Ecological aspects of the formation of the helminth fauna of *Perca fluviatilis* (Actinopterygii: Perciformes) of the Usinsky Bay (Kuibyshev Reservoir, Russia)

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Abstract. The fauna of the multicellular parasites of European perch *Perca fluviatilis* (Perciformes) of the Usinsky Bay of the Kuibyshev Reservoir was studied in 2019–2020; nine taxa of helminths were found. The parasite prevalence of most of the intestinal helminth species, associated with the zooplankton community, did not exceed 12–25%. In the fish with a body length of 117–200 mm, fish juveniles and benthos organisms played a significant role in the parasite transmission. The Usinsky Bay was a buffer zone at the margin of the “river-reservoir” system and had a specific hydrological regime. This promoted favorable conditions for the spreading of alien species of aquatic organisms in the ecosystem of the reservoir; in some cases this led to an increase in the invasion of indigenous fish (European perch) by invader parasites. As a result of this process, the invasive species of trematode *Apophallus muehlingi* became dominant in the helminth fauna of the European perch. High degree of infestation of European perch by this parasite indicated wide distribution of its first intermediate host, the alien mollusk *Lithoglyphus naticoides*, in the Usinsky Bay. Other species of parasites, associated with this invader, were not found in *Perca fluviatilis*. Helminths of the European perch can be used as biological markers to identify migratory activity, the vector of the invasion of some alien species, the range of their hosts, the population abundance, and indirect infection by alien hosts in different water bodies of the Volga River basin.

1. Introduction
The study of the fauna of fish parasites and the ecology of aquatic organisms under changing environment due to anthropogenic load and other factors is one of the key issues for the water bodies of the middle and lower Volga River regions [1]. Parasites are important components of the ecosystem, they are able to precondition the ecological relationships of aquatic organisms to certain extent, and to affect the community structure [2]. Fish helminths may serve as biological markers in revealing the main features of the host ecology and structural and functional changes in ecosystems [3, 4]. The knowledge on the composition of intestinal helminths of fish makes it possible to characterize the trophic links of the host [5]. The degree of infection of fish by larval stages of trematodes characterizes other ecological relations between the parasite and the host, for example, their general confinement to certain biotope [6].
Nowadays, the composition of the parasite fauna and the ecology of fish change mainly due to the anthropogenic load that affects significantly the functioning of aquatic ecosystems [7]. A long-term multifactor anthropogenic impact in the Volga River basin has led to a manifold increase in the income of toxic substances with wastewater from industrial enterprises, as well as fertilizers and pesticides [8]. The development of shipping, mechanized excavation, the operation of river ports, the construction of dams and bridges have led to changes in the hydrological regime and thus contributed to the transformation of the ecosystems of the Volga River reservoirs and tributaries. The consequences of human activity arose the issue of biological invasions in the Volga River basin. Suffice it to say that the number of invader parasite species here has tripled over the past twenty years [9]. Disturbance of the habitat of aquatic organisms had changed the fish infection and deteriorated the epizootic and epidemiological state of the water bodies [10]. The structure and functioning of lake ecosystems have been most studied to date, but the ecosystems of reservoirs, to a lesser extent. River ecosystems remain unjustifiably poorly studied, since they are more complexly organized due to the peculiarities of hydrology and different dimensionality. The study of the features of their functioning is necessary for practical reasons and to development of a general theory of the functioning of ecological systems [11].

The Usinsky Bay is a body of water formed after the flooding of the lower reaches of the Usa River (right-bank tributary of the Volga River) during the establishing of the Kuibyshev Reservoir [12]. The river bed is regulated in the lower reaches by a temporary soil dam, which leads to the reshaping of the river channel, silting, and destruction of the banks. The reservoir is navigable from the mouth to the Mezhdurehensk village, the 20-km route is included in the list of waterways of the Russian Federation [12]. The wave and wind regimes are similar to those for the river section of the Saratov Reservoir. The "blooming" of the Usinsky Bay is very intense in summer; Cyanoprokaryota (up to 99% of phytoplankton biomass) contribute the most [13]. Water quality of the Usa River, assessed by specific combinatorial index of water pollution (SCIWP) in the upper and lower reaches, corresponds to IV class, category "a" ("dirty"); on average, III class, category "b" ("very polluted") [14]. On one hand, the Usinsky Bay is affected by the influence of reservoir waters, but exhibits typical river conditions on the other. This contributes to the formation of a hydrological regime characteristic of a low-flow water body.

The study of the helminth fauna of the European perch *Perca fluviatilis* Linnaeus, 1758 was carried out within the framework of a complex hydrobiological study of the waters of the Priplotinny Ples Reach of the Kuibyshev Reservoir. European perch is a typical representative of the ichthyofauna of the Volga River reservoirs, including the Kuibyshev Reservoir and its tributaries [15]. Species composition of fish of the Usa River and its tributaries is diverse and represented by 47 species; *Perca fluviatilis* belongs to the group of dominant species in the ichthyofauna of the Usa River (16.9%) [14]. In the Priplotinny Ples Reach of the Kuibyshev Reservoir, where the Usinsky Bay flows into, commercial and amateur fishing is performed all the year round (excluding the spawning period) [16]. European perch in one of the main commercial species. The peculiarities of the biology and ecology of *Perca fluviatilis* have been studied for water bodies of different types [17, 18, 19]. The species belongs to facultative predators with no particular food preferences. The food spectrum is determined only by the availability and abundance of food organisms (zooplankton, macrozoobenthos, and juvenile fish) [15, 20]. The composition of parasites of European perch from the water bodies of Eurasia is quite diverse [21, 22]. In total, 165 species belonging to 17 taxa were found in *Perca fluviatilis* within the boundaries of the Arctic Province [23].

The study aims to analyze the species composition of *Perca fluviatilis* helminths, their abundance, and the peculiarities of the functioning of parasite systems associated with this host in the Usinsky Bay. The study is highly relevant due to the lack of modern parasitological data for the Usinsky Bay, the location of the reservoir in the zone of different types of anthropogenic impact, and to special hydrological regime.
2. Materials and Methods
The studies have been performed in the Usinsky Bay. Its length exceeds 45 km, from the mouth of the Tisherek River (a tributary of the Usa River) up to the Priplotinny Ples Reach; the bay is located in the zone of maximum backwater of the Kuibyshev Reservoir (figure 1).

![Usinsky Bay: the site of junction with the Priplotinny Ples Reach of the Kuibyshev Reservoir](image)

The width of the Usinsky Bay is 2–4 km, the depth at the junction with the reservoir reaches 23 m, increasing up to 8 m towards the upper part. The water resources of the bay are used for fishery, household, recreational purposes (dispensaries, recreation centers). In this work, we have used the materials collected in 2020 during the complex scientific cruise of the R/V "Pobeda" along the Kuibyshev Reservoir and its tributaries (including the Usinsky Bay). Ichthyological and parasitological material for the work was obtained at two stations in the Usinsky Bay. In May—June 2019, 16 specimens were caught with a hook tackle nearby Mezhdurechensk (53°16′31.4″ N 49°06′09.2″ E) (station no. 1). In July-August 2020, 18 specimens were caught downstream of the Usa River in the area of the unexploited camp site "Impuls" (53°17′47.0″ N 49°15′19.1″ E) (station 2). In total, 34 specimens of *Perca fluviatilis* were examined by the method of incomplete parasitological dissection. The fixation and processing of the parasitological material was carried out by standard methods; the length of the fish body was measured from the end of the snout to the end of the scale cover [24]. The stages of maturity of the gonads of fish were determined using reference literature [25]. In 2019, perch was represented by specimens with a body length of 154–200 mm. In 2020, individuals with a body length of 117–193 mm were examined. Neutral red was used for vital dyeing of parasites. The parasites were identified according to the taxonomic key [26], taking into account up-to-date data of the Fauna Europaea website [27]. The fish taxonomy was verified with the FishBase website [28]. The fish infestation was assessed qualitatively by generally accepted indicators: parasite prevalence (EI%), which was the number of the infected host by certain parasite species to the total number of fish in the sample [29] and the parasite abundance (The average number of parasites of one species in all studied individuals, including uninfected ones). The data in the tables are presented as $m \pm SE$ (mean ± error of the mean) [30].

In 2020, samples of zooplankton were collected in the pelagic and littoral zones in the surface water layer (0-0.5 m) with a graduated cylinder. Thirty liters of water was filtered through a plankton net (mesh size of 64 μm) and fixed with 96% ethanol. Sample processing was carried out according to the standard methods [31, 32]. The zooplankton species were identified according to the recent taxonomic keys [32, 33, 34]. The original data for 2020 were supplemented by up-to-date literature data on the composition of the zooplankton community in the Usinsky Bay [14].
The index of similarity of the species composition of the helminth fauna was calculated based on the Sørensen index (at a significance level of 50%) using Statistica 8.0 program.

3. Results
The infestation by helminths of *Perca fluviatilis* in the Usinsky Bay of the Kuibyshev Reservoir was investigated. Nine taxa of helminths were found, eight taxa were identified down to species level, belonging to four taxonomic groups: Trematoda – 4 species (*Rhipidocotyle campanula* (Dujardin, 1845), *Bunodera luciopercae* (Muller, 1776), *Ichthyocotylurus variegatus* (Creplin, 1825)), Apophallus muehlingi (Jagerskiold, 1899)), Nematoda – 3 species (*Camallanus lacustris* (Zoega, 1776), *Camallanus truncatus* (Rudolphi, 1814), *Contracaecum microcephalum* (Rudolphi, 1819)), Crustacea – 1 species (*Argulus foliaceus* (Linnaeus, 1758)), and Bivalvia – 1 species (Unionidae sp. larvae) (table 1).

| Helminth species                      | Tissue                        | Station no. 1                   | Station no. 2                   |
|---------------------------------------|-------------------------------|--------------------------------|--------------------------------|
| *Rhipidocotyle campanula*             | intestine                     | 25±11.18                       | 0                              |
|                                       |                               | 0.56±0.28                      |                                |
| *Bunodera luciopercae*                | intestine                     | 12.5±8.54                      | 22.22±10.08                    |
|                                       |                               | 1.38±0.97                      | 0.45±0.25                      |
| *Ichthyocotylurus variegatus*         | swim bladder wall, adipose tissue, outer intestinal wall, mesentery, fins, operculum, gill rakers, subcutaneous tissue of the body, outer shell of the eyes | 43.75±12.84                      | 61.11±11.82                    |
| mtc                                   |                               | 1.63±0.54                      | 2.06±0.54                      |
| *Apophallus muehlingi* mtc            |                               | 81.25±10.08                    | 94.45±5.55                     |
|                                       |                               | 69.44±15.09                    | 201.33±72.56                   |
| *Camallanus lacustris*                | intestine                     | 12.5±8.54                      | 50.0±12.13                     |
|                                       |                               | 0.19±0.14                      | 0.17±0.18                      |
| *Camallanus truncatus*                | intestine                     | 18.75±10.08                    | 16.67±9.04                     |
|                                       |                               | 0.19±0.14                      | 1.17±0.37                      |
| *Contracaecum microcephalum* larvae*  | liver                         | 25.0±11.18                     | 0                              |
|                                       |                               | 0.75±0.36                      |                                |
| *Argulus foliaceus*                   | fins                          | 0                              | 11.11±7.62                     |
|                                       |                               | 0                              | 0.11±0.08                      |
| Unionidae sp. larvae                  | gill rakers                   | 0                              | 5.56±5.56                      |
|                                       |                               | 0.11±0.11                      |                                |

The numerator is the parasite prevalence, %; the denominator is the parasite abundance, ind.

Most of the parasites found in the study area were widely specific and might be recorded in different fish species. The parasites of Percidae were *Bunodera luciopercae*, *Camallanus lacustris*, and *Camallanus truncatus*. Seven out of nine species have complex life cycles (table 2). The definitive hosts of four helminth species are fish, three species of helminths are transmitted along the trophic chains to fish-eating birds, including one species that may finish its life cycle in mammals and humans as well [38] (table 2). The life cycles of parasites of European perch are facilitated by the presence of hosts of all levels (table 2). According to our observations, total abundance of rotifers *Euchlanis dilatata* Ehrenberg, 1832 and *Keratella cochlearis cochlearis* (Gosse, 1851), as well as Cyclopoida (*Thermocyclops oithonoides*, *Acanthocyclops americanus*) (Marsh, 1892) reaches 404·10³ ind./m³, biomass, 2.16 g/m³. These results fit well with the literature data [14], evidencing on higher quantitative indicators of the zooplankton community at the sampling sites comparing with those in the upper and middle sections of the Usa River. Benthos community in the lower reaches of the Usa River, including the Usinsky Bay, is less diverse than that in the upper
reaches; in total, 51 species have been recorded. The abundance of benthic organisms is high, reaching \(6 \cdot 10^3\) ind./m\(^2\), biomass, 5.0 g/m\(^2\), mainly due to invading species [14]. The Ponto-Azov invader, mollusk *Lithoglyphus naticoides* (C. Pfeiffer, 1828), found in the Usa River [41], may serve as the intermediate host of parasites of European perch (table 2). Mollusk *Valvata piscinalis* (O.F. Müller, 1774) is the first intermediate host of *Ichthyocotylurus variegatus*, which has not been recorded in the Usinsky Bay. However, high prevalence (43–61%) of trematode larvae in European perch indicates a wide distribution of mollusks in the study area.

**Table 2.** Life cycles of helminths of *Perca fluviatilis* \(^a\)

| Helminth species | Life cycle |
|------------------|------------|
| *Ichthyocotylurus variegatus* | Intermediate host I - mollusk *Valvata piscinalis* (O.F. Müller, 1774), intermediate host II – Cuprinidae, Percidae, and other fish species, definitive host – gulls and sterns Intermediate host I – mollusks *Unio* \(^b\), *Anodontia* (*Anodonta mutabilis* Clessin, 1877, *A. anatina* Stabile, 1845, *A. seisanensis* Kobelt, 1911), intermediate host II – Cuprinidae, and other fish species, definitive host – predator freshwater species. |
| *Rhipidocotyle campanula* | Intermediate host I – mollusks *Sphaerium corneum* (Linnaeus, 1758), *S. rivicola* (Lamarck, 1818), *Pisidium annicum* \(^b\) (O.F. Müller, 1774), *P. casertanum* Annandale, 1918, *P. lilljeborgii* Esmark & Hoyer, 1886, *P. personatum* Malm, 1855, intermediate host II – *Simopeplus vetulus* (O.F. Müller, 1776), *Eudiaptomus graciloides* (Lilljeborg, 1888) \(^b\), *Daphnia* (*Daphnia*) *pulex* (Leydig, 1860), *Daphnia* (*Daphnia*) *galeata* Sars, 1864 \(^b\), *Daphnia* (*Daphnia*) *cucullata* Sars, 1862, *Eury cercus* (*Eury cercus*) *lamellatus* (O.F. Müller, 1776), *Thermocyclops oithonoides* (Sars, 1863) \(^b\), *Thermocyclops crassus* (Fischer, 1853) \(^b\), definitive host – predator fish, mostly *P. fluviatilis* |
| *Bunodera luciopercae* | Intermediate host I – mollusk *Lithoglyphus naticoides* (C. Pfeiffer, 1828) \(^b\), intermediate host II – fishes, definitive host – Laridae, mammals, humans Intermediate host I – *Mesocyclops* (*Mesocyclops leuckarti* (Claus, 1857)), *Megacyclops* \(^b\) (*Megacyclops viridis* (Jurine, 1820)), *Macrocyclops* \(^b\), *Acanthocyclops* \(^b\), *Eycyclops*, *Cyclops*, facultative hosts – Harpacticoidea, Isopoda, Odonata, definitive host – Percidae and other predator fish species |
| *Apophallus muehlingi* | Intermediate host I – mollusk *Lithoglyphus naticoides* (C. Pfeiffer, 1828) \(^b\), intermediate host II – fishes, definitive host – Laridae, mammals, humans Intermediate host I – *Mesocyclops* (*Mesocyclops leuckarti* (Claus, 1857)), *Megacyclops* \(^b\) (*Megacyclops viridis* (Jurine, 1820)), *Macrocyclops* \(^b\), *Acanthocyclops* \(^b\), *Eycyclops*, *Cyclops*, facultative hosts – Harpacticoidea, Isopoda, Odonata, definitive host – Percidae and other predator fish species |
| *Camallanus lacustris* | Intermediate host I – *Mesocyclops* \(^b\) (*Mesocyclops leuckarti*), *Megacyclops* \(^b\) (*Megacyclops viridis*), *Macrocyclops*, *Cyclops*, possible reservoir host - fish *Leuciscus*, *Abramis*, definitive host – Percidae and other predator fish species Intermediate host I – *Thermocyclops oithonoides*, *Dacyclops bicuspidatus* (Claus, 1857), facultative host – larvae of Ephemeroptera \(^b\), reservoir host – larvae of Ephemeroptera \(^b\), Trichoptera, fish, definitive host – herons, night herons, and cormorants |
| *Camallanus truncatus* | Intermediate host I – *Mesocyclops* \(^b\) (*Mesocyclops leuckarti*), *Megacyclops* \(^b\) (*Megacyclops viridis*), *Macrocyclops*, *Cyclops*, possible reservoir host - fish *Leuciscus*, *Abramis*, definitive host – Percidae and other predator fish species Intermediate host I – *Thermocyclops oithonoides*, *Dacyclops bicuspidatus* (Claus, 1857), facultative host – larvae of Ephemeroptera \(^b\), reservoir host – larvae of Ephemeroptera \(^b\), Trichoptera, fish, definitive host – herons, night herons, and cormorants |
| *Contracaecum microcephalum* | Intermediate host I – *Mesocyclops* \(^b\) (*Mesocyclops leuckarti*), *Megacyclops* \(^b\) (*Megacyclops viridis*), *Macrocyclops*, *Cyclops*, possible reservoir host - fish *Leuciscus*, *Abramis*, definitive host – Percidae and other predator fish species Intermediate host I – *Thermocyclops oithonoides*, *Dacyclops bicuspidatus* (Claus, 1857), facultative host – larvae of Ephemeroptera \(^b\), reservoir host – larvae of Ephemeroptera \(^b\), Trichoptera, fish, definitive host – herons, night herons, and cormorants |

\(^a\) Life cycles are given according to: [35, 36, 37, 38, 39, 40].

\(^b\) Intermediate hosts found in the fish from the Usinsky Bay, according to: [14, 41, original data]
Most of the parasite species (four out of seven) belong to the class Trematoda. Two species are found in European perch at the stage of metacercaria. This indicates that the fish visit bottom biotopes, where mollusks live, which are the first intermediate host for trematodes. The European perch is infected by metacercariae of the trematodes *Ichthyocotylurus variegatus* and *Apophallus muehlingi* directly, bypassing trophic links.

*Apophallus muehlingi*, originally found by us for the first time in the European perch in 2019 in the Usinsky Bay, is an alien species in the Volga River reservoirs (figures 2, 3).

![Figure 2. Alien trematode A. muehlingi from perch in Usinsky Bay (general view, length 0.67 mm)](image1)

![Figure 3. V-shaped excretory vesicle with an S-shaped curved posterior section and rounded testes on the sides](image2)

This trematode species parasitizes the perch at the metacercaria stage. Prevalence of this parasite in perch is very high and reaches 81–94% (table 1). The maximum number of parasites found in one host is 1,296 specimens. The invader occupies a dominant position in the fauna of European perch helminths in the studied areas of the Usinsky Bay. The trematode causes fish disease, leading to the death of juvenile fish at high infestation rate [42]; it also poses a potential danger to carnivorous mammals and humans [38]. The trematode *Ichthyocotylurus variegatus* and the parasitic crustacean *Argulus foliaceus* are also dangerous for fish as they may cause epizootic diseases. Three helminth species, inhabiting the digestive tract of the fish (*Bunodera luciopercae*, *Camallanus lacustris*, and *C. truncatus*), use zooplankton organisms as intermediate hosts. In addition to planktonic crustaceans, benthos organisms (Ephemeroptera larvae) may also be intermediate hosts of *Contracaecum microcephalum*. However, zooplankton organisms make up a significant part of the diet of European perch only up to a certain size/age of fish [43]. When the body length reaches 150 mm, European perch actively includes juvenile fish in its diet. We have examined individuals of the size group of 117–200 mm. There are no published data on the perch feeding in the Usinsky Bay. In the Kuibyshev Reservoir, invertebrates make a significant part of the diet of European perch with a body size of 100–150 mm, but fish are the main food object after perch reaches a body length of 150 mm [18]. Direct trophic relationships between the zooplankton community and medium- and large-sized European perch are weakened to a certain extent. The parasites infect perch of this size both indirectly, when they inhabit the juveniles of Cyprinidae and/or the juveniles of perch, and directly at metacercaria stage of trematodes, which are the parasites with a direct life cycle.

There was the same number of parasite species (7) of European perch in both studied areas of the Usinsky Bay, but the species lists were different (table 1). At station no. 1, no parasites with direct life cycle have been found. The parasite prevalence of all helminth species, except *Contracaecum microcephalum*, was lower than that observed at station no. 2. The prevalence of *Contracaecum microcephalum* was quite high and amounted to 25%. Prevalence of *Bunodera luciopercae*,

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Camallanus lacustris, and C. truncatus was much lower (12–18%). Rhipidocotyle campanula and Contracaecum microcephalum were not found in European perch at station no. 2, and the prevalence of Camallanus lacustris was high (50%) (table 2). The Sørensen similarity index of the European perch helminth fauna in Usinsky Bay was 43% when comparing different years (2019 versus 2020).

The pathways of helminths of Perca fluviatilis may change in the water body affected by invasion of alien species of aquatic organisms [14]. In order to search for the role of invading fish in the spreading of perch parasites in the Usinsky Bay, the similarities between the species composition of the helminth fauna of Perca fluviatilis and the alien Neogobius melanostomus (Pallas, 1814) [44] were analyzed; the Sørensen similarity index was 29%.

4. Discussion
Fish helminths are able to reflect the most important structural and functional changes in the biocenosis of a water body, such as the dynamics of the abundance and biomass of zooplankton and zoobenthos, the composition of ichthyocenosis [45, 46, 47], and the transformation of trophic relationships in fish [48]. Analysis of the fauna of helminths of Perca fluviatilis, which is ecologically plastic and widespread species, makes it possible to assess trophic and biotope relationships in the biocenosis, to analyze the composition of zooplankton and benthos communities, and to reveal the participation of invading species in the trophic relationships of fish and parasitic systems [6].

The feeding peculiarities of the European perch are an important factor determining the composition of its helminth fauna. The food spectra of Perca fluviatilis is preconditioned both by the abundance and availability of food items in the water body [20]. In the Usinsky Bay, perch has low or medium rates of prevalence of most intestinal helminths, which use trophic links as the invasion pathways. According to our observations, the food spectra of European perch with a body size of 154–200 mm at the station no. 1 is represented by juvenile fish, followed by benthic organisms (Chironomidae, Gammaridae, Oligochaeta), but singly, by zooplankton. Perch with a body size of 117–193 mm at station no. 2 feeds mainly on juvenile fish; mollusks and zooplankton organisms are recorded singly as the food items. This indicates that juvenile fish is an important channel for the invasion of perch by intestinal helminths in the reservoir in different seasons of the year and in different biotopes. This food object may serve for perch as a transmission link for helminth passing through the digestive tract, particularly, for Bunodera luciopercae, Rhipidocotyle campanula, Camallanus lacustris, C. truncatus, and Contracaecum microcephalum. The Cestoda representatives, which are common for Perca fluviatilis in the Volga River reservoirs [49], are completely absent in the studied individuals. Obligate intermediate hosts of helminths of this taxonomic group are zooplankton organisms. The weakening of the trophic links of the perch and the zooplankton community, the low abundance and / or low prevalence of parasites in planktonic crustaceans (the intermediate hosts of parasites) may be possible reasons for the low prevalence / absence of these parasites in Perca fluviatilis. The seasonal change of zooplankton community may be another possible reason for the low parasite prevalence in perch. In addition, perch tends to consume much benthos in the Kuibyshev Reservoir, which joins the Usinsky Bay [18]. Forming of tight ecological links (nutrition, habitat) between Perca fluviatilis and the benthos community in the reservoir is facilitated by the sufficient abundance and diversity of components of the latter. According to the benthos abundance the water body is assessed being of medium feeding capacity [14]. Against the background of the average prevalence of parasites in Perca fluviatilis, regard must be paid to the invading trematode Apophallus muehlingi, which invades fish in an active (non-trophic) way and is characterized by the highest prevalence. Therefore, dominance of this trematode in the helminth fauna of the European perch is another evidence of the tight biotope-related links of Perca fluviatilis with the benthos community. At the same time, no representatives of the class Acantchocephala have been found in perch, although benthic crustaceans are the intermediate hosts of these helminths. For example, Acanthocephalus lucii (Muller, 1776) and Neoechinorhynchus rutili are common parasites of perch in other water bodies [49, 50], but these helminths are absent in the perch from the Usinsky Bay. This indicates a low abundance / absence of crustaceans Asellus aquaticus (Linnaeus, 1758),
Ostracoda (genus *Cypria*), as well as some Megaloptera (Insecta) and Gammaridae, which are intermediate hosts of these parasites, in the benthic communities of the study area [50].

Seasonal dynamics of the fish feeding and the life cycles of parasites are important factors preconditioning the infection of *Perca fluviatilis* with intestinal helminths. In 2019, 69% of total sample were mature females after spawning (stage VI). In the Kuibyshev Reservoir, perch spawns at the end of April—beginning of May [18], during spawning, the perch almost stop feeding. Accordingly, intestinal helminths do not enter the *Perca fluviatilis* population during this period. Perhaps, this contributes to the elimination or poor survival of intestinal helminths: no intestinal parasites have been found in 31% of the examined fish. Mature *Bunodera lucioperca* leave perch in June and July [51], which also leads to a sharp decrease in the trematode prevalence in early summer. In late summer (2020), young stages of *Bunodera lucioperca* begin to enter the perch population. This is reflected in the prevalence rates, which have increased up to 22.2% (table 2).

Significant changes have been observed in the last two decades in the ecosystem of the Kuibyshev Reservoir, as well as in other Volga River reservoirs; they are associated with the penetration of alien species, including parasites [9, 52, 53]. In the Usinsky Bay, invasive species of the Pontic-Caspian complex mainly were recorded in almost all communities, i.e. zooplankton, zoobenthos, and fish communities [14]. In zooplankton, various stages of *Eurytemora caspia* Sukhikh & Alexeev, 2013 and *Heterocope caspia* Sars GO, 1897 (Copepoda) were noted. In the macrozoobenthos community, alien crustaceans, belonging to Cumacea, Gammaridea (*Stenogammarus dzjubani* (Sars, 1894)), and representatives of Mollusca (*Lithoglyphus naticoides*, *Dreissenopsis polymorpha* (Pallas, 1771), *Monodacna colorata* (Eichwald, 1829)) have been registered [41]. In the Kuibyshev Reservoir, the Ponto-Azov invader *Lithoglyphus naticoides* was first discovered in the mid-1990s. [54]. In aquatic and terrestrial ecosystems, there are frequent cases of invasion meltdown, when the naturalization of one or several species leads to the introduction of others [55, 56], which become members of the recipient system communities, together with their hosts or independently [57]. *Lithoglyphus naticoides* has brought at least three trematode species to the Volga River reservoirs: *Apophallus muehlingi* (Jagerskiold, 1889), *Apophallus donicus* (Skrjabin & Lindtrop, 1919) (syn.: *Rossikotrema donicum* Skrjabin & Lindtrop, 1919), and *Nicolla skrjabini* (Ivanitzky, 1928); this mollusk species serves as an obligate first intermediate host [58]. The formation of a new parasitic system “alien mollusk—*Apophallus muehlingi*—fish—fish-eating birds (possibly mammals, humans)” was a result of such invasion meltdown in the study area. The dominance of *Apophallus muehlingi* in the perch helminth fauna indicates successful naturalization, wide distribution, and rather high prevalence of trematodes in *Lithoglyphus naticoides* inhabiting the Usinsky Bay. The functioning of the system, where both alien species “*Lithoglyphus naticoides*—conjugate parasites” and *Perca fluviatilis* participate, varies in the water bodies of different types, characterized by different hydrological parameters, species composition, and ecology of aquatic organisms. In the lower reaches of the Volga, perch is infested with three parasite species associated with *Lithoglyphus naticoides* (*Apophallus muehlingi*, *Apophallus donicus*, *Nicolla skrjabini*) [58], in the Saratov reservoir, by *Apophallus muehlingi*, *Nicolla skrjabini* [6], in the Usinsky Bay, by *Apophallus muehlingi* only (original data).

The ichthyofauna of the Kuibyshev Reservoir includes eight invasive species, mainly of the Pontic-Caspian origin, including gobies of the family Gobiidae [14, 15]. Alien species of aquatic organisms are usually included in the diet of both native and invasive fish. An increase in the proportion of alien species (Mysidacea, gobies of the family Gobiidae, and *Clupeonella cultriventris* (Nordmann, 1840)) was noted in the ration of perch of the Kuibyshev Reservoir, regardless of the year of study [18]. Invasive fish may participate actively in the infestation of perch with helminths. Such a process is observed in the Saratov Reservoir, when *Perca fluviatilis* feeds on gobies Gobiidae [6]. The infection rate of *Neogobius melanostomus* with helminths, which are also found in *Perca fluviatilis*, is low: the prevalence of *Rhododocotyle campanula* is 1.85%, of *Camallanus lacustris*, 5.56%, and of *C. truncates*, 1.85% [44]. Therefore, the potential role of *Neogobius melanostomus* as the source of invasion for *Perca fluviatilis* is insignificant. The invasive trematode *Nicolla skrjabini* (Iwanitzky, 1928) dominates in helminth fauna of *Neogobius melanostomus* (the parasite prevalence is 72.22%).
“Passenger” pathway for this trematode would have led to significant infestation of perch feeding on *Neogobius melanostomus*. However, this parasite was not found in *Perca fluviatilis* in the Usinsky Bay. The similarity of the helminta fauna of the invader *Neogobius melanostomus* and *Perca fluviatilis*, caught at the same site, was quite low (Sørensen similarity index of 29%). The composition of parasites of these fish species differs due to specific parasites of *Neogobius melanostomus* and invasive parasite species.

*Apophallus donicus*, belonging to helminta, whose life cycle obligatory includes *Lithoglyphus naticoides*, has not been found in the perch of the Usinsky Bay, although this invading trematode tends to infect mainly Percidae [58]. The life cycle of *Nicolla skrjabini*, in addition to the intermediate host (*Lithoglyphus naticoides*), includes another additional hosts in the Volga River, *Pontogammarus crassus* (Sovinsky, 1904) and *Dikerogammarus haemobaphes* (Eichwald, 1841) [58]. In the Kuibyshev Reservoir, *Dikerogammarus haemobaphes* is widespread and is one of main components of the zoobenthos community [59]. These crustaceans have not been found in the Usinsky Bay [14, 60]. However, the high prevalence of the trematode *Nicolla skrjabini* in the alien fish *Neogobius melanostomus* and its absence in the native *Perca fluviatilis* in the same water area of the Usinsky Bay indicates the patchy (mosaic) distribution of representatives of Gammaridea (additional hosts of the trematode). There is also the ecological niche decoupling of the parasites transmitted through *Lithoglyphus naticoides*, since the trematodes have a different range of intermediate and definitive hosts (fish).

In 2019, significant fluctuations in the water level were noted in the Kuibyshev Reservoir. Low water level was main feature of this year (below the average by 2.5 m), even during the flood. The maximum water levels were recorded on April 22—23, 2019. The maximum discharge through the Zhigulevsky hydroelectric power plant occurred at the end of April—beginning of May (22,500—23,100 m³/s), which was lower than the average long-term maximum. The spillway dam was closed on May 14, which was almost a month earlier than the average long-term dates [16]. The Usinsky Bay is located in the zone of maximum backwater of the reservoir. Undoubtedly, high variability of the water regime of the reservoir influenced the functioning of the zooplankton and benthos communities. In turn, this affected the helminta fauna of European perch (table 1). Prevalence of most intestinal parasites in 2019 was much lower compared to 2020, even though the prevalence and abundance of parasites in larger fish should be slightly higher in 2020. When comparing perch helminths in 2019 and 2020, Sørensen similarity index was low (43%), which indicated specific ecological conditions of the habitat of aquatic organisms that served as the hosts of parasites in different years.

5. Conclusion

Primary original data have been obtained on the qualitative and quantitative composition of the helminta fauna of *Perca fluviatilis* in the Usinsky Bay. Interannual and biotope-related differences in the infestation of perch with helminta indicate a variety of habitat conditions for parasites and hosts (organisms of zooplankton, benthos, and fish) in the studied water body. Parasite prevalence in European perch is also preconditioned by the season of the year, the size of the fish, and the composition of the fodder base in the reservoir. *Perca fluviatilis* prefers to predate in benthic communities, despite both zooplankton and zoobenthos are quite diverse and abundant. The composition of the fauna of fish helminta indicates that stable systems "parasite-fish-predatory fish" and "parasite-fish-fish-eating birds" exist in the reservoir.

Human activity contributes to the penetration of invading aquatic organisms into the ecosystem of the Usinsky Bay and to an increase in the role of the parasites in regulating the structure of both parasite fauna and the fish community. The formation of new parasitic systems with the participation of both native and alien hosts and alien helminta is a result of this process. The functioning of the parasitic system “alien mollusk–alien parasites–fish–fish-eating birds / mammals, humans” differs significantly from other water bodies of the Volga-Kama reservoir cascade.

Currently, particular alien species of parasites (*Apophallus muehlingi*) dominate in the perch helminta fauna. This indicates the presence of favorable conditions in the reservoir for the
development of populations of all types of hosts, including alien ones. According to our observations, the Usinsky Bay is included in the system of water bodies that form the Volga River "invasion pathway", along which invader species disperse actively. The vector of distribution of alien species is directed from the Kuibyshev Reservoir to the tributaries. The invaders of the Ponto-Caspian complex predominate. The process of distribution of alien species in the bay is characterized by several peculiarities: (1) naturalization of invasive species occurs later than in the reservoir from which they penetrate into the bay and (2) there is an ecological niche decoupling in alien parasite species introduced by one obligate intermediate host.

Fish helminths with a complex developmental cycle are often used as biological markers for assessing the ecology of the hosts and changes in the biocenosis of the reservoir. The analysis of obtained dataset of parasite fauna makes it possible to predict further distribution and increase in the number of alien species of aquatic organisms, increasing their role in the structural and functional organization of the ecosystem of the Usinsky Bay and in the entire Kuibyshev Reservoir.

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Compliance with ethical standards
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