Transmission pathways of the helminths of the digestive system of the European perch *Perca fluviatilis* (Actinopterygii: Perciformes) in the fish communities of the water bodies of the national park "Samarkskaya Luka" (Russia)

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**Abstract.** Studied the dynamics of infection of the European perch *Perca fluviatilis* (Perciformes) by the helminths of the digestive system and their invasion of 13 native and 2 alien fish species in the water bodies of the National Park "Samarkskaya Luka". The similarity of the composition of the fauna of helminths of the digestive system of the European perch and other fish species has been analyzed for the period of 1990–2016. Peculiarities of the distribution of *Perca fluviatilis* parasites along the trophic chains of the fish community at different stages of ecosystem succession were revealed. Human activity promoted the penetration of alien species of aquatic organisms into the water bodies, their incorporation into the trophic chains and parasitic sub-systems "fish – helminths of the digestive system". The historically established trophic relations of carnivorous fish with *Perca fluviatilis* are nowadays weakened; usual food objects are replaced by the invasive fish species. Invasive species participate actively in the formation of trophic chains of the ecosystem; in some cases, it leads to an increase in the invasion rates of indigenous hosts by alien parasites.

1. **Introduction**

The study of the species composition of parasites, various aspects of their transmission in the aquatic ecosystems, and the characteristics of the functioning of parasitic systems are among the main directions in modern parasitology [1]. Important factors for parasite dispersal are the habitat itself, distance from the source of origin [2], and increasing anthropogenic impact on the habitat [3, 4]. Studies of the patterns of the parasite cycle in the ecosystem reveal the role of particular host species in helminth life cycles and the direction of invasion pathways [5, 6]. Helminths of the digestive system of fish are of significant interest as biological markers that reveal the characteristic features of the host ecology, the degree and direction of structural and functional changes in the ecosystem of the water body [7, 8]. When choosing helminths as bioindicators of ecological forms of the host fish, it is also necessary to understand clearly the possible ways of their infection. Underestimation of such information can lead to a distortion of research results and reduce their reliability [9].

The problem of searching for the reasons that precondition the composition of parasites in the host populations belongs to the urgent tasks of ecological parasitology [10]. Species richness in parasitic communities is facilitated by a lower degree of specificity, due to which the exchange of parasites...
among interrelated host species is possible [11, 12]. A non-uniform manifestation of the specificity of parasites preconditions the tendency to master a wider range of hosts and to develop adaptations to the new habitat conditions. Important factors determining the composition of parasites include the host species and the habitat conditions [2, 11, 13], as well as its feeding and behavior peculiarities [14, 15, 16].

The trophic chains are the gate for the fish infection by helminths of the digestive system. Similar food spectra of the parasite hosts preconditions similar composition of their helminths [17]. Interchange of parasites between phylogenetically close species is possible, the degree of similarity of parasitic communities of these species is governed by the characteristics of host biology and the degree of overlapping of their ecological niches [18, 2]. High abundance of the same potential intermediate hosts in the food spectra of ecologically similar species of final hosts is one of the key elements contributing to the similarity of helminth infra-communities in different hosts with overlapping ecological niches [19]. The feeding strategy of fish within a population varies, since not all the specimens use the same food objects. The trophic differentiation of the fish populations depends on the type of the water body [20] and on the variability of abundance and biomass of the benthic organisms [21]. The evolution of complex life cycles in helminths transmitted with food objects has its own characteristics pre conditioned by the change in both the habitat and the host [22]. Changes in the food webs of aquatic ecosystems, including those affected by anthropogenic impact, are becoming increasingly important as a factor determining the transmission of helminths in the ecosystem [23, 24]. Parasites can significantly affect trophic interactions, food chains, competition, biodiversity, and form a community structure [25]. An analysis of fish infection with helminths of the digestive system makes it possible to quantify the «parasite – host» relationships and to determine the food spectrum of fish [26].

The parasite fauna of fish changes during the ecological succession of the water body; the rate and nature of these changes depend mainly on the degree of the anthropogenic load [27, 3, 4]. This makes it possible to use fish helminths effectively as a test object for assessing the ecology of hosts and the state of a water body [7, 28, 29]. Such studies are especially relevant in connection with the increasing changes in the Saratov Reservoir ecosystem associated with the introduction of alien species of aquatic organisms [30]. Over the past two decades, the number of alien parasites in the Volga River Basin has tripled [31]. The increasing number of invasive species of parasites is due to an increase in the number of alien fish species and invertebrates, which are their intermediate hosts. The impact of invasive species on the ecosystems is expressed by the changes both of the habitat and of the structure of trophic links [32, 33].

European perch *Perca fluviatilis* Linnaeus, 1758 is a widespread Palearctic species, it is a typical representative of the ichthyofauna of the water bodies of the National Park «Samarskaya Luka». The species range in Russia includes the basins of the Arctic Ocean, the Baltic Sea, the Black Sea, and the Caspian Sea. In the waters of Australia, New Zealand, and other territories, it is an introduced species [34, 35]. Biological features of *Perca fluviatilis*, including its trophic links, have been studied in various water bodies [36, 37, 38]. It is a facultative predator, which food spectrum and diet depend mostly on the abundance and accessibility of certain food objects [39, 40]. The composition of the helminth fauna of *Perca fluviatilis* was studied in different types of water bodies of Eurasia [41, 42], including those outside the native range [43]. There was reported on a close relationship between the species composition of the helminths of *Perca fluviatilis* and the fish species richness of the water body [44]. Meantime, the works studying the helminth invasion pathways [20, 45] and their biocenotic relationships in the ecosystems [46, 42] are scarce. The study aims to analyze the pathways of distribution of the helminths of the digestive system of the European perch in the fish community of the National Park «Samarskaya Luka» in 1990–2016 taking into account the long-term data on the composition of helminths of the digestive system of *Perca fluviatilis* and other fish species, which allows reveal the nature and trends of changes in the parasitic and trophic relationships.

2. Materials and Methods
Material for the study was collected in the buffer zone of the Saratov Reservoir within the southwestern part of the National Park "Samarskaya Luka", Studeny Yerik passage, Lake Melkoe Gusinoe (located near the Mordovo village, 53.1000 N, 49.2700 E). The sampling has been performed through the entire year in 1996–1997, in January-February 2009, in May-September/October 2002, 2012–2016. All the listed water bodies form a joint system characterized by similar environmental conditions [47]. In 1996–1997, the fish were caught by fixed nets with 30-mm, 40-mm, and 50-mm mesh size and by a fishing rod; starting in 2002, the sampling was performed by a fishing rod and a spinning rod. Parasitological material was fixed and processed using generally accepted methods; fish length was measured from the end of the snout to the end of the scaly cover [48]. The method of incomplete parasitological autopsy has been applied for 1133 specimens of *Perca fluviatilis*. Archival parasitological data (1990–1992) were included into analysis, comprising the data on 1579 specimens of the European perch caught in the study area; the archival data were presented by the Institute of Ecology of the Volga River Basin of the Russian Academy of Sciences (table 1).

### Table 1. Number of the fish (ind.) studied in the water bodies of the National Park "Samarskaya Luka" (1990–2016).

| Fish species          | Study periods and number of fish studied ind. | Total number of fish, ind. |
|-----------------------|-----------------------------------------------|----------------------------|
|                       | 1990–1992  | 1996–2009  | 2012–2016 | Total number of fish, ind. |
| *Perca fluviatilis*   | 1579      | 827        | 306       | 2712                          |
| *Sander lucioperca*   | 0         | 31         | 95        | 126                           |
| *Sander volgensis*    | 0         | 6          | 69        | 75                            |
| *Esox lucius*         | 0         | 82         | 11        | 93                            |
| *Gymnocephalus cernua* | 0        | 49         | 53*       | 102                           |
| *Silurus glanis*      | 0         | 2          | 18        | 20                            |
| *Leuciscus idus*      | 0         | 26         | 8         | 34                            |
| *Leuciscus aspius*    | 0         | 0          | 4         | 4                             |
| *Lota lota*           | 0         | 0          | 6         | 6                             |
| *Abramis brama*       | 0         | 0          | 21        | 21                            |
| *Scardinius erythrophthalmus* | 0      | 0          | 9         | 9                             |
| *Squalius cephalus*   | 0         | 0          | 11        | 11                            |
| *Tinca tinca*         | 0         | 0          | 30        | 30                            |
| *Alburnus alburnus*   | 0         | 0          | 32        | 32                            |
| *Perccottus glenii*   | 0         | 57         | 77        | 134                           |
| *Clupeonella cultriventris* | 0 | 0         | 23        | 23                            |
| Total number of fish, ind. | 1579      | 1080       | 773       | 3432                          |

*primary data courtesy by O. Mineeva [49].

In order to determine the transmission pathways of helminths of the digestive system of the European perch in the Saratov Reservoir, an incomplete parasitological autopsy was performed at 3222 fish specimens belonging to 13 native fish species and 157 specimens of the two invasive fish species (table 1). We apply the term "parasites of the digestive system" here since the commonly used term "intestine/intestinal parasites" refers exclusively to those inhabiting the gastro-intestinal tract (mostly intestine). We have studied the parasite fauna of the entire digestive system that includes also the mouth, oral cavity, pharynx, esophagus, stomach, intestines, rectum, and adnexa, which play an important role in digestion (for example, pyloric appendages in the European perch).

Intravitral staining of parasites was performed in a weak solution of neutral red. Helminth species identification was carried out according to Scarlato [50], fish species, according to Reshetnikov [36]. The system of helminths is presented in accordance to the "Fauna Europaea" [51]. The fish taxonomy has been verified with the "FishBase" [52]. The parasite prevalence (%) was used as a characteristic of fish infection with helminths, which was the percentile representation of infected hosts divided by
hosts examined multiplied by 100 [53]. The similarity of the helminths composition was analyzed as follows: the total number of species of helminths of the European perch was set as 100%, and the share of this species list in the other fish species was calculated. Species richness of helminths and fish has been assessed by the Sørensen-Chekanovsky index. The data in the tables are presented as m ± SE (mean ± standard error) [54]. The dendrograms of the similarity of the composition of the helminth fauna based on the Sørensen-Chekanovsky index (at a significance level of 50%) were plotted using amalgamation (linkage) rule, single linkage, in Statistica 8.0. An ANOSIM test was performed using ‘vegan’ R package, R version 2.4-1, to check for significant difference between two or more groups of samples [55, 56].

3. Results

The species composition of helminths of the digestive system of the European perch Perca fluviatilis is represented by 19 taxa belonging to six higher taxonomic groups: six species of Cestoda (Proteocephalus perca (Muller, 1780), Triaenophorus nodulosus (Pallas, 1781), Bothriocephalus acheilognathi Yamaguti, 1934, Cestoda sp.), seven species of Trematoda (Bucephalus polymorphus von Baer, 1827, Rhipidocotyle campanula (Dujardin, 1845), Bunodera luciopercae (Muller, 1776), Nicolla skrjabini (Iwanitzky, 1928), Allocotylus transversae (Rudolphi, 1802), Sphaerostomum globiporum (Rudolphi, 1802), Trematoda sp.), five species of Nematoda (Camallanus lacustris (Zoega, 1776), Camallanus truncatus (Rudolphi, 1814), Raphidascaris acus (Bloch, 1779), Contracaecum microcephalum (Rudolphi, 1819), Nematoda sp.), and three species of Acanthocephala (Neoechinorhynchus rutili (Muller, 1778), Echinorhynchus cinctulus Porta, 1905, Acantocephalus lucii (Muller, 1776) (table 2). Sixteen taxa are identified down to the species level, except juveniles indicated as Cestoda sp., Trematoda sp., and Nematoda sp. Most of these parasites are widely specific and can be found in different fish species. The specific helminth fauna of Perca fluviatilis is represented by the cestode Triaenophorus nodulosus. According to literature data [57], Dichelyne minutus (Rudolphi, 1819) has been registered in the European perch in the study area in the early 1990s, but this parasite was not found in our samples. The cluster analysis of the species richness of helminths of the European perch allowed us to determine the main trends in the dynamics of "Perca fluviatilis – helminthes" system over the entire period of research (1990–2016) (figure 1).

Figure 1.

Dendrogram of the species similarity of the community of the helminths of Perca fluviatilis (1990-2016). The X-axis is the Euclidean distance, the Y-axis, the species composition of helminths of the European perch. Correlation coefficient r = 0.93.
The correlation between the test statistics R of intergroup similarity, calculated on the basis of the Sørensen-Chekanovsky index for parasite species of *Perca fluviatilis*, was 0.78 (p < 0.001).

Seven typical parasite species of the European perch were the most common species, comprising cestodes *Triaenophorus nodulosus*, *Proteocephalus perca*, trematode *Bunodera luciopercae*, nematodes *Camallanus lacustris*, *C. truncatus*, *Raphidascaris acus*, and thorny-headed worm *Acanthocephalus lucii*. These parasites were recorded in *Perca fluviatilis* during the entire study period. The changes in helminth fauna were due to the absence of species recorded in 1990–1992 only (*Echinorhynchus cinctulus*, *Dichelyne minutus*) and with appearance of a group of trematodes registered in 1996–2009 (*Bucephalus polymorphus*, *Allocreadium transversale*, *Sphaerostomum globiporum*). In addition, new native species of parasites have been registered for the period of 1996–2016 (*Rhipidocotyle campanula*, *Neoechinorhynchus rutili*).

Finally, the formation of the modern composition of helminths in 2012–2016 was due to the appearance of the native nematode *Contracaecum microcephalum*, the alien trematode *Nicolla skrjabini*, and the cestode *Bothriocephalus acheilognathi*. The Sørensen-Chekanovsky index of the species composition of helminths of the digestive system of the European perch was significantly high (> 70%, p < 0.001). (table 2).

**Table 2.** Sørensen-Chekanovsky index (%) of the species composition of helminths of digestive system of the European perch *Perca fluviatilis* in the water bodies of the National Park "Samarskaya Luka" in 1990–2016.

| Years          | 1990–1992 | 1996–2009 | 2012–2016 |
|---------------|-----------|-----------|-----------|
| 1990–1992     | 100       | 79        | 83        |
| 1996–2009     | 75        | 100       | 75        |
| 2012–2016     | 83        | 79        | 100       |

The dynamics of infection of *Perca fluviatilis* by parasites was analyzed for the period of 1990–2016. Three different species lists of helminths of the digestive system have been registered, which differed significantly both qualitatively and quantitatively (table 3).

In 1990–1992, nine parasite species have been registered in the European perch, in 1996–2009 and 2012–2016, there were twelve species, but their composition and infection rates were different. Seven parasite species were constantly recorded ones (figure 1) until nowadays (2012–2016). However, the prevalence of some varied greatly or has significantly decreased (table 3). Infection by the nematode *Camallanus truncatus* steadily decreased during the period of 1992–2016. The cestode *Triaenophorus nodulosus* was not registered after 2013. For these species, there was a tendency to disappear from the helminth fauna of *Perca fluviatilis*. The cestode *Bothriocephalus acheilognathi* was recorded only within the present study in 2013. The trematode *Nicolla skrjabini* has been registered in the European perch for the first time in 2012 with the prevalence of 4.17%, by 2016, the last parameter has increased by 2.8 times.

Trends in the parasite species composition and helminth prevalence in *Perca fluviatilis* have been observed (table 3). Since the 1990s, steadily high infection rate was a characteristic of trematode *Bunodera luciopercae* and cestode *Proteocephalus percae*; the prevalence of the nematode *Camallanus lacustris* has increased by 3.7 times. In some species recorded in 1990–1992, a decrease in their prevalence was subsequently noted, or even their disappearing from the parasite fauna at all. A constant decrease in the infection rate of *Perca fluviatilis* by the nematode *Camallanus truncatus* (dominant species in 1990) was observed; in 2013, this parasite was not registered; currently, it belongs to endangered species. The period of 2012–2016 was characterized by the largest scale of changes in the species composition and infection of *Perca fluviatilis* by helminths, the appearance of new native and alien species. The prevalence of certain parasite species recorded in 2012 and later on is increasing by now (for example, by 3.9 times in *Nicolla skrjabini*).
Table 3. Species composition and average annual prevalence (Pmean, %) of helminths of the digestive system of *Perca fluviatilis* in different study periods in the water bodies of the National Park "Samarskaya Luka".

| Species of helminths | 1990–1992 Pmean (%) | 1996–2009 Pmean (%) | 2012–2016 Pmean (%) |
|----------------------|----------------------|----------------------|----------------------|
| *B. lucioperca*       | 53.51 ± 2.33         | *C. lacustris* 60.01 ± 4.62 | *C. lacustris* 56.10 ± 2.84 |
| *C. truncatus*        | 44.97 ± 2.08         | *B. lucioperca* 39.51 ± 4.35 | *B. lucioperca* 42.18 ± 2.83 |
| *A. lucii*            | 36.87 ± 2.25         | *C. truncatus* 25.75 ± 3.65 | *C. microcephalum* 33.01 ± 2.69 |
| *C. lacustris*        | 15.27 ± 1.58         | *A. lucii* 23.75 ± 3.67 | *P. perca* 13.68 ± 1.97 |
| *P. perca*            | 14.47 ± 1.63         | *P. perca* 8.90 ± 2.54 | *A. lucii* 12.71 ± 1.91 |
| *T. nodulosus*        | 7.71 ± 1.26          | *T. nodulosus* 3.28 ± 0.97 | *Nicolla skrjabini* 5.27 ± 1.28 |
| *D. minutus*          | 5.90 ± 0.10          | *R. campanula* 4.35 ± 1.10 | *C. truncatus* 4.98 ± 1.25 |
| *R. acus*             | 0.33 ± 0.21          | *R. acus* 0.91 ± 0.56 | *R. acus* 4.80 ± 1.22 |
| *E. cinctulus*        | 0.23 ± 0.23          | *A. transversale* 0.65 ± 0.34 | *R. campanula* 3.73 ± 1.09 |
| *N. rutili*           | 0.43 ± 0.21          | *T. nodulosus* 0.42 ± 0.37 | *N. rutili* 0.21 ± 0.26 |
| *B. polymorphus*      | 0.35 ± 0.02          | *S. globiporum* 0.11 ± 0.11 | *B. acheilognathi* 0.21 ± 0.26 |

Only the taxa identified down to the species level are presented; the species are arranged in order of decreasing Pmean values; *a* infection rate by *D. minutus* is given according to literature data [57]; *b* parasite species absent in the European perch or decreasing their abundance; *c* alien parasite species.

Subsequently, a decrease in the prevalence or even a loss of some helminths species found in the 1990s has been recorded; a constant decrease in the infection rates of *Perca fluviatilis* has been noted for *C. truncatus*, which was the dominant species in 1990s. This parasite was not observed in the European perch in 2013, it has been considered nowadays an endangered species.

A three-step change of the dominant species of helminths of the digestive system of the European perch has been observed: *Camallanus truncatus* (1990) → *Bunodera lucioperca* (1991–1992) → *Camallanus lacustris* (1996–2016). Dominating of *C. lacustris* nematode for the period of 1996–2016 was ensured by two factors: wide distribution of intermediate hosts (planktonic crustaceans) and constant presence of alien goby species (family Gobiidae) infested with this parasite [47]. Among these alien goby species, *Ponticola gorlap* (Iljin, 1949) was the most infected (prevalence of 8.98%) with *C. lacustris* [58]; therefore, it played a significant role in the European perch invasion since the last fish species fed on the first one. *Ponticola gorlap* was infected also with the parasites of the European perch, *Bunodera lucioperca* (prevalence of 0.73%), *Rhipidocotyle campanula* (0.73%), *Camallanus truncatus* (2.92%), and *Acanthocephalus lucii* (4.71%); *Neogobius melanostomus* (Pallas, 1814), by *C. lacustris* (0.94%) [59, 58, 60]. However, feeding of *Perca fluviatilis* on these invaders does not yet contribute much to the increase of the infection of the European perch due to the low degree of invasion of these alien fish species. High rates of infection (prevalence of 19.05–62.04%) of the European perch by the native nematode *Contraecacum microcephalum* were also supported, in particular, by feeding on these goby species [58]. The life cycle of the alien parasite *Nicolla skrjabini* also takes place with the participation of an invasive mollusk species *Lithoglyphus naticoides* (Pfeiffer, 1828), which plays the role of an intermediate host [61]. The crustaceans of Gammaridae family serve as an additional host, and the fish, as definitive host. In the Saratov Reservoir, the trematode prevalence in *Ponticola gorlap* is 86.3%, in *Neogobius melanostomus*, 60.0% [60]. Infections of *Perca fluviatilis* by trematode are predicted to increase, since the infection may occur through two pathways: when consuming benthic invertebrates and/or invasive species of Gobiidae family.
The infection of 13 indigenous fish species by the helminths of the digestive system of *Perca fluviatilis* was studied for *Esox lucius* Linnaeus, 1758; *Sander lucioperca* (Linnaeus, 1758); *Sander volgensis* (Gmelin, 1789); *Gymnocephalus cernua* (Linnaeus, 1758); *Silurus glanis* Linnaeus, 1758; *Lota lota* (Linnaeus, 1758), *Leuciscus aspius* (Linnaeus, 1758); *Abramis brama* (Linnaeus, 1758); *Scardinius erythrophthalmus* (Linnaeus, 1758); *Leuciscus idus* (Linnaeus, 1758); *Squalius cephalus* (Linnaeus, 1758); *Tinca tinca* (Linnaeus, 1758); *Alburnus alburnus* (Linnaeus, 1758), as well as of two invasive fish species: *Clupeonella cultriventris* (Nordmann, 1840) and *Perccottus glenii* Dybowskii, 1877.

A cluster analysis of the degree of similarity in the species composition of helminths of the digestive system of *Perca fluviatilis* and 15 fish species in the water bodies of the National Park "Samarskaya Luka" was carried out for the entire study period (figure 2). The correlation between test statistics R of intergroup similarity, calculated on the basis of the Sørensen-Chekanovsky index, was 0.62 (p < 0.0001).

Generally, the Sørensen-Chekanovsky index of the species composition of helminths of the digestive system of *Perca fluviatilis* and other fish species was high in different time periods and exceeded 58.5%. Minimal similarity was observed for *Clupeonella cultriventris* (12.1%) due to the minimal diversity of the parasite fauna of this alien species. A high similarity exceeding 80.6% was noted for *Perca fluviatilis* and predator species *Esox lucius* and *Sander lucioperca*, for which the European perch was an important component of their food spectra.

![Tree Diagram for 16 Variables](image)

**Figure 2.**
Dendrogram of the species similarity of the community of the helminths of the digestive system of *Perca fluviatilis* and other fish species (1990-2016). The X-axis is the Euclidean distance, the Y-axis, the fish species. Correlation coefficient $r = 0.85$.

The greatest similarity of the fauna of helminths of the digestive system was observed in *Perca fluviatilis* and the predator *Esox lucius*, as well as other representatives of Percidae family, predators *Sander lucioperca* and *S. volgensis* and bottom-feeder *Gymnocephalus cernua*. The number of parasite species that are common for *Perca fluviatilis* and other predatory fish (*Silurus glanis* and *Lota lota*) is much lower. Even a greater difference in the species composition of parasites was noted between *Perca fluviatilis* and the species of Cyprinidae family. The lowest similarity was observed for the invasive species *Clupeonella cultriventris* and *Perccottus glenii* (table 4).
Table 4. Share of the common helminth species (%) of the digestive system in *Perca fluviatilis* and other fish species in the water bodies of the National Park "Samarskaya Luka" in different periods (1990–2016).

| Fish species               | Years/Similarity of parasite species list (%) | 1990–1992 | 1996–2009 | 2012–2016 |
|----------------------------|-----------------------------------------------|-----------|-----------|-----------|
| Sander lucioperca          | 44.51                                         | 41.71     | 66.75     |           |
| S. volgensis               | 55.62                                         | 8.35      | 33.30     |           |
| Esox lucius                | 44.54                                         | 50.01     | 16.79     |           |
| Gymnocephalus cernua      | 66.73                                         | 50.01     | 58.38     |           |
| Silurus glanis            | 33.34                                         | 8.30      | 50.02     |           |
| Leuciscus idus            | 33.37                                         | 50.01     | 25.07     |           |
| Leuciscus aspius          | 22.29                                         | –         | 8.36      |           |
| Lota lota                 | 77.87                                         | 8.37      | 33.36     |           |
| Abramis brama             | 22.29                                         | –         | 0         |           |
| Scardinius erythrophthalmus| 22.27                                         | –         | 8.35      |           |
| Squalius cephalus         | 22.26                                         | –         | 8.33      |           |
| Tinca tinca               | 11.16                                         | –         | 8.37      |           |
| Alburnus alburnus         | 22.28                                         | –         | 8.334     |           |
| Percottus glenii          | –                                             | 8.36      | 16.74     |           |
| Clupeonella cultriventris | 0                                             | –         | 12.31     |           |

In 1990–1992, the composition of the helminths of the digestive system of predators *Lota lota*, *Esox lucius*, *Sander lucioperca*, *S. volgensis* was similar to that of *Perca fluviatilis* by 44.51–77.87%; between *Perca fluviatilis* and the bottom-feeder *Gymnocephalus cernua* it was also significant (66.73%). A similarity of up to 33.30% was noted for the fauna of helminths of the digestive system of *Perca fluviatilis* and a group of the fish species differing in the food spectra: predators *Silurus glanis* and *Leuciscus aspius*; planktivorous *Alburnus alburnus*; and the species that include juvenile fish in their diet, namely *Leuciscus idus*, *Abramis brama*, and *Squalius cephalus*. The community of helminths of the digestive system in *Perca fluviatilis* and the bottom-feeder *Tinca tinca* was as low as 11.16%. No similarity in the composition of helminths of the digestive system was found in *Perca fluviatilis* and the invading planktivorous species *Clupeonella cultriventris*.

In 1996–2009, the 50.01% similarity of the fauna of helminths of the digestive system was noted for *Perca fluviatilis* and *Esox lucius*, *Gymnocephalus cernua*, and *Leuciscus idus*. More than 40.0% of parasite species found in the European perch have been reported for *Sander lucioperca*. In *S. volgensis*, *Silurus glanis*, and *Lota lota*, the proportion of parasites common with *Perca fluviatilis* decreased by 4–9 times. In the other fish species, there were no parasites found that were common with the European perch, with the only exception of *Percottus glenii* infected with the trematode *Rhipidocotyle campanula*. The localization of immature parasites in the lower intestine indicated that this invader played the role of an eliminator in the life cycle of this trematode species.

In 2012–2016, the maximum similarity of the composition of helminths of the digestive system has been found in *Perca fluviatilis* and the representatives of Percidae family, namely, *Sander lucioperca* (66.75%), *Gymnocephalus cernua* (58.38%), as well as to *Silurus glanis* (50.02%). The species number of helminths of the digestive system common for *Perca fluviatilis* and *Esox lucius* decreased by 3 times compared with the period of 1996–2009. There was also a similarity of the fauna of helminths of the digestive system in *Perca fluviatilis* and the alien species *Clupeonella cultriventris*, when *Camallanus truncatus* (prevalence of 8.70%) has been found in both fish species. Common parasites for *Perca fluviatilis* and *Percottus glenii* were the native trematode *Rhipidocotyle campanula* and the alien cestode *Bothriocephalus acheilognathi*. Compared to the period of 1990–1992, the share of helminths of the digestive system of *Perca fluviatilis* in other predators, *Lota lota*...
and \textit{Leuciscus aspius}, decreased by 2.3–2.7 times, in other cyprinids, by 1.3–2.3 times. There were no common species of helminths found in \textit{Perca fluviatilis} and \textit{Abramis brama}.

4. Discussion

Helminths of the digestive system of fish use their trophic relationships as the pathways of invasion. Studies on the ecology of the fish feeding in the basin of the Saratov Reservoir are scarce. Literature data refer only to certain aspects, for example, to the trophic relationships of some invasive fish species [62, 63]. The available data on the relationships of planktonic crustaceans with helminths of the digestive system of \textit{Perca fluviatilis} make it possible to assess the degree of participation of zooplankton in the trophic links of the European perch and some other fish species [47]. The trophic relationships in the fish communities were studied in detail in 1972–1980 [64]. Currently, trophic relations in the fish community and their grazing/predatory press in the water bodies of National Park «Samarskaya Luka» remain poorly understood. When comparing the results of the original parasitological studies with the literature data on the fish feeding of the Saratov Reservoir, it became clear that there were changes in the trophic relationships during the period of 1972–2016. According to literature data [64], in 1972–1980, the largest similarity of the food spectra among predatory fish was found for the pairs \textit{Esox lucius} ↔ \textit{Sander lucioperca} and \textit{Silurus glanis}, \textit{S. volgensis} ↔ \textit{Lota lota}, and \textit{Perca fluviatilis} ↔ \textit{S. glanis}. However, there was almost no competition for food due to the divergence of the ecological niches in habitats, the size of the consumed food objects, and the timing of intensive feeding. Growth period of active predators (\textit{Esox lucius}, \textit{S. lucioperca}, \textit{L. lota}, \textit{S. glanis}, and \textit{L. aspius}) occurred mainly due to the fish species of low commercial value, such as \textit{Perca fluviatilis}, \textit{Gymnocephalus cernua}, \textit{Alburnus alburnus}, \textit{Rutilus rutilus} (Linnaeus, 1758), \textit{Clupeonella cultriventris}, and the gobies of Gobiidae family. The share of alien species in the ration of \textit{Perca fluviatilis} exceeded significantly this parameter in \textit{Esox lucius} and \textit{S. lucioperca}. That is why the helminths of the digestive system of \textit{Perca fluviatilis} can serve as the valid biological markers that make it possible to assess the degree and nature of changes in the trophic relationships of carnivorous fish, which are caused, in particular, by the colonization process of alien species. The results of our study (Fig. 2) evidence that general features of trophic relationships between predator and non-predator fish in the studied ecosystem in 1990–2009 were consistent with the published data [64, 57]. Analysis of the dynamics of the similarity / differences in the composition of helminths of the digestive system of \textit{Perca fluviatilis} and other fish species (Table 4) testify for the recent structural rearrangements of trophic links in the fish community of the reservoir in 2012–2016.

The most significant changes have been observed for the trophic relationship of \textit{Esox lucius} ↔ \textit{Perca fluviatilis}. The similarity of the composition of the helminths of the digestive system of these species was about 50% in 1990–2009, in 2012–2016, it has decreased by almost three times (Table 4). Regard must be paid to the significant similarity of food and biotope spectra of \textit{Esox lucius} and \textit{Perca fluviatilis} in 1972–1980, when the European perch was also one of the main components of pike food spectrum [64]. The helminths species composition and their prevalence in the digestive system of \textit{Esox lucius} in 1990–2009 was largely due to its active feeding on \textit{Perca fluviatilis} and the fish of Cyprinidae family. A significant proportion of the European perch in the diet of \textit{Esox lucius} during this period is indicated by infection with the specific cestode \textit{Triaenophorus nodulosus} (prevalence of 34.4%). \textit{Gymnocephalus cernua} was an additional pathway for the infection of \textit{Esox lucius} with this parasite (18.6%), since the specimens of \textit{G. cernua} were repeatedly registered in the stomach of this predator in our study. In the life cycle of this parasite, \textit{Perca fluviatilis} plays the role of an obligate additional (intermediate II) host, and \textit{Esox lucius} is an obligate definitive host. The infection of the pike by \textit{Proteocephalus percae}, \textit{Camallanus lacustris}, \textit{C. truncatus}, \textit{Acanthocephalus lucii}, and, possibly, \textit{Dichelyne minutus} indicates regular feeding on \textit{Perca fluviatilis} during these years. The infection of \textit{Esox lucius} by the nematode \textit{C. lacustris} (2.5%) could also occur when it feeds on \textit{Scardinius erythrophthalmus} [57]. The finding of the nematode \textit{Raphidascaris acus} in \textit{Esox lucius} indicates the feeding of this species on the European perch and Cyprinidae fish (\textit{Rutilus rutilus}, \textit{Abramis brama}, \textit{Leuciscus idus}, \textit{Squalius cephalus}, \textit{Tinea tinca}, and \textit{Alburnus alburnus}). The pike is
infected by *Rhipidocotyle campanula* when it consumes *Perca fluviatilis, Abramis brama,* and *Squalius cephalus* [57]. The trematode *Bucephalus polymorphus* did not infect much *Esox lucius* due to the low degree of invasion in the European perch (prevalence of 0.35%). The infection occurred mainly during the feeding of this predator by the fish of Cyprinidae family. The absence of trematode *Bunodera luciopercae* in *Esox lucius* indicates that the parasite does not take root in this host. This is confirmed by the data obtained from other water bodies [65].

The dynamics of the composition of *Esox lucius* parasites reflected two steps of the change in the dominant species in the fauna of helminths of the digestive system of *Perca fluviatilis: Camallanus truncatus* (1990) → *C. lacustris* (1996–2016). The nematode *C. truncatus* was recorded in *Esox lucius* in 1990–1992 (prevalence 12.5%), *C. lacustris*, in 1996–2009 (28.0%). The dominance of the trematode *Bunodera luciopercae* in 1991–1992 in the fauna of helminths of the digestive system of *Perca fluviatilis* was not reflected in the composition of the parasites of *Esox lucius*, since the predator played the role of the eliminator of the parasite.

In 2012–2016, *Raphidascaris acus* and *Acanthocephalus lucii* were the helminths of the digestive system of the European perch that were still found in *Esox lucius*. Moreover, according to our data, the infection by *R. acus* was mainly associated with the feeding of this predator on *Scardinius erythrophthalmus* and *Leuciscus idus*. Infection can also occur when feeding on *Rutilus rutilus* [57]. After 2009, the specific cestode *Triaenophorus nodulosus* was not observed in the fauna of helminths of the digestive system of *Esox lucius*. It was replaced by the cestode *Triaenophorus crassus* Forel, 1868 (prevalence of 73.3%) a parasite of gobies. In the study area, in 2009–2015, the prevalence of this parasite in *Ponticola gorlap* (Iljin, 1949), *Neogobius melanostomus* (Pallas, 1814), and *Proterorhinus marmoratus* (Pallas, 1814) ranged as 13.8–50.0% [66]. The replacement of *Triaenophorus nodulosus* by *T. crassus* fits well with the data on a sharp decrease in the infection of the European perch by *T. nodulosus* by 2009 [47]. After 2013, this parasite is nearly extinct in the fauna of helminths of *Perca fluviatilis*. Thus, the disappearance of *T. nodulosus* from the helminth fauna of the obligate definitive host, *Esox lucius*, led to the loss of this species in the additional host, *Perca fluviatilis*. In 2012–2016, the nematode *Camallanus lacustris*, a dominant species in the fauna of helminths of the digestive system of the European perch, has also disappeared from the helminths fauna of *Esox lucius*. Also, the similarity of the composition of the helminths of the digestive system of *Esox lucius* and *Perca fluviatilis* has decreased by 3 times. This indicates a significant weakening of the trophic links of this predator with *Perca fluviatilis*. Currently, there has been a change in the food spectrum of *Esox lucius*. In the 1980s-1990s, *Perca fluviatilis* and *Rutilus rutilus* formed the basis of the predator's diet [64, 57]. According to our observations, the share of *Perca fluviatilis* in the ration of *Esox lucius* has decreased significantly in 2012–2016, its diet is mainly represented currently by *Rutilus rutilus* and invasive goby species of Gobiidae family.

There were also changes in the relationships *Perca fluviatilis* ↔ helminths of the digestive system ↔ other fish species due to the structural rearrangements of the trophic chains and the similarity / divergence of the fish habitats. In 1990-1992, all the studied species (with the exception of *Clupeonella cultriventris*) participated in the life cycles of helminths of the digestive system of *Perca fluviatilis*. The degree of such participation and the role in the infection spreading are different in certain fish species. Infection of predatory fish with parasites occurred during the feeding by *Perca fluviatilis* and non-predatory Cyprinidae family. The similarity of the fauna of helminths of the digestive system of *Perca fluviatilis* and the fish Cyprinidae family in 1990–2009 was based on a certain similarity of the composition of aquatic invertebrates in their food spectra. Parasitological data indicate a maximum discrepancy in the composition of helminths of the digestive system of *Perca fluviatilis* and cyprinids in 2012–2016 in comparison with 1990–1992. This is due to differences in fish food spectra and thus indicates indirectly the tendency to move to benthic biotopes for *Perca fluviatilis*. A significant similarity of the composition of the parasites of *Perca fluviatilis* and *Gymnocephalus cernua* also indicates that the European perch prefers to live close to benthic communities in the studied water bodies, since the similarity of the nature of changes in the composition of the helminth fauna of these two species was noted. These changes include the
disappearance of the cestode *Triaenophorus nodulosus* and the appearance of the nematode *Contracaecum microcephalum*. In addition, the replacement of *Camallanus truncatus* by *C. lacustris* was noted in *Gymnocephalus cernua*. In *Perca fluviatilis*, the prevalence of *Camallanus truncatus* was reduced down to 1.45%, this parameter of *C. lacustris* has increased and exceeded 50%. The current tendency to inhabit benthic biotopes by the European perch is also indicated by its infection by *Nicolla skrjabini*. Earlier, this parasite was discovered by A. Buryakina [57] in a typical benthos-feeder *Gymnocephalus cernua*. The European perch is another species, in which this trematode is registered. Since the invasion occurs when feeding on benthic crustaceans of Gammaridae family, the increase in the infection of *Perca fluviatilis* with this trematode evidences on its feeding in benthic biotopes and thus preferring these habitats.

The decrease in the similarity of the helminth fauna of *Perca fluviatilis* and *Esox lucius, Sander volgensis, Lota lota, Leuciscus aspius* in 2012–2016 is due to a decrease in the share of the European perch in the diet of some predatory fish against a background of more active feeding by the invasive goby species. The species composition and characteristics of infection with the specific helminths of the digestive system evidence that Lota lota and Silurus glanis either retained or increased the proportion of *Perca fluviatilis* in their diet.

The infection of fish by *Dichelyne minutus* is the issue of particular interest. This nematode was noted by A. Buryakina [57] in the 1990s in *Perca fluviatilis, Esox lucius, Sander volgensis*, and *Lota lota*. Apparently, the infection of predatory fish occurs during the feeding on the invasive goby species, which are the main hosts of this parasite [67]. Later, this nematode species was absent in the sixteen fish species in the same study area. The life cycle of *Dichelyne minutus* includes polychaeta and fish. It is characterized by a short infection period, low survival rate of nematode larvae, and the death of mature nematodes immediately after spawling in autumn [68]. In addition, polychaeta are not widespread in the buffer zone of the Saratov Reservoir. Their share in the total biomass of the soft-bodied benthos was about 13% in 2009-2011 [69]. Apparently, the deterioration of the conditions for the implementation of its life cycle is a possible reason for the disappearance of this nematode after the 1990s.

Active consumption of the invasive fish species by the predators of the upper levels of the trophic chains led to a redistribution of invasion pathways. For example, in the early 1990s, the nematode *Camallanus truncatus* has been met in five fish species: *Perca fluviatilis, Esox lucius, Sander lucioperca, S. volgensis*, and *Gymnocephalus cernua*. In 2012–2016, most of the infection flux of *C. truncatus* was distributed mainly in the populations of *Sander lucioperca, S. volgensis*, and *Perca fluviatilis*. Moreover, the European perch plays nowadays a small role in the distribution of *C. truncatus* due to low parasite prevalence. Since the 1970s and until now, the growth period of *Sander lucioperca* in the buffer zone of the Saratov Reservoir is characterized by feeding mainly on *Clupeonella cultriventris* [64]. Therefore, infection of this invader by *C. truncatus* (prevalence of 8.7% in 2012) led to the accumulation of this parasite mainly in the populations of *Sander lucioperca* and closely related *S. volgensis* in 2012–2016. The infection of fish by the nematode *Camallanus lacustris* is another example of a change in parasitic fluxes in the studied water bodies. Since 1996, *Ponticola gorlap* has played a significant role in the spreading of this parasite in the studied water bodies of the National Park «Samarskaya Luka» and in the buffer zone of the Saratov Reservoir. Since 2012, invasive goby species have also contributed to the abundance of the nematode *Contracaecum microcephalum* in addition to native fish.

Invasive fish species participate actively also in the transmission of indigenous parasites. By 2012–2016, the goby has served as reservoir / final hosts for five species of helminths of the digestive system of the European perch, namely, *Camallanus lacustris, C. truncatus, Bunodera luciopercae, Acanthocephalus lucii, and Contracaecum microcephalum*. The infection of *Clupeonella cultriventris* by the nematode *C. truncatus* maintains the parasite abundance in the population of this fish species in the ecosystem. *Percottus glenii* is an eliminator in the life cycle of *Rhipidocotyle campanula*.

Alien species of aquatic organisms have become a channel of infection of indigenous fish species by invasive species of parasites. The invasive trematode *Nicolla skrjabini* was widely distributed in
the buffer zone of the Saratov Reservoir due to the resettlement of the first intermediate host, the alien mollusk *Lithoglyphus naticoides* [70]. This led to an expansion of the list of the hosts and to an increase in infection of fish by this parasite in the studied water bodies. In the early 1990s, *Nicolla skrjabini* was found in *Gymnocephalus cernua* [57], which has tight trophic links with benthic invertebrates. In 2012, a trematode was first noted in *Perca fluviatilis* (original data). Since 2009, *Silurus glanis* and *Sander lucioperca* were also infected by *Nicolla skrjabini*; a high prevalence of this parasite was observed in the invasive goby species *Neogobius melanostomus* (prevalence of 48.65–87.34%) and *Ponticola gorlap* (73.33–100.0%) [71, 72]. In 2012–2016, in the study area, the lists of the hosts of *Nicolla skrjabini* expanded significantly. It included four species of Percidae family (*Perca fluviatilis*, *Sander lucioperca*, *S. volgensis*, *Gymnocephalus cernua*), three species of Cyprinidae family (*Leuciscus idus*, *Squalius cephalus*, *Alburnus alburnus*), and one species of Siluridae family (*Silurus glanis*). The prevalence of this parasite in *Sander lucioperca* varies greatly [73], since the parasitic subsystem «*Sander lucioperca – Nicolla skrjabini*» is not stable enough due to the new link establishing. *Nicolla skrjabini* expands its distribution in the reservoir rapidly due to forming of tight biotopic links between the fish and the invasive mollusk *Lithoglyphus naticoides*, whose number in the buffer zone of the reservoir currently increases [74]. This situation indicates the active feeding of fish of Cyprinidae family on benthic invertebrates (Gammaridae), and carnivorous fish, on the gobies. The high parasite prevalence (53.14%) of the alien trematode *Nicolla skrjabini* in the typical planktivorous species *Alburnus alburnus* indicates a significant proportion of benthic invertebrates in its diet. The almost complete absence of parasites reflecting feeding on zooplankton indicates a change in the type of feeding of *Alburnus alburnus* to benthic invertebrates. *A. alburnus* switched from feeding on plankton to benthos in the early 1990s [57]. Currently, only infection by the nematode *Contracaecum microcephalum* indicates the consumption of planktonic organisms by *Alburnus alburnus*.

Such a change in the type of feeding in planktivorous fish indicates a lack of zooplankton stock and production in the water bodies of the National Park «Samarskaya Luka», including the buffer zone of the Saratov Reservoir. In 1972-1980, fish consumed insignificant part of mollusk production (2.8–9.4%) [64]. Small-sized non-commercial fish were quite abundant. The production of soft-bodied benthic organisms was used in full (40–90%), the production of zooplankton, much less (16–40%). The stock of fodder planktonic organisms was absent due to their low abundance. According to our data, during 1990–2016, the proportion of helminths of the digestive system of *Perca fluviatilis* associated with zooplankton decreased from 78% down to 50–67% [47]. It also indicates indirectly on the increase in the tension of trophic links between fish and zooplankton. This situation develops against the background of an increase in the total abundance and biomass of benthos in the buffer zone of the Saratov Reservoir due to the development of the alien mollusk *Lithoglyphus naticoides* [75].

Infection of fish by the helminths of the digestive system of *Perca fluviatilis* can occur in two ways depending on the type of feeding. Non-predatory fish and juvenile predators are infected via consuming aquatic invertebrates, which are the intermediate hosts of parasites. Infection of predators and euryphagous fish (facultative predators) occurs when feeding on non-predatory fish and on *Perca fluviatilis*.

There is an elongation of trophic chains of fish due to the inclusion of invasive fish species, which leads to a complication of the life cycles of particular indigenous species of helminths of the digestive system. This gives a definite advantage when parasites reach their final host and end their life cycle in changing environmental conditions. Three possible options for the implementation of the life cycles of individual indigenous / alien helminths with the participation of alien fish species were observed. The first way is the inclusion of new facultative reservoir / additional hosts (invasive fish species) after the intermediate host (aquatic invertebrates) and the transmission of the parasite to the final host (predatory fish) by eating. The second way is possible, when the life cycle of the parasite may complete up to the end in the same invasive host species (for example, the gobies of Gobiidae family), which increases the parasite chances to participate in the reproduction process. The third way is the
elimination of native parasites by invasive fish species playing the role of an abortive host (for example, *Percottus glenii – R. campanula*).

5. Conclusion

Three periods, 1990–1992, 1996–2009, and 2012–2016, defined within the present study, corresponded to the stages of ecosystem succession, when the fauna of helminths of the digestive system of fish significantly differed both in quantitative and qualitative composition. Significant similarity of the helminth composition of *Perca fluviatilis* and other fish species in 1990–2009 was due to the high ecological plasticity of the European perch in regard to the preferred habitats and food objects, as well as to the wide specificity of most of its parasites. Significant changes in the common fauna of helminths of the digestive system of *Perca fluviatilis* and other fish observed in 2012–2016 testified for tight interconnection of trophic and parasitic links, supported by a reliable data on the involvement of certain alien species (fish, mollusks) in them. Some alien species of parasites have occupied a significant position in the helminth fauna of some key fish species. This indicates an increase in the share of invasive fish in the diet of carnivorous fish, and the spreading of both indigenous and alien intermediate hosts of parasites in the studied water bodies. Predatory fish have also switched to consume invasive fish species instead of *Perca fluviatilis*.

There is an active process of formation of new parasitic systems, where both native and alien fish and helminth species participate. The habitat conditions for both parasites and hosts in the water bodies are affected by anthropogenic impact, in some cases, it leads to the expansion of the number of the host alien species of fish parasites and to the replacement of indigenous species (parasites and fish) by alien species in the trophic chains. Finally, redistribution of parasitic flows occurs.

The use of helminths of the digestive system of fish occupying the upper level of trophic chains as biological markers allows one to determine the presence of structural rearrangements of the trophic chains of the reservoir ecosystem. Thus, in the 1980s, invasive fish species, namely, gobies of Gobiidae family and *Clupeonella cultriventris*, occupied a great place in the diet of carnivorous fish, but this had little effect on the composition of fish helminths. Significant changes in the fauna of fish parasites observed currently are due to an increase in the number of new species of hydrobionts (fish, parasites, mollusks) and their wider distribution in the water body, as well as to the strengthening of their positions in the trophic chains and altering the helminth life cycles. The increase in the significance of the parasitic factor, high activity of invasive species in the formation of the structural and functional organization of the ecosystem of the studied water bodies is proposed.

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