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**FEATURES OF THE PARASITE FAUNA FORMATION  
IN THE EUROPEAN SMELT *OSMERUS EPERLANUS* (L.)**

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The structural features of the parasite fauna of the European smelt are considered. The parasite fauna of the smelt is taxonomically quite diverse, comprising 65 species of 14 classes. Cestodes, trematodes, nematodes and acanthocephalans are the most numerous, constituting 71 % of the total number of species. The fraction of species-, genus- and family-specific osmerid parasites constitutes 7 % of the total number of smelt parasitic species. Protozoans are a small group (9 species), but diverse in relation to the number of higher taxa (6 classes). Monogeneans, leeches, and bivalves are represented by a single species in each class. Ecologically, the parasite fauna of the smelt is also diverse, with three major groups of species: parasites of the Arctic freshwater complex, associated with salmonids, coregonids, osmerids and lotids; boreal flatland faunal complex, associated with percids, esocids and cyprinids (dominants in the fish population of sub-Arctic freshwater bodies); and marine faunal complex typical of marine fish and mammals living in northern seas. Parasites of salmonoid fish are the primary contributors to the parasite fauna of the smelt.

*Key words:* European smelt *Osmerus eperlanus* (Linnaeus, 1758), parasite fauna, structure and diversity.

ОСОБЕННОСТИ ФОРМИРОВАНИЯ ПАРАЗИТОФАУНЫ  
ЕВРОПЕЙСКОЙ КОРЮШКИ *OSMERUS EPERLANUS* (L.)

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Рассмотрены особенности структуры паразитофауны европейской корюшки. Фауна паразитов корюшки разнообразна в таксономическом отношении — 65 видов относятся к 14 классам. Наиболее многочисленны цестоды, трематоды, нематоды, скребни — 71 % от общего числа видов. Доля специфичных к виду, роду и семейству корюшковых составляет 7 % от общего числа видов в ее фауне. Простейшие — малочисленная группа видов (9), но разнообразная по числу высших таксонов (6 классов). Моногенеи, пиявки и двустворчатые моллюски представлены одним видом в каждом из классов. Паразитофауна европейской корюшки неоднородна в экологическом отношении и представлена тремя основными группами видов: паразиты арктического пресноводного комплекса, приуроченного к лососевым, сиговым, корюшковым и налимным рыбам; бореального равнинного фаунистического комплекса, приуроченного к окуневым, щуковым и карповым — доминирующим представителям рыбного населения субарктических пресноводных водоемов и паразиты морского фаунистического комплекса, характерного для морских рыб и млекопитающих северных морей. Ведущая роль в формировании паразитофауны европейской корюшки принадлежит паразитам лососеобразных рыб.

*Ключевые слова:* европейская корюшка *Osmerus eperlanus* (Linnaeus, 1758), паразитофауна, структура и разнообразие.

The smelt, or the European smelt *Osmerus eperlanus* (Linnaeus 1758) is one of major harvested fish species in water bodies of the European North, widely distributed from France (the Loire) to the Baltic, White and Barents Seas, including the south-eastern part of the Scandinavian Peninsula and southwestern Ireland. Distribution of these fish in Russia exceeds the distribution in all the above-mentioned seas. The species occurs in the Kola Peninsula, is widespread in Karelia and water bodies from the Northern Dvina to the Pechora and lakes of Bolshezemelskaya tundra (Atlas..., 2003; Sidorov, Reshetnikov, 2014). In the past few decades, smelt have been actively dispersing (Reshetnikov, Popova, 2012; Hagenlund et al., 2015), colonizing not only new water bodies but even new zoogeographic provinces. Smelt's wide ecological valence, high abundance, and biomass provide it with competitive advantage in comparison with native species, profoundly modifying the structure and trophic relations in the fish community (Reshetnikov et al., 1982; Sterligova et al., 2002; Kriksunov et al., 2005).

The present paper continues a series of authors' publications concerning parasites of the European smelt *Osmerus eperlanus* (L.). Our previous publications contain an annotated list of parasites found in the European smelt, based on own material and data published in journal reviews, scientific papers, conference proceedings, and academic theses. Each parasite species was described briefly,

its occurrence in different smelt ecoforms, sample provenance and author were stated. For the higher taxa, an attempt was made to analyze the taxonomic diversity and distribution of European smelt parasites (Anikieva, Ieshko, 2017). The parasite fauna was analyzed in two ecoforms of the European smelt: the anadromous (sea-going) smelt from the North Sea drainage basin and two landlocked forms — smelt proper from lakes Ladoga, Onego and Pyaozero, and dwarf (lake) smelt from lakes Beloye, Vozhe and Chudskoye (Peipus). Smelt ecoforms differed in the set of parasites and the taxonomic structure of parasite diversity, which was estimated by the composition of higher taxa. The greatest differences were detected between the anadromous form inhabiting waters with different salinities and the landlocked forms of the smelt. It was shown that ecoform-specific features of the parasite fauna of the smelt resulted from its ecological plasticity enabling the fish to live in both marine and fresh waters (Anikieva et al., 2017).

The aim of this study was to investigate the formation of the parasite fauna in the European smelt *Osmerus eperlanus* and assess the contribution of parasites associated with different fish species to the species diversity of the parasite fauna.

## MATERIAL AND METHODS

The parasite fauna was analyzed in relation to the annotated species list of parasites found in the European smelt, compiled previously for different parts of the species range, viz. lakes of Karelia, Kola Peninsula and Vologda Region, Baltic Sea bays and coastal waters of the North Sea (Anikieva, Ieshko, 2017), using known data on the distribution and biology of parasite species.

The role of parasites associated with different taxonomic and ecological groups of fish in the parasite fauna of the smelt was assessed. The parasites were analyzed in relation to host specificity: specialists of certain host species or genera, those confined to a single taxonomic group of hosts, or species parasitizing in a variety of host systematic and ecological groups. In terms of the frequency of occurrence, parasites were grouped into two categories: frequent species (present in more than a half of sample sets with over 30 % prevalence and rare species). The contribution of parasites associated with different taxonomic and ecological groups of fish to the species diversity of parasites in the smelt was estimated by a principal component analysis (Korosov, Gorbach, 2010).

## RESULTS

Records from the entire range of the European smelt include 65 species of parasites belonging to 14 classes (fig. 1). The parasite fauna of the smelt is composed mainly of species with a complex life cycle — cestodes, trematodes, nematodes, acanthocephalans. They represent over 70 % of the total number of species parasitizing in the smelt. Nematodes, both marine and freshwater, adults and larvae are represented most widely. Protozoans (Kingdom Protista) are a small group (9 species), but diverse in terms of the number of higher taxa (6 classes). Monogeneans, leeches and bivalves are represented by a single species in class.

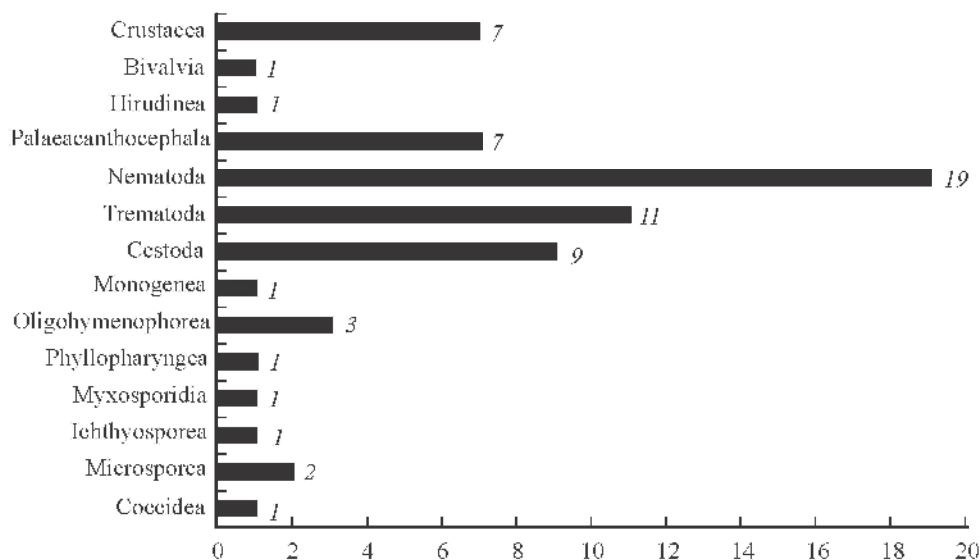


Fig. 1. Number of species in individual taxonomic groups of parasites found in the European smelt.

Five species are specialists of their host species, genus, or family of osmerids. They belong to the freshwater ecological group and constitute 7 % of the total number of species in the parasite fauna of the smelt. One of these species is represented by the Sporozoa Leuckart, 1879 type — coccidian *Eimeria osmeri* Molnar et Fernando, 1974 (class Coccidea Leuckart, 1879) and two species, by Microspora Balbiani, 1882 type, class Microsporea — *Glugea hertwigi* Weissenberg, 1921 and *Pleistophora ladogensis* Voronin, 1978.

Among numerous species of the class Coccidea parasitic in fish, osmerids are known to host a single species, *Eimeria osmeri*, detected for the first time in the rainbow smelt *Osmerus mordax* (Mitchill, 1815) from Lake Ontario (Molnar, Fernando, 1974). Low-intensity infections with *E. osmeri* were found in the European smelt from lakes of Karelia (Ladoga, Onego, Pyaozero) (Rumyantsev, 2007).

Similarly to *E. osmeri*, *Glugea hertwigi* is parasitic in fish of the genus *Osmerus* Linnaeus, 1758, but its distribution range is wider. It occurs in lakes of northwestern Russia, Finland, and North America. In some lakes it has repeatedly caused epizootic events (Voigt, 1975; Nellbring, 1989; Sterligova et al., 1992; Rumyantsev, Ieshko, 1997; Ieshko et al., 2000). In Fennoscandian waters, *G. hertwigi* has been reported from coregonids: the vendace *Coregonus albula* (L.) from the Kem River basin — Lakes Kerkkies (27 %) and Kopati (33 %) (Rumyantsev, 1964) and whitefish *C. lavaretus* (L.) from Lake Vagatozero (7 %) (Schulman et al., 1974), Lake Onego (7 %) (Rumyantsev, Ieshko, 1997).

*Pleistophora ladogensis* is parasitic in the European smelt and the only landlocked gadid species — the burbot *Lota lota* (L.). Current data on the distribution of *P. ladogensis* are scanty. The parasite was found in the dwarf smelt from lakes Ilmen, Seliger, Pestov, and in the European smelt from lakes of Karelia (Onego and Ladoga) and from the German coast of the North Sea (Khlopina, 1920; Sprengel, Liichtenberg, 1991; Kerstan, 1992; Rumyantsev, 2007; Costa et al., 2016). The species is most frequently found in juveniles and causes epide-

mic events. The only findings from the burbot were from Lake Vrevo (Leningrad Province). The host-specific differences in the shape of *P. ladogensis* spores indicate morphological heterogeneity of the species (Voronin, 1978).

Two other smelt specialists belong to monogenean and cestode classes. Monogeneans are one of the leading groups in the parasite fauna of freshwater fish, and many of them are strict specialists. Only a single monogenean species has been recorded from the European smelt — *Gyrodactylus osmeri* Rumyantsev, Schulman & Ieshko 1998 (Rumyantsev, Ieshko, 1997). In the smelt's distribution range, *G. osmeri* was found in three lakes of Karelia (Ladoga, Onego and Pyaozero) and in the Gulf of Bothnia (Rumyantsev et al., 2001; Rumyantsev, 2007; Valtonen et al., 2012). The species is morphologically similar to the coregonid parasite *Gyrodactylus lavareti* Malmberg, 1957 (Anikieva, Ieshko, 2017).

The cestode *Proteocephalus tetrastomus* (Rudolphi 1810), parasitizing in representatives of the family Osmeridae, occurs in the European smelt *Osmerus eperlanus*, the Japanese smelt *Hypomesus nipponensis* McAllister, 1963 from Lake Suwa, Japan, and the rainbow smelt *Osmerus mordax* (Mitchill, 1815) from the Gulf of St. Lawrence, Canada (Scholz et al., 2004), and has a Holarctic distribution. The species is widespread in the European smelt's range (Willemse, 1969; Anikieva, 1998). Findings from the northeastern periphery of the range came from Lake Goluboye (Pechora River basin) (Anikieva, Dorovskikh, 2009). *P. tetrastomus* is the only *Proteocephalus* species with craspedote proglottids. Studies of the intraspecies variation in *P. tetrastomus* from the European smelt from lakes Ladoga and Goluboye revealed the species' heteromorphism and the existence of intraspecies forms (Anikieva, Dorovskikh, 2009).

Infection with larvae (glochidia) of the duck mussel *Anadonta anatina* (Linnaeus, 1758) was found only in anadromous smelt from the Elbe delta (Anders, Möller, 1991; Anders, Wiese, 1993). *A. anatina* is widespread in Europe and a part of Asia. Its population densities are the highest in the German coast of the North Sea. The species demonstrates wide ecological valence, and can inhabit both oligotrophic and eutrophic waters. The identification of a glochidium from European smelt gills as *Anadonta anatina* is the only case of down-to-species identification of mussels as *Osmerus eperlanus* parasites.

As to other fish of the region, unidentified glochidia were found only on the two-spotted goby *Gobiussculus flavescens* (Fabricius, 1779) (Palm et al., 1999), as well as in the European smelt from Lake Onego (Rumyantsev, 2007), and the dwarf smelt from Lake Beloye (Radchenko, 2002). These were rare, low-intensity glochidial infections. The mussels were thought to employ a wide range of fish species as hosts for metamorphosis of their larvae. Recent studies have shown, however, that only a few fish species are suitable hosts for glochidia (Douda, 2013). Affiliations with specific fish hosts need to be thoroughly investigated. Many authors report a wide assortment of hosts for larvae. At the same time, species ranges of Unionoidea are strongly narrower than those of fish. The morphology and ecology of glochidial development have been studied insufficiently. In this situation, we shall avoid determining *Anadonta anatina* glochidia as smelt specialists.

The majority of species in the parasite fauna of the European smelt are broad generalists, utilizing fish hosts belonging to different taxonomic and ecological groups (fig. 2). There are 34 of such species. Of these, 14 species can be attributed as representatives of the freshwater ecological group. Five species infu-



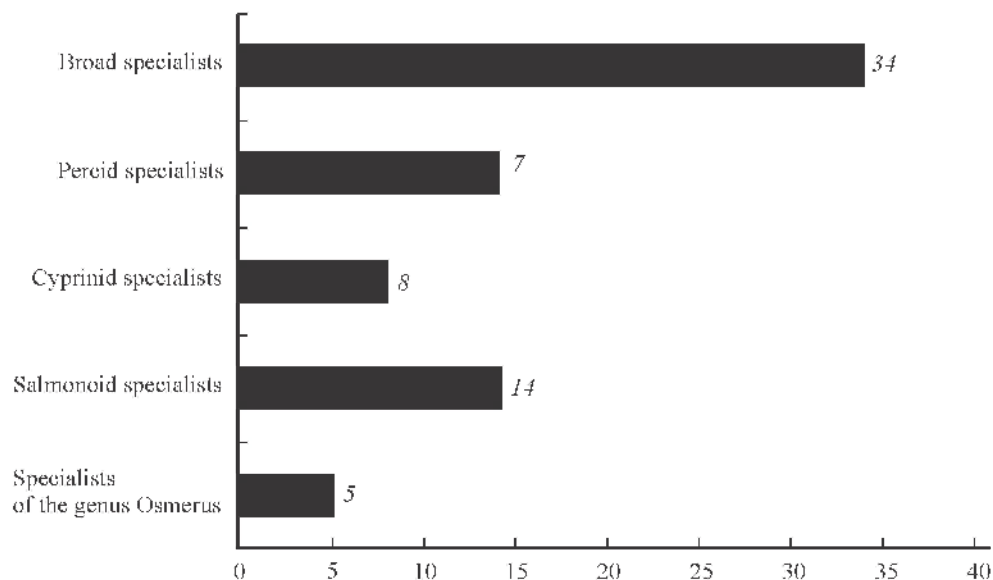


Fig. 2. Host specializations of parasites found in the European smelt.

sorians *Capriniana piscium* (Butschli, 1889), *Trichodina pediculus* Ehrenberg, 1838, leech *Piscicola geometra* (Linnaeus, 1761), crustaceans *Ergasilus sieboldi* Nordmann, 1832 and *Argulus foliaceus* (Linnaeus, 1758) possess the direct life cycle, the other 9 species use a wide range of planktic and benthic invertebrate hosts, primarily crustaceans — copepods, mysids, gammarids, including the relict *Pontoporeia affinis* Lindström, 1855, *Palasea quadrispinosa* Sars, 1867. The widest range of intermediate and paratenic hosts belong to the nematode *Raphidascaris acus* (Bloch, 1779): oligochaetes, mollusks, crustaceans, larvae of aquatic insects. Only three parasite species are widespread and common in the smelt — metacercariae of the trematodes *Diplostomum baeri* Dubois, 1937 and *Diplostomum spathaceum* (Rudolphi, 1819) and the nematode *R. acus*.

Nineteen species belong to the marine ecological group: trematodes *Brachyphallus crenatus* (Rudolphi, 1802), *Cryptocotyle lingua* (Creplin, 1825), nematodes *Eustrongylides mergorum* (Rudolphi, 1809), *Hysterothylacium aduncum* (Rudolphi, 1802), *Hysterothylacium cf. cornutum* (Stossich, 1904), *Contracaecum osculatum* (Rudolphi, 1802), *Anisakis simplex* (Rudolphi, 1809), *Pseudoterranova decipiens* (Krabbe, 1868), *Porrocaecum* ssp., *Cosmocephalus obvelatus* (Creplin, 1825), *Paracuaria tridentate* (Linstow, 1877), *Anguillicoloides crassus* Kuwahra, Niimi et Itagaki, 1974, *Spinitectus* sp., acanthocephalans *Echinorhynchus gadi* Müller, 1776, *Corynosoma semerme* (Forssell, 1904), *Corynosoma strumosum* (Rudolphi, 1802), crustaceans *Lepeophtheirus* sp., *Caligus elongatus* Nordman, 1832, *Lernaeocera branchialis* (Linnaeus, 1758).

Three of the species (crustaceans *Lepeophtheirus* sp., *Caligus elongatus*, *Lernaeocera branchialis*) have a direct life cycle. The life cycles of 16 species are complex and highly variable. They can involve one or two intermediate hosts. The definitive hosts are marine fish, aquatic mammals, and piscivorous birds. Their life cycle also include paratenic and post-cyclic hosts.

The core of the marine group of parasites is represented by nematodes (11 species). Five of the nematode species recorded from the European smelt parasitize in marine mammals: *Contracaecum osculatum* s. lato, *Anisakis simplex*, *Pseudoterranova decipiens* (Krabbe, 1868) s. lato, a tuna fish specialist *Hysterothylacium* cf. *cornutum*, and the parasite of aquatic and terrestrial vertebrates (parasitic in invertebrates at the larval stage) *Spinitectus* sp. Four nematode species are parasitic in piscivorous birds of various orders, dwelling over sea spaces or at freshwater bodies: *Eustrongylides mergorum*, *Porrocaecum* spp., *Cosmocephalus obvelatus*, *Paracuarria tridentate*, and a single species — *Hysterothylacium aduncum* — is predominantly parasitic in marine fish (clupeids, gadids, gobiids, etc.). The European smelt has lately been invaded by *Anguillicoloides crassus* introduced to Europe from Japan via the Japanese eel *Anguilla japonica* Temming et Schlegel, 1846 (Hartmann, 1994). All the above-mentioned species are noted for high ecological plasticity. *Anisakis simplex*, *Hysterothylacium aduncum*, *Contracaecum osculatum* occur in almost all fish species inhabiting the North Sea. Some nematode species associated with marine fish can also infest freshwater fish either visiting or residing in brackish waters. *C. osculatum* larvae have been found in both the Northern and the Southern hemisphere, primarily in marine fish, but also in fish pertinent to brackish and fresh waters. They have also been reported from freshwater fish farms.

Nematodes associated with marine mammals, piscivorous birds, and marine fish use the European smelt as a paratenic host. Larvae encyst in its stomach walls, muscles, and body cavity. Larvae of spiruroid nematodes are found in the European smelt most frequently (Obiekiezie et al., 1992). Some publications also mention a high rate of mortality among nematode larvae in the smelt (Kuhn et al., 2013).

Particularly noteworthy is the parasitism of anisakid nematode larvae in smelt. Infection of humans with anisakid nematodes has happened in many countries around the world. Members of genera *Anisakis*, *Contracaecum*, *Hysterothylacium*, *Porrocaecum*, and *Pseudoterranova* are pathogenic for humans, fish, and animals, and have medical and economic importance.

Special members of the marine group of parasites include acanthocephalans of the genus *Corynosoma* Lühe, 1904 — *C. semerme* and *C. strumosum*. They are widespread in seal populations. Their intermediate host is amphipods of the genus *Pontoporeia* Kohlm., whereas an additional or second intermediate hosts include different marine, migratory, as well as landlocked fish living in the lower flow of rivers and relict continental basins (Identification..., 1987). Osmereids are paratenic hosts of these two acanthocephalan species (Skorobrechova, Nikischin, 2011). In German coastal waters of the North Sea, the acanthocephalan *C. semerme* was found only in the eel *Anguilla anguilla* (L.) and in the European smelt, and *C. strumosum* only in the European smelt. *Corynosoma* acanthocephalans (not identified as a species) have been retrieved from gobiids *Gobies niger* (Linnaeus, 1758), *Pomatoschistus microps* (Kroyer, 1838), *P. minutus* (Pallas, 1770), the flounder *Platichthys flesus* (Linnaeus, 1758), the nine-spined stickleback *Pungitius pungitius* (Linnaeus, 1758), and the European eelpout *Zoarces viviparus* (Linnaeus, 1758) (Palm et al., 1999). In Lake Ladoga, both species were found in the European smelt, the pike *Esox lucius* L., the zieg *Pelecus cultratus* (Linnaeus, 1758), the burbot, the pike-perch *Sander lucioperca* (Linnaeus, 1758), and the ruffe *Gymnocephalus cernuus* (Linnaeus, 1758);

the Atlantic salmon *Salmo salar* Linnaeus, 1758 hosted only *C. semerme*, and the perch, only *C. strumosum* (Rumyantsev, Ieshko, 1997).

The European smelt has been mentioned as a paratenic host for the trematode *Cryptocotyle lingua* (Anders, Möller, 1991), whose definitive hosts are terrestrial and aquatic mammals and piscivorous birds. Only two species — the trematode *Brachyphallus crenatus* and the acanthocephalan *Echinorhynchus gadi* occur in European smelt as adults. Both species are widespread in fish of northern seas (Gibson, Brey, 1986; Shostak et al., 1986).

Among parasites found in the European smelt, 26 species parasitize in a single taxonomic group of freshwater fish. The majority (14) of the species (21 % of the total number of European smelt parasites) are parasites with salmonoid fish as predominant hosts. This group is taxonomically diverse, including the myxosporidian *Chloromyxum coregoni* Bauer, 1948, cestodes *Triaenophorus crassus* Forel, 1868, *Eubothrium crassum* (Bloch, 1779), *E. salvelini* Schrank, 1790, *Diphyllobothrium dendriticum* (Nitzsch, 1824), *D. ditremum* (Creplin, 1825), *Proteocephalus longicollis* (Zeder, 1800), trematodes *Phyllodistomum umblae* (Fabricius, 1780), *Ichthyocotylurus erraticus* (Rudolphi, 1809), nematodes *Pseudocapillaria salvelini* (Poljansky, 1952), *Cystidicola farionis* Fischer, 1798, *Sterliadochona ephemeridarum* (Linstow, 1872) (after: Sokolov et al., 2012), *Philonema sibiricum* (Bauer, 1946), acanthocephalan *Echinorhynchus salmonis* Müller, 1780. *Sterliadochona ephemeridarum* represents the Boreal piedmont faunal complex. Other parasites are psychrophilic, belonging to the Arctic faunal complex, possessing Holarctic or Palaearctic distribution. The majority of these species occur in the smelt at a significantly lower population density degree and intensity than in their preferred hosts. The most frequent findings include cestodes of the genera *Eubothrium* and *Diphyllobothrium*, *Proteocephalus longicollis*, the nematode *Cystidicola farionis*, and the acanthocephalan *Echinorhynchus salmonis*, whose life cycles involve crustaceans, including relict ones.

Eight of the species in the parasite fauna of the European smelt are predominantly parasitic in cyprinids (12 %): infusorians *Tripartiella copiosa* Lom, 1959, *T. lata* Lom, 1963, larvae of the trematodes *Bucephalus polymorphus* Baer, 1827, *Ichthyocotylurus pileatus* (Rudolphi, 1802) and *Tylodelphys clavata* (Nordmann, 1832), nematode *Pseudocapillaria tomentosa* (Dujardin, 1843), acanthocephalan *Pomphorhynchus laevis* (Müller, 1776), crustacean *Ergasilus briani* Markewitsch, 1932. These species are widespread in the Palaearctic in different genera of the cyprinid family, and belong to the boreal flatland complex. For five species possessing the complex life cycle, the European smelt is an intermediate and reservoir host, and the other three species (*Tripartiella copiosa*, *T. lata*, and *Ergasilus briani*) have a direct life cycle. All parasites in this group are rather rare and scanty in the smelt. The nematode *Pseudocapillaria tomentosa* was found in the smelt only in Lake Onego.

Four parasite species found in the European smelt (6 % of the total number of species) mostly specialize on predaceous fish, like the pike *Esox lucius* and the perch *Perca fluviatilis* Linnaeus, 1758: they include the cestode *Triaenophorus nodulosus* (Pallas, 1781), the trematode *Bunodera luciopercae* (Müller, 1776), nematodes *Camallanus lacustris* (Zoega, 1776) and *C. truncatus* (Rudolphi, 1814). They belong to the boreal flatland faunal complex and are widespread in the Palaearctic region. They employ a wide variety of intermediate hosts.



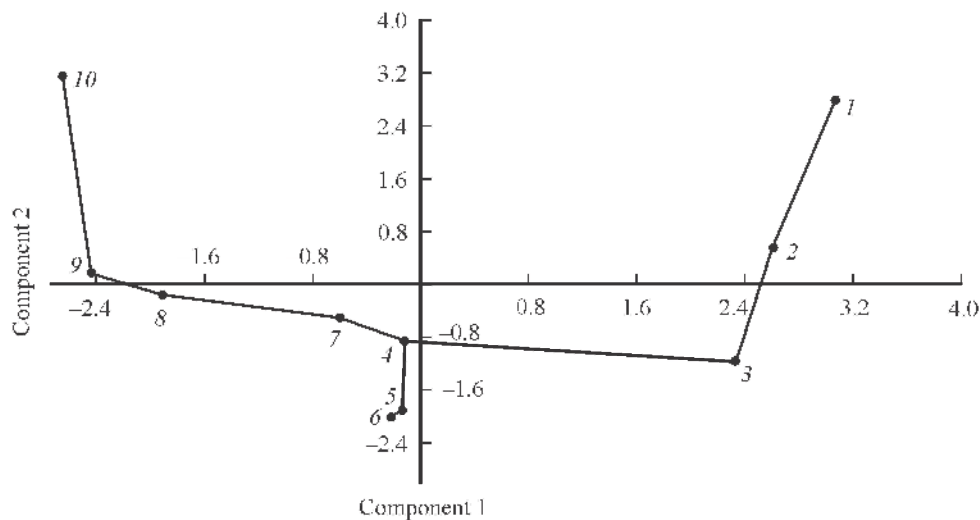


Fig. 3. Ordination of objects (the fauna of parasites of individual groups of hosts) in PCA coordinates.

1 — *Osmerus eperlanus*, 2 — Salmonidae, 3 — Coregonidae, 4 — Thymallidae, 5 — Cyprinidae, 6 — Esocidae, 7 — Percidae, 8 — Gasterosteidae, 9 — Cottidae, 10 — marine fish (Clupeidae, Gadidae, Pleuronectidae etc.).

The cestode *T. nodulosus* is one of few parasites frequently found in the European smelt. It is present throughout the distribution range of its definitive host, the pike. The highest *T. nodulosus* infection rates in the smelt were reported from Lake Ladoga (prevalence 87 %, abundance index 1.7 worms) (Barysheva, Bayer, 1957). The other three parasite species infect the smelt locally and at low population density.

Significance of different host species in the formation of the parasite fauna of the European smelt is demonstrated in fig. 3. Principal component analysis has demonstrated that the structure of the parasite species diversity in the smelt is the most similar to that in salmonid and coregonid fish, and is also relatively close to that in the grayling *Thymallus thymallus* (Linnaeus, 1758). A separate cluster is formed by parasites associated with the dominant members of the freshwater fish community — the perch, the pike, and cyprinids (the roach *Rutilus rutilus* (L.) and the bleak *Alburnus alburnus* (L.)). The similarity of the parasite species composition in the smelt and in these fish species arises from the wide occurrence of typical freshwater parasites hosted by predaceous fish and belonging to the boreal flatland faunal complex: *T. nodulosus* and *D. latum*, metacercariae of trematodes of genera *Diplostomum* and *Thylodelphys*, *Ichthyocotylurus pileatus* metacercariae, trematode *Bunodera luciopercae*, nematodes *Raphidascaris acus*, *Camallanus lacustris*, *C. truncatus*. The European smelt is an intermediate or paratenic host for these parasites.

The most remote and least significant contributors to the parasite fauna of the European smelt are parasites of sticklebacks *Gasterosteus aculeatus* Linnaeus, 1758 and *Pungitius pungitius* (Linnaeus, 1758), gobies and other marine fishes, whose parasite fauna comprises marine and brackish-water species. This group is formed of marine trematodes, nematodes, and crustaceans. The European smelt mostly acts as a paratenic host for these parasite species.

## DISCUSSION

Our studies have demonstrated that the contribution of specialist species to the parasite fauna of the European smelt is low. The parasite fauna is mostly formed of broad generalists. Parasites with a complex life cycle, infesting the smelt either with food or by active invasion are most widespread.

Zoogeographically, the parasite fauna of the European smelt is heterogeneous, being a combination of four faunal complexes. A prevalent group of species (40 %) belongs to the freshwater boreal flatland complex, which was formed in the first half of the Oligocene. Its representatives are distributed widely across the Holarctic or Palaearctic, being represented by eurybiotic and broad generalists. The freshwater Arctic complex (the youngest faunal complex) contributes 26 % of the parasite fauna of the European smelt. It has been formed during the Quaternary period. According to Yakovlev (1961, 1964) this complex is a derivative of the boreal piedmont complex and invasive marine species. Members of the Arctic freshwater complex are psychrophilic and oxyphilic. The smallest number of species (4) belongs to the boreal piedmont faunal complex. They are oxyphilic, psychrophilic, and stenohaline. They rarely occur in the European smelt. The marine faunal complex comprises 30 % of the smelt's parasite fauna. The main hosts of the marine parasites found in the European smelt include common fish species in the orders Clupeiformes, Gadiformes, Perciformes, Scorpaeniformes, and Pleuronectiformes.

The European smelt was widely dispersed across Northern Europe since the last deglaciation and grew adapted to various ecological conditions, differentiating into the anadromous, lacustrine-riverine, and lacustrine forms (Klyukanov, 1977; Atlas..., 2003; Fishes in the nature reserves of Russia, 2010). The species composition of parasites in different ecoforms of the smelt, as well as the structure of their diversity, were strongly shaped by the environmental conditions, the structure of the fish community, and the coenotic relationship between its components (Anikieva et al., 2017).

Analysis of the contributions of individual fish species to the parasite fauna of the European smelt proves that the fauna of its parasites was forming through a system of coenotic relations with the fauna of northern freshwater ecosystems. The dominant role in the establishment of the parasite fauna of the smelt belongs to salmonids, prevailing in the fish communities of northern water bodies. The smelt shares 42 parasite species with salmonids and coregonids, i. e. 64 % of its parasite fauna. This number includes six out of the nine protozoan species known from the European smelt. Some of them occur also in fish of other taxonomic groups: esocids, cyprinids, gasterocephalids, and percids. Six out of nine cestode species known for the smelt are typical parasites of salmonoid fish. Seven of eleven trematode species in the smelt are shared with salmonid fish. They include metacercariae of the genera *Diplostomum* and *Tylodelphys*, common parasites of freshwater fish, and typical parasites of salmonids and coregonids *Phyllodistomum umblae* and *Ichthyocotylurus erraticus*. The parasite fauna of both the smelt and salmonids includes the marine species *Brachyphallus crenatus* and the freshwater parasite of percids *Bunodera luciopercae*. Three of 19 nematode species in the smelt are associated with salmonids, 8 species are shared with salmonoid fish and are broad generalists. All the common acanthocephalan and crustacean species are generalists.

The limited number of specialist parasites, the dominance of generalists, the low prevalence of infection in the smelt, and the low abundance of the majority of parasite species suggest that the formation of the parasite fauna of the European smelt is not completed and the contemporary fauna reflects the current results of the complex formation process. The wide distribution ranges of many parasite species found in the smelt (reaching far beyond its own range), and the fact that the smelt mostly acts as a paratenic host in the life cycle of parasites serve as an evidence that the parasite fauna of the European smelt is evolutionarily quite young.

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