum and maximum) per infected host individual, specimens (Bush et al., 1997; Margolis et al., 1982). If a parasite was found in only one pike fingerling in the sample, the minimum II value was taken as 0.

For statistical data analysis, one-way analysis of variance and Tukey's test, Spearman's correlation coefficient, and coefficient of variation were used.

RESULTS

The total number of macroparasite species found in pike fingerlings and the prevalence of invasion notably increased from the upstream to the downstream (estuary) section of the river. The average number of parasites per fish changes in a non-unidirectional manner - the maximum value (78.6 specimens) is observed in individuals from the middle section of the river. The main abundance is provided by just one species of trematodes (Trematoda) - *Phyllodistomum folium* , without which this indicator is almost identical in fingerlings from the upper (7.5 ± 3.2) and middle (6.5 ± 2.4) sections of the river. Differences in the average number of parasites per fish between different river sections are highly significant (one-way ANOVA, $p = 0.0001$), with the lowest indicator in the sample from the upper section differing from indicators in samples from both the middle and lower sections (Tukey's test, $p = 0.0002$ and 0.0300 respectively). Pike samples from

different sections varied significantly in the variability of invasion intensity between individuals (coefficient of variation of parasite numbers per fish, %). The highest variability was observed in the sample from the upper section - 162%, while in individuals from the middle and lower sections it decreased significantly to 89% and 57% respectively.

The body length of pike fingerlings from different sections of the river continuum differed significantly (ANOVA: $p < 0.0001$; Tukey's test: the length of fish from the upper reaches differed from the length of individuals from the middle section, $p = 0.0001$; the same level of significance in differences was observed between the middle and lower sections). The highest average length of pike fingerlings was in the middle part of the river; in the upper and lower reaches it was significantly lower and did not differ significantly. The sample from the upper reaches was characterized by the highest variability in fish length (coefficient of variation 52.4%), in the lower reaches it was the lowest (16.9%), in the middle part - 21.0%.

The infection rate of fish (MI) did not significantly depend on their size (Spearman's correlation coefficient: $p > 0.05$). Also, no correlation was observed between the abundance of the most numerous parasite *P. folium* and fish size (Spearman's correlation coefficient: $p = 0.51$). It should be noted that the structure of component parasite communities in the lower section of the river differed significantly from their structures in the upstream sections. In pike fingerlings in the upper (four species of macroparasites) and middle parts of the river (five species), only one species of trematodes predominated in abundance - *P. folium* : 87 and 92%, respectively. In the lower section, with a much richer component community of macroparasite species (15 species), there were no such pronounced dominants (Table 1). Only fingerlings from the lower section of the river had seven species of trematodes at larval stages, completely absent in other zones. The different ratio of adult and larval forms of parasites in pike fry from different river zones is noteworthy (Table 2). In the upper and middle reaches of the river, fry were dominated by parasites of adult

developmental stages, while in the lower reaches of the river, half of all parasite species were represented by larvae.

DISCUSSION

A river is a heterogeneous environment in which boundaries between biotopes can be sharp (horizontal transverse, vertical gradients) or blurred/gradual (along

Table 1. Parasites of pike fingerlings *Esox lucius* from different zones (sections) of the Ild River

Taxon	Life cycle stage	Localization	Upper reaches		Middle reaches		Lower reaches	
			PI, %	MI (II), specimens	PI, %	MI (II), specimens	PI, %	MI (II), specimens
Monogenea								
Dactylogyrus sp.	Adult	Gills			7.1	0.07 (0–1)		
Tetraonchus monenteron	Same	Same	20.0	0.33 (1–2)	21.4	1.07 (0–5)	45.0	2.60 (1–17)
Gyrodactylus lucii	"	Skin					80.0	6.80 (1–30)
Digenea								
Azygia lucii	"	Stomach					30.0	1.50 (1–12)
Phyllodistomum folium	"	Urinary bladder	40.0	6.50 (3–32)	78.6	72.10 (11–187)	20.0	0.25 (1–2)
Bunodera luciopercae	"	Intestine					10.0	0.15 (1–2)
Ichthyocotylurus sp.	Larva	Mesentery					10.0	0.15 (1–2)
Bucephalus polymorphus	Same	Muscles					15.0	0.30 (1–3)
Paracoenogonimus ovatus	"	Same					90.0	24.60 (1–90)
Tylodelphys clavata	"	Vitreous body					25.0	0.75 (1–5)
Posthodiplostomum brevicaudatum	"	Retina					20.0	0.35 (0–1)
Diplostomum sp. 1	"	Lens					30.0	0.45 (1–2)
Diplostomum sp. 2	"	Vitreous body					20.0	0.60 (1–5)
Acanthocephala								
Acanthocephalus lucii	Adult	Intestine	6.7	0.27 (0–4)	28.6	3.30 (3–20)		
Chromadorea								
Raphidascaris acus	Larva	Liver	26.7	0.33 (1–2)	50.0	2.07 (2–9)	5.0	0.05 (0–1)

Copepoda								
Ergasilus sieboldi	Adult	Gills					90.0	6.10 (1–27)
Branchiura								
Argulus foliaceus	Adult	Skin					45.0	0.70 (1–3)

Note. EI - extensity of invasion; AI - abundance index, II - intensity of invasion (min-max).

Table 2. Parameters of the parasite community structure and size of pike fingerlings *Esox lucius* in different zones of the Ild River

Parameter	Upper reaches (*n* = 15)	Middle reaches (*n* = 14)	Lower reaches (*n* = 20)
Standard body length of fingerlings, mm*	92.5 (48.0)	167.1 (24.0)	107.8 (18.0)
	60–210	109–207	74–148
Number of parasite species:			
– larvae	1	1	8
– adult individuals	3	4	7
– total	4	5	15
Average number of parasite larvae in one fish, spec.	0.13	2.07	27.20
Total prevalence of invasion, %	66.7	92.9	100
Total abundance index, spec.	7.5	78.6	44.8

Note. *n* – number of examined fingerlings, spec.; * above the line – mean value and standard deviation (in brackets), below the line – limits of parameter variation.

river – continuum) (Vannote et al., 1980; Krylov et al., 2007; Statzner, Higler, 2011; Pavlov, Mikheev, 2017). Both adult fish and juveniles can move along the continuum in search of an optimal biotope. The main factors determining the suitability of a biotope are considered to be the ratio of resource availability and predator pressure (Kramer et al., 1997; Giam, Olden, 2016). Parasites rarely cause direct damage to the host fish population comparable to predators, but they can be influential regulators of predator-prey relationships through manipulation of the host phenotype (Moore, 1995; Barber et al., 2000; Poulin, 2010). Parasites as "ecological catalysts" change the availability of hosts to predators, open the way for infections, affect different aspects of behavior – defensive, feeding, social, migratory (Moore, 1995; Poulin, 2010; Mikheev, 2011).

We found that in a river continuum, the diversity of macroparasites and the infection rate of pike fingerlings increases from upstream to downstream, which may determine the significance of parasites as regulators of biotic interactions. From the diverse set of parasites in the lower reaches of the river, some have been identified (e.g., trematodes of the Diplostomidae family) that increase the vulnerability of hosts to predators (birds, large piscivorous fish), which probably select the largest fingerlings (Seppälä et al., 2004). Other parasites (*Azygia lucii*) may increase the accessibility of the smallest fingerlings to predators, making them vulnerable to larger conspecifics prone to cannibalism (Odening, Bockhardt, 1976; Zhokhov, Pugacheva, 2023). Thus, in the lower reaches of the river, predator pressure may be high on both the largest and smallest fingerlings. Apparently, this is related to the low variability (coefficient of variation) in body length among pike fry in the lower reaches of the river found in our study.

In the upper reaches, where parasite infection and diversity are the lowest, and the abundance of predators is probably also low (Krylov et al., 2007; Mikheev et al., 2013), the size variability of pike fingerlings is the highest. The highest variability in infection rates was also observed there. The prevalence of infection with a small number of parasite species (no more than four) in the upper reaches did not exceed 66.7%, while in the lower reaches it reached 100%. It is obvious that with low average parasite abundance in the upper reaches, their spatial distribution is very heterogeneous, which allows many fingerlings to avoid high infection rates. Even if the upper reaches are generally less productive than the lower reaches, localized food concentrations (large invertebrates, juvenile fish from the order Cypriniformes) can form there, attracting individual pike fingerlings (Krylov et al., 2007; Mikheev et al., 2013). Under such conditions, a few but most active individuals may consume smaller conspecifics. Cannibalism dramatically accelerates the growth of young pike (Ivanova, Svirskaya, 2013). Therefore, alongside small individuals, very large ones are also found there, comparable to the largest fingerlings in the lower reaches. The upper reaches

likely serve as a refuge from major threats (enemies: predators and parasites), giving young fish an advantage even with lower average resource availability. As body size increases and vulnerability to predators decreases (Fuiman, Magurran, 1994), along with strengthening of the immune system (Magnadottir et al., 2005; Zapata et al., 2006), young pike can move to more productive biotopes in the lower reaches of the river (Dodson, 1997; Kramer et al., 1997; Krylov et al., 2007; Mikheev et al., 2013).

In studies on pike ecology in river conditions, their tendency for a sedentary lifestyle and gravitation toward macrophyte-rich lower reaches of rivers (with abundant resources and biotopic diversity) is emphasized, where adult ambush predators find conditions for hunting, and juveniles find abundant and diverse food and shelter from predators (Miller et al., 2001; Vehanen et al., 2006). In studies of marked pike movements, it has been established that their sedentary nature is often exaggerated, and when habitat conditions deteriorate, pike actively move between biotopes (Vehanen et al., 2006). The high macroparasite infestation of young-of-the-year pike in the lower reaches of the river found in our study suggests that at the earliest stages of ontogenesis, when fish juveniles are particularly vulnerable to both predators and parasites, movement to less productive but safer biotopes may provide an advantage. In small rivers, such biotopes may be associated with the upper reaches, where early juveniles can migrate along the shoreline against the current or immediately find themselves in the upper reaches if part of the pike population finds suitable spawning grounds there. These assumptions require special verification.

By all main indicators, the component communities of macroparasites in young-of-the-year pike from different sections of the Ild River differed significantly. From the upper to the lower section, the number of parasite species and the prevalence of infection increased, but the infection intensity (mean abundance) reached its maximum in the middle section and decreased again in the lower section. It should be noted that this maximum was associated with only one species (the

trematode *P. folium* accounted for more than 90% of the parasite abundance). Excluding this trematode, the mean abundance, like other quantitative indicators of infection, gradually increased from the upper to the lower reaches. The absence of a relationship between the abundance of *P. folium* and the length of young-of-the-year pike suggests that these parasites do not have a direct negative effect on the feeding and growth of the latter. The maximum abundance of *P. folium* in the middle course of the river is probably associated with the high abundance of their host – the mollusk *Pisidium amnicum* . The large cercariae of this trematode with a dixenous life cycle are readily consumed by young pike.

It is important to note that the observed difference in the ratios of adult and larval forms of parasites in young-of-the-year pike in different river zones indicates different strategies of host utilization by parasites. Adult stages of heteroxenous parasites do not exhibit pronounced pathogenic effects on the host, trying to preserve it as a habitat (Mikheev, 2011). Parasites at larval developmental stages have the opposite strategy, manipulating the phenotype of the intermediate host to ensure it becomes prey for the definitive host.

The negative impact of trematode larvae parasitizing fish is especially noticeable in the fingerling stage. There are known examples when young fish infected with trematode larvae exhibited reduced growth rates, physiological disorders, and increased mortality (Harrison, Hadley, 1982; Lemly, Esch, 1984; Coleman, Travis, 1998; Johnson, Dick, 2001). Among the seven species of trematode metacercariae infecting young-of-the-year pike in the lower reaches of the river, there are representatives of the Diplostomidae family (*Posthodiplostomum* , *Diplostomum*). Trematode larvae of these and related species can alter host behavior, reduce total lipid levels, and stimulate oxygen consumption (Lemly, Esch, 1984). Trematode larvae parasitizing in pike muscles, *Bucephalus polymorphus* and *Paracoenogonimus ovatus* , like other species with similar localization, increased glycogen content in muscles, slowed the growth of young-of-the-year pike,

and caused their mortality (Coleman, Travis, 1998; Johnson, Dick, 2001; Tyutin, Izvekova, 2013). It is characteristic that the trematode *P. ovatus* was the dominant species by abundance in pike at the river mouth. The low mobility of pike as an ambush predator increases the probability of its infection with trematode cercariae in biotopes saturated with various mollusks - intermediate hosts of trematodes. Such biotopes predominate in the lower reaches of the river.

A characteristic feature of the parasite fauna of pike fingerlings in the lower reaches of the river was the presence of two species of crustaceans (*Ergasilus sieboldi* , *Argulus foliaceus*), which feed on fish blood and cause significant damage to them (Kabata, 1981). Almost half of the pike fry carried large crustaceans *A. foliaceus* on their skin with an invasion intensity of 1-3 specimens. The actual invasion intensity could be significantly higher, as the crustaceans easily detach from the fish when it is caught. The size of these crustaceans (length up to 7 mm) indicates that the damage they cause is quite substantial and can lead to fish mortality at an early juvenile age, as the crustaceans prefer to attack specifically the fry. In general, the favorable living conditions of pike fingerlings in highly productive biotopes in the lower reaches of the river with elevated temperature and abundance of food may be associated with a high risk of parasite infection and greater parasitic pressure with pronounced negative consequences.

More and more evidence is accumulating in favor of the hypothesis about the influence of parasites as one of the leading factors initiating and modifying the migratory activity of animals (Altizer et al., 2011; Poulin et al., 2012; Poulin, de Angeli Dutra, 2021; Wille, Klaassen, 2022). The obtained data on the variability of the size structure of pike fingerlings and their infestation with macroparasites in different parts of the river continuum suggest that the role of parasites as regulators of defensive, feeding, and migratory behavior of these fish may be significant. Testing this assumption will require comprehensive field and experimental studies of fish feeding and migratory activity under conditions of different parasite infestation.

CONCLUSION

The heterogeneous distribution of resources and threats in space is pronounced in small river ecosystems, where fish can inhabit both highly productive areas (biotopes) with high predator pressure and low-food areas with few predators over relatively short distances. The arrangement of such areas along the river (river continuum) enables fish to move and choose between different tactics – staying in a rich biotope, investing more resources in defensive behavior under conditions of high food availability, or moving to safer but less productive biotopes. The division of the population according to these tactics can lead to the formation of intrapopulation groups, in particular, to migratory polymorphism. Our results on the variability of fish parasite infection within the river continuum showed that the influence of parasites can be no less important a factor causing polymorphism than trophic interactions.

Even pike prone to sedentary life (Vehanen et al., 2006) can leave food-rich biotopes and migrate to areas where there is less risk of parasite infection and predation. This tactic can be used by young individuals who find it difficult to resist both parasites and predators (Fuiman, Magurran, 1994; Zapata et al., 2006). The heterogeneous environment of small rivers allows fish to move freely and choose biotopes with different combinations of biotic factors. Migrations both upstream and downstream can be performed even by juvenile fish with their small energy reserves. Biotopes in the upper reaches of the river, where the risk of parasite infection is lower, can be accessible to both juvenile fish and adult individuals during the spawning migration.

Among the factors forming biotopic heterogeneity in the river continuum and conditions for the emergence of intrapopulation polymorphism, parasite load may be no less important than feeding conditions and predator pressure. In addition to direct effects on fish metabolism, morphology and behavior, parasites can modify the nature of intra- and interspecific interactions, changing prey accessibility for fish, manipulating their defensive, social and migratory behavior.

There is little information about the role of various parasites as ecological regulators, therefore, continuation of field and experimental research in this direction is highly relevant. Small rivers, which play an important role as spawning and feeding biotopes for many fish species, are especially attractive as heterogeneous but "permeable" ecosystems with a wide range of biotic and abiotic conditions. As research objects, small rivers are relatively accessible and convenient for a complex of field and experimental work.

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COMPLIANCE WITH ETHICAL STANDARDS

All manipulations with the research objects were carried out in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals (http://oacu.od.nih.gov/regs/index.htm). The work was approved by the IBIW RAS Bioethics Commission, protocol No. 13 dated January 30, 2024.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflict of interest.

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