DISCOVERY OF *EUDONTOMYZON* SP. (PETROMYZONTIDAE) LARVAE IN LAKES AND A CHARACTERISATION OF THEIR HABITATS

Aleksandr O. Zvezdin[1,*], Natalia V. Polyakova[1], Aleksandr V. Kucheryavyy[1], Vladimir R. Khokhryakov[2], Anzhelika V. Kolotei[1], Dmitriy S. Pavlov[1]

[1]*A.N. Severtsov Institute of Ecology and Evolution of RAS, Russia*
[2]*Smolenskoye Poozerye National Park, Russia*
e-mail: a.o.zvezdin@gmail.com

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The extended freshwater life of Petromyzontiformes larvae (ammocoetes) takes place mainly in lotic waters where it has been studied in detail. Information on ammocoetes in lentic habitats is extremely limited, with few data on the occurrence of specimens in ponds or large lakes. The area of the Smolenskoye Poozerye National Park has a dense network of lakes and rivers, with streams abundantly populated by lamprey larvae of the genera *Lampetra* and *Eudontomyzon*. In this paper, we evaluate the habitability of lakes belonging to such systems and the manner in which they are populated by lamprey. Larval habitat identification and documentation (bed analysis where ammocoetes exist, including ground composition and biotic and abiotic habitat characteristics) were carried out, resulting in the first documentation of larvae and metamorphic specimens of *Eudontomyzon* sp. inhabiting littoral areas of small lakes. These specimens were found in the fringe biotopes between the river mouth and lakes. One peculiarity that distinguishes the lentic habitats from the typical river ones is the absence of distinct currents. Freshwater flows diffusely into lakes, mixing continuously at the sites we studied. Preferred habitats for *Eudontomyzon* sp. consisted of swales filled with debris carried from inflowing streams and deposited as current diminished. In ammocoete beds of this type, the examined larvae had a good trophic position. Such habitats can be both permanent and ephemeral as tributary water levels changes. During flood events, elevated velocity can flush debris and ammocoetes away from these fringe habitats and further into a lake. No accentuated active decomposition was found in the areas where the ammocoetes were present. The results of the study indicate that Petromyzontiformes larvae may be more common in lentic habitats than is currently documented.

Key words: ammocoetes, ammocoetes bed, lake habitat, lampreys, relocation mechanism, migration, settlement mechanism

Introduction

Petromyzontiformes larvae (ammocoetes) are common in the benthic habitats of streams (Torgersen & Close, 2004; Mundahl et al., 2006) and are most abundant in slow but flowing stretches (Nazarov et al., 2016; Reid & Goodman, 2017). Substrate particle size is one of the most important determinants of larval distribution (Almeida et al., 2002) with fine, loose sediments composed of a mixture of silt and sand with good aeration being preferred. More developed, larger ammocoetes can thrive in habitats with more coarse sediments including sand-gravel and gravel (Almeida & Quintella, 2002). In addition, larval lamprey can populate lentic water bodies, such as small ponds (Shandikov & Goncharov, 2008; Reid & Goodman, 2017) as well as littoral zones of lakes (Wagner & Stauffer, 1962; Bond & Kan, 1973; Lee & Weise, 1989; Lorion et al., 2000; Fodale et al., 2003; Cochran & Lyons, 2004), move towards river mouths and lentic areas with age (Kelso & Todd, 1993; Quintella et al., 2003; Jones, 2007) or in rare cases may be hatched there (Beamish, 1982; Russell et al., 1987).

The Smolenskoye Poozerye National Park, located in the north of the Smolensk Region of Russia, is a territory rich with watersheds including more than 35 lakes of glacial origin and many rivers and streams in the Western Dvina River Basin (Baltic Basin). The south-eastern borders of the Smolenskoye Poozerye National Park are adjacent to the Black Sea Basin. Due to its geographical position spanning these two basins, there are two lamprey genera, which inhabit the Smolenskoye Poozerye National Park: *Lampetra* (from the Baltic Sea Basin) and *Eudontomyzon* from the Black Sea Basin (Kucheryavyy et al., 2019).

The lakes, rivers, and streams of the Smolenskoye Poozerye National Park are interwoven into a dense hydrographic network. Since all of these lakes are small (maximal area of 3.04 km^2), and exist within a network of streams where larvae of the genera *Lampetra* and *Eudontomyzon* are abundant and sympatric in some rivers, we assume that lamprey are able to navigate and inhabit these lakes at different stages of their migratory cycle, at least as transitional habitats (Pavlov et al., 2019).

At present, there is very little published literature on the life history of ammocoetes in lake habitats. The purpose of this study was to document ammocoete populations in lake habitats, and to investigate the characteristics of those habitats. The objectives of this paper included: i) searching for ammocoetes and characterising their use of lake habitats adjacent to river mouths and outlets of streams; ii) determining the taxonomic position of ammocoetes; iii) evaluating possible mechanisms for ammocoete resettlement from streams to the littoral zone of lakes.

Material and Methods

The study was performed in the Smolenskoye Poozerye National Park in May – June 2019 and August – September 2020. Several lakes and their tributaries, and one river out-flowing from the lake were surveyed.

Ammocoetes were surveyed in four small lakes and adjacent streams (Fig. 1, Table 1): 1) in the north-eastern Lake Dgo at the source of River Ilzhitsa (55.584006° N, 31.780675° E); 2) in the south-eastern part of Lake Sapsho, at the point where it meets the River Sapshanka (55.491289° N, 31.858169° E); 3) in the northern part of Lake Baklanovskoe at the point where it meets the River Senokositsa (55.504992° N, 31.669128° E); 4) in the north-western portion of Lake Petrovskoe at the egress of an unnamed stream (55.510275° N, 31.680639° E), as well as in the lower course of this stream where spawning grounds of *Eudontomyzon* sp. were documented. The location of habitats where larvae were found was documented (GPS and straight-line distances) relatively to stream mouth and the shoreline of the lake, and the density of larvae was noted. The primary sampling gear used to collect lamprey specimens was the dip net (Kinalev net) (rebar frame 0.5 × 0.7 m stretched with net of 3-mm mesh), commonly used in such studies to catch ammocoetes age 1+ and older. In contrast to the electrofishing method, the dip net allows to withdraw the grounds from a certain area, along with all its inhabitants, organic material and inorganic substrate.

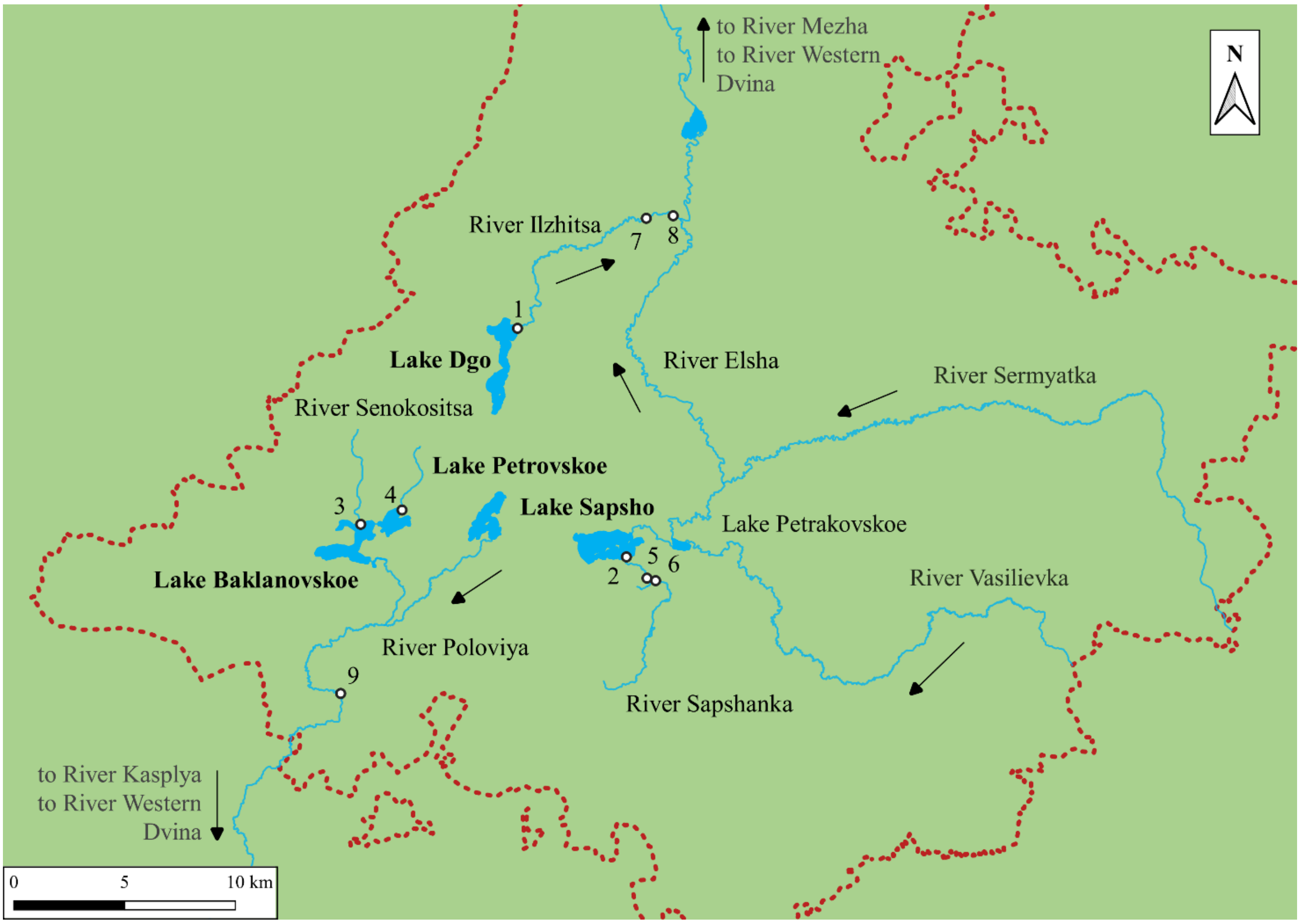

Fig. 1. Map of the Smolenskoye Poozerye National Park and the study sites. Designations of the sample collection sites: Dgo (1), Sapsho (2), Baklanovskoe (3), Petrovskoe and Unnamed Stream (4), Sapshanka (5) and its Unnamed tributary (6), Ilzhitsa (7, 8), Poloviya (9). Arrows indicate the currents direction. The red dotted line indicates the borders of the Smolenskoye Poozerye National Park.

Table 1. Sample size on the study sites in the Smolenskoye Poozerye National Park

Year	Petrovskoe	Baklanovskoe	Sapsho	Dgo
2019	35 / 65	–	–	0 / 20
2020	1+(2) / 45	42 / 50	0 / 40	–

Note: number of the caught ammocoetes / total number of samples (sweeps of a net). The number of ammocoetes from the Unnamed Stream (Petrovskoe) is shown in brackets. Dash means no research.

Abiotic conditions were observed in some study sites. In these areas, the water depth of the habitat and the depth of ammocoete immersion in the substrate were documented. The velocity and direction of any current present was recorded using a Valeport Model 801-FT. The type of ammocoete bed (i.e. place of aggregation with relatively constant use by larvae) and the fractional composition of the substrate were analysed by the ground sifting method. The rate of gas release from the substrate was estimated by the frequency of bubbles rising from the substrate when under pressure (Reid & Goodman, 2017). The organic matter content of the sediment was calculated using ash-free dry mass (AFDM) (Logue et al., 2004) to estimate the ratio between the dry mass of the sample and mass of its ash after combustion in a muffle furnace. Among the biotic parameters investigated at each biotope were the distribution of aquatic flora and riparian vegetation, as well as the composition of benthic invertebrates and zooplankton (Alekseev & Tsalolikhin, 2010, 2016). These characteristics may further be useful for better understanding of the environmental conditions in the ammocoetes habitats and ecological interactions between species.

Life stages of the estimated specimens are used according to Clemens (2019). The taxonomy of ammocoetes was determined based on known data on adults captured in the Smolenskoye Poozerye National Park (Kucheryavyy et al., 2019). Further, comparison was made between features of sampled larvae and specimens of *Lampetra fluviatilis* (Linnaeus, 1758) larvae originating from rivers in the Baltic Sea basin (within Leningrad Region) and by features specified in Renaud (2011), i.e. pigmentation of head, branchial region and caudal fin, as well as structure of tongue precursor. In ammocoetes, the total length (TL, mm) and body weight (W, g) were measured. The degree of fullness of the digestive tract was visually evaluated on the six-point Lebedev (1936) scale. The components of the bolus were sorted under a Micromed 3 microscope and measured quantitatively. In Lake Petrovskoe, samples were taken twice, in early May 2019 (ten ammocoetes) and in early August 2020 (one specimen directly from the lake and two from the stream that flows into the lake). In Lake Baklanovskoe, ten ammocoetes were analysed in early August 2020. The collected specimens are now archived in the collection of the Laboratory of Behaviour of Lower Vertebrate of the Severtsov Institute of Ecology and Evolution of RAS (Moscow, Russia) (Table 2).

Results

Documenting of ammocoete habitats

In 2019–2020, study sites included three lakes near the inflow of streams, and one lake area near a river outlet. Portions of the streams either entering or exiting each lake were also surveyed. All lakes were small (0.94–3.04 km^2), with mean depths of 16.5–28.7 m and either had moderate (Lake Baklanovskoe, Lake Sapsho) or low retention time (Lake Petrovskoe, Lake Dgo) (GOST 17.1.1.02-77; geoportal.poozerie.ru). The survey rivers and streams associated with these lakes are classified as the smallest (less than 25 km) and small (25–100 km) streams, based on Kurdov (1995). Ammocoetes were found in Lake Baklanovskoe and Lake Petrovskoe, and we studied habitat use in these areas. No ammocoetes were found in the study areas of Lake Dgo and Lake Sapsho.

Table 2. Lamprey samples collected in the Smolenskoye Poozerye National Park in 2019–2020

Study site	Collection site	Year	Life stage	N	Sample number in IEE
River Ilzhitsa	8	2019	adult	172	19051001
	7	2019	larva	11	19051002
		2020	transformer	7	20080701
		2020	larva	8	20080507
River Poloviya	9	2019	adult	16	19050701
River Sapshanka	5	2019	larva	26	19050801
Lake Baklanovskoe	3	2020	larva	24	20080801
		2020	transformer	18	20080802
Lake Petrovskoe	4	2019	larva	11	19050901
		2020	larva	1	20080707
Unnamed Stream (Petrovskoe)	4	2020	larva	2	20080706

Note: Designations of the sample collection sites: Dgo (1), Sapsho (2), Baklanovskoe (3), Petrovskoe and Unnamed Stream (4), Sapshanka (5) and its Unnamed tributary (6), Ilzhitsa (7, 8), Poloviya (9); IEE – Severtsov Institute of Ecology and Evolution of RAS.

Lake Dgo was investigated at the source of the River Ilzhitsa (Fig. 2A). In June 2019, the outlet of the lake was an extensive overgrown grassy marshland. When pressure was applied to the ground, many gas bubbles were released. Over 20 m of the lake shoreline was covered with *Phragmites australis* (Cav.) Trin. ex Steud. No ammocoetes were found. Earlier in 2019 however, lamprey *Eudontomyzon* sp. spawning was observed in downstream reaches of the River Ilzhitsa (Site 7, Site 8), and ammocoetes were found (Table 2).

Lake Sapsho was studied at the mouth of the River Sapshanka and the adjacent shoreline (Fig. 2B). In August 2020, the connection between the river and the lake was reduced due to the low water level in the river, with extensive growth of aquatic and riparian vegetation in the mouth and lower reach of the River Sapshanka. The mouth area was a wetland, covered mostly with *Phragmites australis*. Many gas bubbles were released from the soil when pressed. We surveyed over 400 m of the lake shoreline in addition to a 150 m reach in the lower section of River Sapshanka. During this effort, no ammocoetes were found, though lamprey *Eudontomyzon* sp. were observed spawning upstream in the River Sapshanka (Site 6) in May 2019, and ammocoetes were found 1.8–2.3 km upstream of the mouth (Site 5).

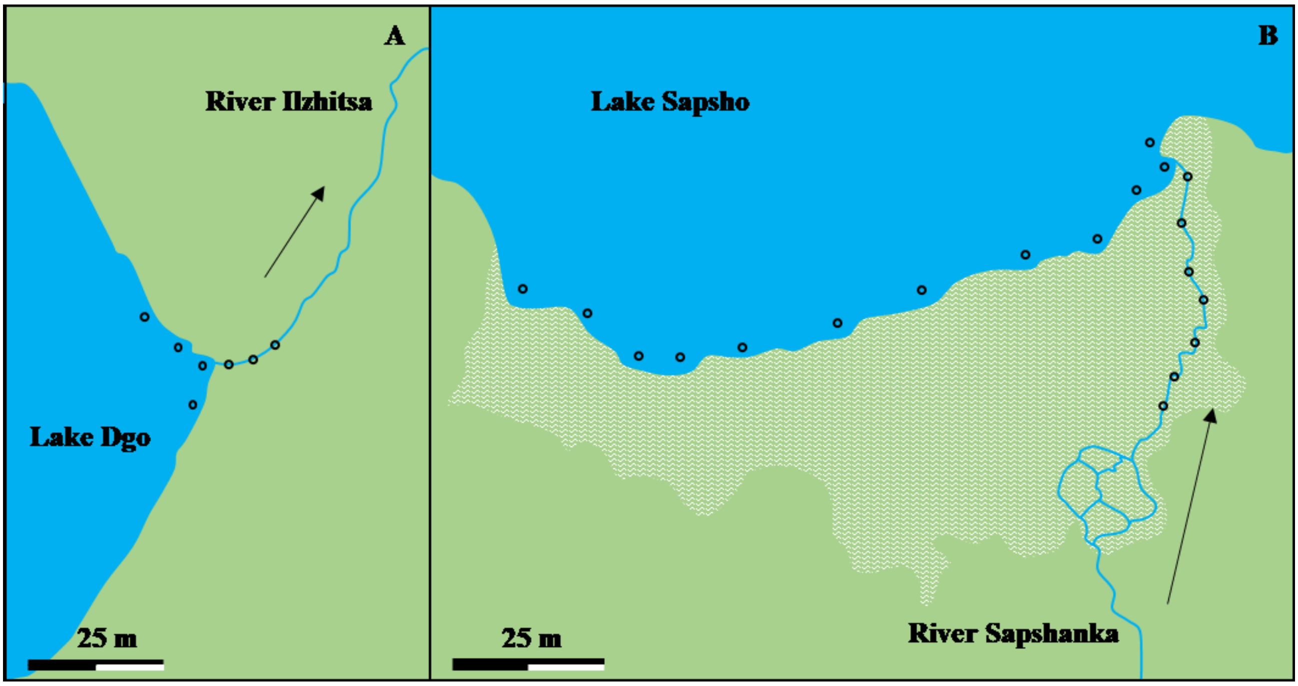

Fig. 2. The studied sites in Lake Dgo (A) and Lake Sapsho (B). Designations: empty dots – sample collection sites with no ammocoetes; shading area – swampy thickets of *Phragmites australis*; arrows indicate current direction of rivers.

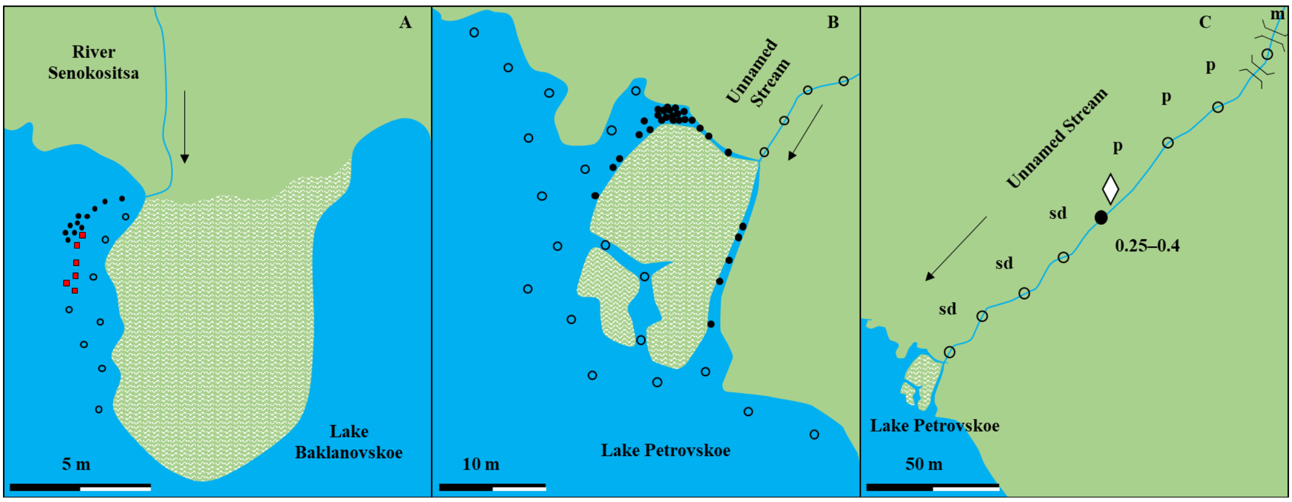

Fig. 3. Map of the ammocoete habitats in Lake Baklanovskoe (A), Lake Petrovskoe (B), and its Unnamed Stream (C). Rotting silt and organic detritus (sd), pebble ground (p), marshy ground in the stream (m); number ranges are for depths (m). Designations: black dots – catches of ammocoetes in swales; red squares – catches of ammocoetes in the sandy swale wall; empty dots – no ammocoetes; white rhombus – sample site for phytoplankton and zooplankton, and benthos; shading area – thickets of *Phragmites australis*; arrows indicate the current direction of rivers.

Lake Baklanovskoe was investigated at the mouth of the River Senokositsa (Fig. 3A). This site was characterised by abundant aquatic and riparian vegetation including *Potamogeton* sp., *Nuphar lutea* L., *Typha latifolia* L., *Persicaria amphibia* L., and *Phragmites australis*. To the south-east of the mouth of the River Senokositsa is a bar which descends into Lake Baklanovskoe to a depth of 12 m and is colonised by a dense patch of *P. australis*, a mass of which floated above the water surface at the time of the survey. Along the vegetation bed, the bottom of the lake forms a shallow fan up to 1.5 m wide. The fan becomes a deep depression in the lakebed where the inflow from the River Senokositsa has scoured a swale. The width of the swale is ~ 1.2 m. Directional flow of the water was not present at the surface or in deeper strata at the survey time. Ammocoetes were found in the lake at the bottom of the swale and within the body of the fan. The River Senokositsa itself was not surveyed due to the abundance of *Heracleum sosnowskyi* Manden. thickets along the riverbanks.

Lake Petrovskoe was investigated where an unnamed stream enters it (Fig. 3B). The shoreline zone of the lake at this site is also densely vegetated with *Phragmites australis*, *Nuphar lutea* and *Potamogeton* sp. At the mouth of the stream, a thick bed of vegetation and *P. australis* was growing in the shallow water. To the right and to the left of the mass vegetation, the water depth increased, by forming two swales extending into Lake Petrovskoe that were free of the vegetation. The outer sides of the swales were formed by beds of *Carex* sp. The current of water over the vegetation and swales was absent in May 2019. In August 2020, ammocoetes were found at the bottom of the swales in the Lake Petrovskoe.

The unnamed stream, which flows into Lake Petrovskoe, was examined in more detail (Fig. 3C). At 160 m and 170 m from the mouth, the unnamed stream flows under two roads in low-flow pipes, making it marshy upstream. No ammocoetes were found in the marshy section of the stream. In the section of the stream downstream from the roads the channel is 2–3 m wide and not more than 0.4 m deep. Before emptying into the lake, the ~ 80-m long section is backwatered, and its flow highly reduced to a speed of 0.05–0.10 m/s. The shallow depth of the water and a significant layer of silt mixed with organic debris (> 0.4 m in depth) leads to decomposition in summer. When the ground was pressed, many gas bubbles were released. No ammocoetes were found in this area of the unnamed stream.

However, 90 m upstream of the mouth, a flowing section (0.20–0.25 m/s) begins with a shallow pebble-sand substrate suitable for the lamprey spawning (Fig. 3C). The length of this section is about 75 m. Ammocoetes have been found at the lower edge of this spawning area. At this point, there was a layer of fine particulate sediment 10–12 cm thick, by overlaying the coarser substrate that was similar to the spawning grounds upstream. The flow rate was ~ 0.2 m/s. Sediment analysis from this area indicates its dominance by sand (1.0 mm to 0.1 mm). The main fractions were 1.0–0.5 mm and 0.50–0.25 mm, totalling more than 50%. The length of this stream section is under 10 m and approximately 25 m^2. The average number of ammocoetes in this area was low (0.08 specimens/m^2).

Ammocoete bed characteristics

Abiotic characteristics of ammocoete beds

In May 2019 in Lake Petrovskoe, and in August 2020 in Lake Baklanovskoe and Lake Petrovskoe, ammocoetes were found in swales filled with a thick debris layer, 0.6 m and 0.5 m deep in each respective lake (Fig. 4A,C) with no signs of substantial decomposition (Table 3). Debris was partly mixed with the sediment forming the lake bottom which included silt and fine sand. Samples from swale habitats collected from beneath the debris layer indicated that Lake Baklanovskoe sediment is dominated by small fractions of fine sands from 0.25 mm to 0.10 mm grain size and smaller (< 0.1 mm), totaling 47%. The total fraction of substrate less than 1 mm in size was 94%. In sediment samples from Lake Petrovskoe, the substrate was predominantly less than 1 mm in size (> 90%) with the main fraction in the 0.50–0.25 mm range, totaling 35.1%. The organic matter content of the samples from Lake Baklanovskoe and Lake Petrovskoe was high, 5.20% and 4.85% respectively. In September 2019, the layer of debris in Lake Baklanovskoe swale was absent, while the bottom of the swale contained large sand and gravel.

The sloping sides of the swale in Lake Baklanovskoe where ammocoetes were found contained loose soil of sand and gravel (Fig. 4A). A sediment sample from this area was dominated by large sands of 1.0–0.5-mm size (52%) and had a high content of gravel 1–5 mm in size (14.93%). Organic matter was completely missing from this sample (Table 3).

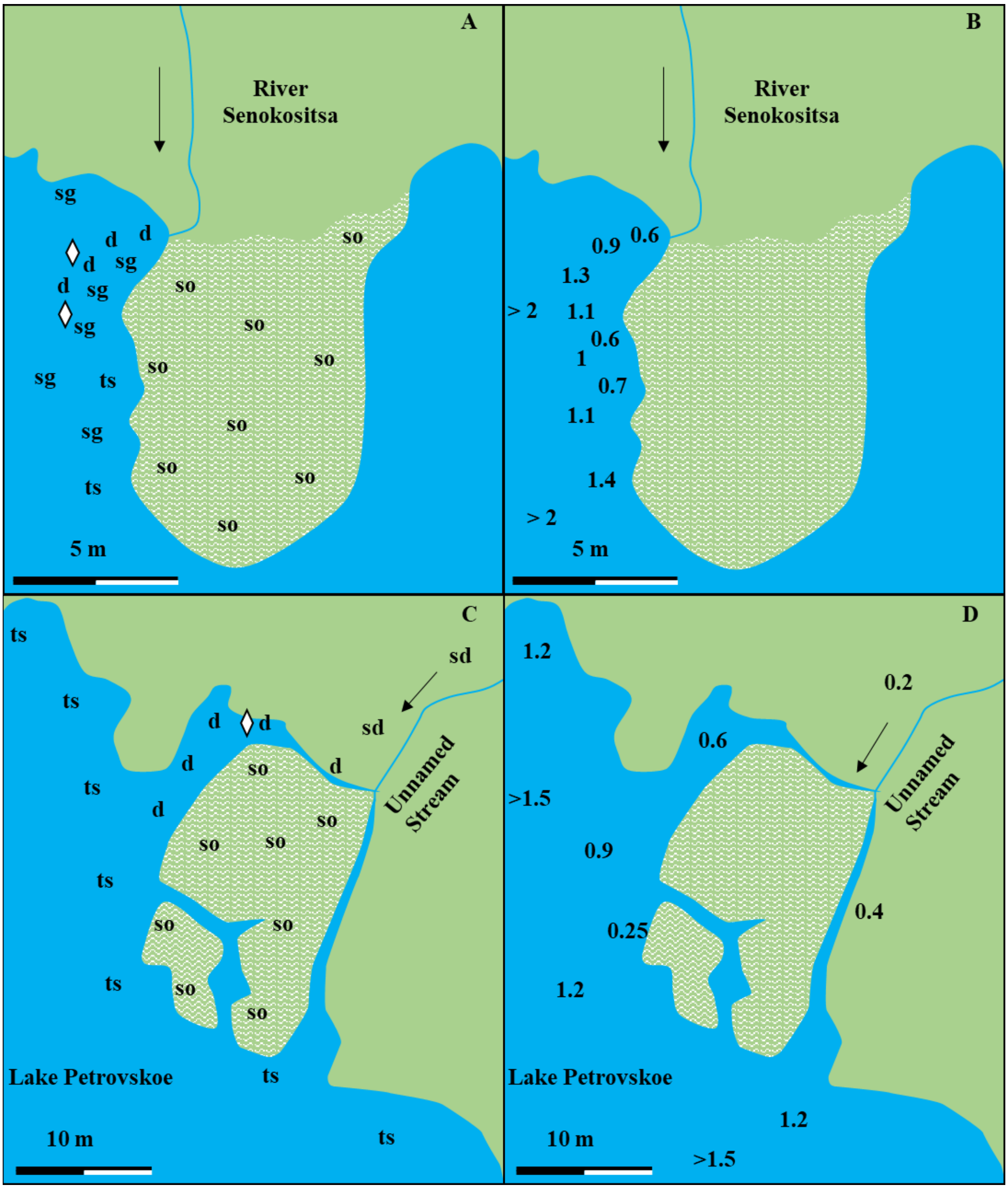

Fig. 4. Substrates and depths in Lake Baklanovskoe (A, B) and Lake Petrovskoe (C, D). Main habitat types: debris (d), rotting silt and debris (sd), tiny sand and silt (ts), coarse sand (sg), reed turf and tiny sand (so). Numbers of ranges are used for depths (m). Designations: white rhombus – sample sites for phytoplankton and zooplankton, and benthos; shading area – thickets of *Phragmites australis*; arrows indicate the current direction of rivers.

Table 3. Abiotic characteristics and ammocoetes abundance of the habitats where ammocoetes were found in Lake Baklanovskoe and Lake Petrovskoe

Biotope characteristics	Lake Baklanovskoe		Lake Petrovskoe
	swale	swale wall	swale
Water depth, m	0.6–1.3	0.6–1.1	0.35–0.70
Substrate	debris	sand	debris
Main ground fraction, mm	0.25–0.10	1.0–0.5	0.50–0.25
Organic component in the ground, %	5.20	0	4.85
Gas bubble emission	low	absent	low
Salinity*, mg/dm^3	231.9–232.8		–
pH*	7.21–8.12		–
Oxygen*, mg/dm^3	7.88–9.04		–
Bed area, m^2	6.6	3.6	36
Burrow depths, m	0.05–0.40	0.05–0.3	0.05–0.30
Averaged ammocoete abundance, specimens/m^2	55	20	5

Note: *parameters are based on Khokhryakov & Antonova (2021); dash means lacking data.

The ammocoete abundance in the swales was 40–70 specimens/m^2 and 1–10 specimens/m^2 in Lake Baklanovskoe and Lake Petrovskoe, respectively (Table 3). In Lake Petrovskoe, ammocoetes aggregated at the head of one of the swales where the average number of individuals exceeded 10 specimens/m^2 (Fig. 3B). In the sloping side of the swale in Lake Baklanovskoe, the larvae abundance was 10–30 specimens/m^2. Additional characteristics of the observed larvae habitats in these lakes are presented in Table 3. The distribution depth of habitats is shown in Fig. 4B,D.

Biotic characteristics of the lake ammocoete habitats

In lakes of the Smolenskoye Poozerye National Park, lampreys are recorded in fish communities with such species as *Esox lucius* Linnaeus, 1758, *Leuciscus idus* (Linnaeus, 1758), *Scardinius erythrophthalmus* (Linnaeus, 1758), *Alburnus alburnus* (Linnaeus, 1758), *Abramis brama* (Linnaeus, 1758), *Blicca bjoerkna* (Linnaeus, 1758), *Rutilus rutilus* (Linnaeus, 1758), *Carassius carassius* (Linnaeus, 1758), *Lota lota* (Linnaeus, 1758), *Sander lucioperca* (Linnaeus, 1758), *Gymnocephalus cernuus* (Linnaeus 1758). It is likely that lamprey larvae can be eaten by at least some of them. It is interesting that lampreys have never been observed in the «perch» lakes, for example, Lake Beloye, Lake Okunevoe, Lake Paltsevskoe, as well as in the habitats of *Misgurnus fossilis* (Linnaeus, 1758) (Kucheryavyy et al., 2019).

Zooplankton sample analysis identified 25 taxa and 18 taxa inhabiting the study areas of Lake Petrovskoe and Lake Baklanovskoe, respectively. Both lakes are dominated by Cladocera (15 species and 11 species respectively) and Copepoda (five species and seven species respectively). Five species of Rotifera were found only in Lake Petrovskoe. The zooplankton density in Lake Petrovskoe is twice that in Lake Baklanovskoe (11 700 specimens/m^3 vs. 6200 specimens/m^3 respectively), though the biomass is higher in Lake Baklanovskoe due to the presence of larger organisms (97.7 mg/m^3 vs. 159.6 mg/m^3). In general, zooplankton taxa are represented predominantly by a typical complex of lentic species. Juvenile stages of the parasitic copepod Ergasilidae were documented in Lake Petrovskoe (200 specimens/m^3).

The abundance of macrozoobenthos in Lake Petrovskoe was significantly higher than in Lake Baklanovskoe (12 500 specimens/m^2 vs. 5500 specimens/m^2, biomass 24.4 g/m^2 vs. 6.8 g/m^2). It should be noted that our study design did not consider large organisms such as *Anodonta* sp., that live on sandy areas of Lake Baklanovskoe (40–60 specimens/m^2) or lamprey larvae. In general, the zoobenthos composition was similar in the lakes. Representative specimens of Oligochaeta, Hirudinea, Gastropoda, Bivalvia, and Crustacea were found. Insects were represented by larvae from the order Diptera (mainly Chironomidae), Ephemeroptera, Megaloptera, Trichoptera, and Coleoptera. Their numbers were dominated by representatives of Tubificidae and mosquito (Chironomidae) larvae. In Lake Petrovskoe, 30% of the total number of individuals were small representatives of Sphaeriidae. Large insect larvae and Mollusca were sporadic, mostly found in qualitative samples. In Lake Petrovskoe, a significant portion of the total biomass was formed by leeches (Hirudinea).

Taxonomic position of ammocoetes

In the present study, within the borders of the Smolenskoye Poozerye National Park, we collected adult lamprey from the River Ilzhitsa and the River Poloviya, belonging to the Western Dvina River Basin (Baltic Sea Basin: Fig. 1). All adults from the River Ilzhitsa were assigned to the genus *Eudontomyzon* based on characteristics of their dentition. Both Lake Baklanovskoe and Lake Petrovskoe flow ultimately into the River Poloviya. The taxonomy of adults is uncertain in the River Poloviya. Adults (both male and female) were caught at a spawning site. Most of them were also classified as *Eudontomyzon*. But it should be noted that four males of this group were identified as *Lampetra fluviatilis*, a resident form (or *Lampetra planeri* Bloch, 1784, according to Renaud, 2011), because they lacked a posterior row of teeth and teeth on the right and left exolateral fields and differed from the other adults with their colouration and pigmentation of the dorsal and caudal fins (Fig. 5).

Comparisons of larvae from the two lakes with *L. fluviatilis* larvae from rivers of the Leningrad Region have shown that they do not belong to *Lampetra*. In the larvae found, the tail fin is sharper and pigmented. The central cirrhi corresponds to representatives of *Eudontomyzon*: its base is triangular and unpigmented, as are the fields along the elastic ridge, upper and lower branchial regions. Further, the dorsal and lateral sides of these larvae are olive-coloured and lighter than in *Lampetra* larvae. Because of the difficulty distinguishing larvae of various species within the *Eudontomyzon* based only on morphological features, we classified them as *Eudontomyzon* sp.

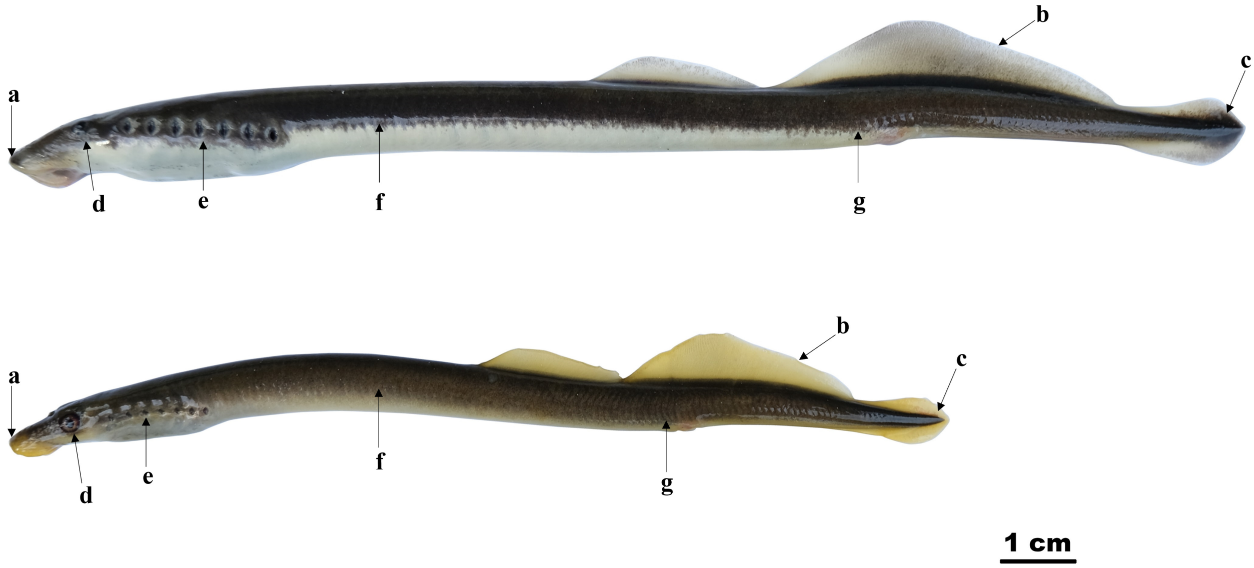

Fig. 5. External view of the adult males of *Eudontomyzon* sp. (top) and resident form of *Lampetra fluviatilis* (bottom) from the Smolenskoye Poozerye National Park. Designations: a – pigmentation of upper part of oral discs; b – colouration and pigmentation of dorsal fins; c – colouration and pigmentation of caudal fins; d – pigmentation of subocular regions; e – pigmentation of lower branchial regions; f, g – dorsoventral dividing line.

Larvae characteristics

The size of captured larvae ranged from 32 mm to 188 mm, while the weight ranged from 0.081 g to 10.24 g. No larvae under one year of age were caught (as said above, that may be due to the used gear), though many individuals were caught with clear signs of metamorphosis, which appears to occur in larvae when they reach a length of ~ 130 mm. This is comparable to the size of metamorphosing larvae observed in the River Ilzhitsa (the minimum TL of a metamorphic specimen in 2020 was 126 mm).

The fullness of the digestive tracts of larvae sampled in Lake Baklanovskoe was high, amounting to 70% of individuals with four points, and the intestines were filled evenly. There were a lot of algae identified in the intestines sampled. Bacillariophyta was dominated by *Navicula*, as well as *Aulacoseira* spp., *Cymbella* sp., *Gomphonema* sp., *Ulnaria* sp., and *Tabellaria* sp. Cyanoprocariota played a significant role in the diet, with a portion of the larval intestine containing masses of single cells, mucous ball colonies, and *Microcystis* sp. In other larvae, intestine contents were primarily caps of filamentous colonies. Colonies of *Woronichinia* sp. were found in all the intestines we sampled. All the larvae sampled had *Eudorina* sp. (Chlorophyta) in their intestines, and some individuals also had Charophyta (order Desmidiales).

The degree of fullness of larval intestines sampled in Lake Petrovskoe was also high. In 2019, intestine fullness was categorised predominantly at four and even five points for sampled individuals, and in 2020, both in Lake Petrovskoe and in its unnamed tributary, intestine fullness was categorised mostly at three points. No differences were observed in fullness by part of the intestines: they were filled evenly. Boli of larvae sampled in Lake Petrovskoe in May 2019 were characterised predominantly by algae, mainly Bacillariophyta and Euglenophyta. In the intestines of some larvae, these taxa represented visually more than half of the total algae. Among Bacillariophyta, *Navicula* was predominant. Other Bacillariophyta representatives that were always present in small numbers were *Nitzschia* spp., *Gomphonema* sp., *Pinnularia* sp., *Pleurostigma* sp., *Ulnaria* sp., and *Closterium* spp. (Charophyta, Desmidiales). In some cases, identified prey items also included Testacea, Nematoda, Rotifera, and Ostracoda. All identified taxonomic forms belong to the group of epifaunal organisms. In August 2020, the number of algae in the intestine of the ammocoetes was considerably lower. Only Bacillariophyta were found, with *Navicula* spp. predominating. A similar pattern was observed in the unnamed tributary to Lake Petrovskoe, but the number of algae in the boli from visual inspection was even lower.

Discussion

Even though ammocoetes live mainly in streams, rivers, and brooks, in the Smolenskoye Poozerye National Park, they have now been found in habitats of two small lakes. We identified three known habitats of Petromyzontiformes larvae in lentic conditions. Shandikov & Goncharov

(2008) mention the population of *Eudontomyzon mariae* (Berg, 1931) in a small pond formed on a stream draining into the River Seversky Donets. Reid & Goodman (2017) discussed conditions for *Entosphenus* sp. larvae in the flowing Hamilton Ponds in detail, an artificial two-pond system, which was created at the mouth of Grass Valley Creek to reduce the flow of sand into the main course of the River Trinity (California, USA). Lentic populations of *Petromyzon marinus* larvae in Lake Superior are well recognised (Lee & Weise, 1989; Fodale et al., 2003). To assess the phenomenon of ammocoete use of lentic habitats, we compared conditions in Lake Baklanovskoe and Lake Petrovskoe with existing theories about preferred habitats of larvae.

Characterisation of lake habitats

A primary limiting factor to ammocoete distribution is the presence of suitable substrate for ammocoete beds (Applegate, 1950; Kan, 1975; Graham & Brun, 2007). Field observations indicate that ammocoetes prefer shoreline areas dominated by sand with an overlayment of organic debris (Leach, 1940; Dendy & Scott, 1953; Hardisty & Potter 1971; Yap & Bowen, 2003; Burr & Shasteen, 2007). Along with the size substrate particles, the selection by ammocoetes is bound by the density of the substrate (Beamish & Lowartz, 1996; Smith, 2009). In rivers, due to the presence of flow, sand is often mixed with mud, but water circulation in the interstices maintains oxygenation and flow.

Ammocoetes inhabiting streams prefer calm areas or pools. Studies conducted by Stone & Barndt (2005) showed that the most preferred areas are those where the current velocity is between 10 cm/s and 20 cm/s, with a maximum larval abundance recorded in low-current/no current area. The most suitable depths for lamprey habitats were 60–80 cm (Stone & Barndt, 2005), though ammocoetes can live at greater depths, of 2 m or more (Taverny et al., 2011) up to 12–22 m (Renaud, 2011; Polyakova et al., 2021).

In Lake Baklanovskoe and Lake Petrovskoe, we documented the largest abundance of larvae in swale features (Fig. 6) in sedimented debris (up to 55 specimens/m^2 and 5 specimens/m^2, respectively), while in the sandy sediments, the abundance was lower, up to 20 specimens/m^2. These data differ from those of Reid & Goodman (2017), who documented that in Hamilton pond systems, ammocoetes preferred sand dominated sediment (27–45 specimens/m^2) and to a lesser extent, silty organic debris. In Lake Superior, larvae of *Petromyzon marinus* preferred soft sediment (sand with a small fraction of silt or clay) located on the slopes of the drop-off. The abundance of larvae in such soil reached 2–5 specimens/m^2 (Fodale et al., 2003).

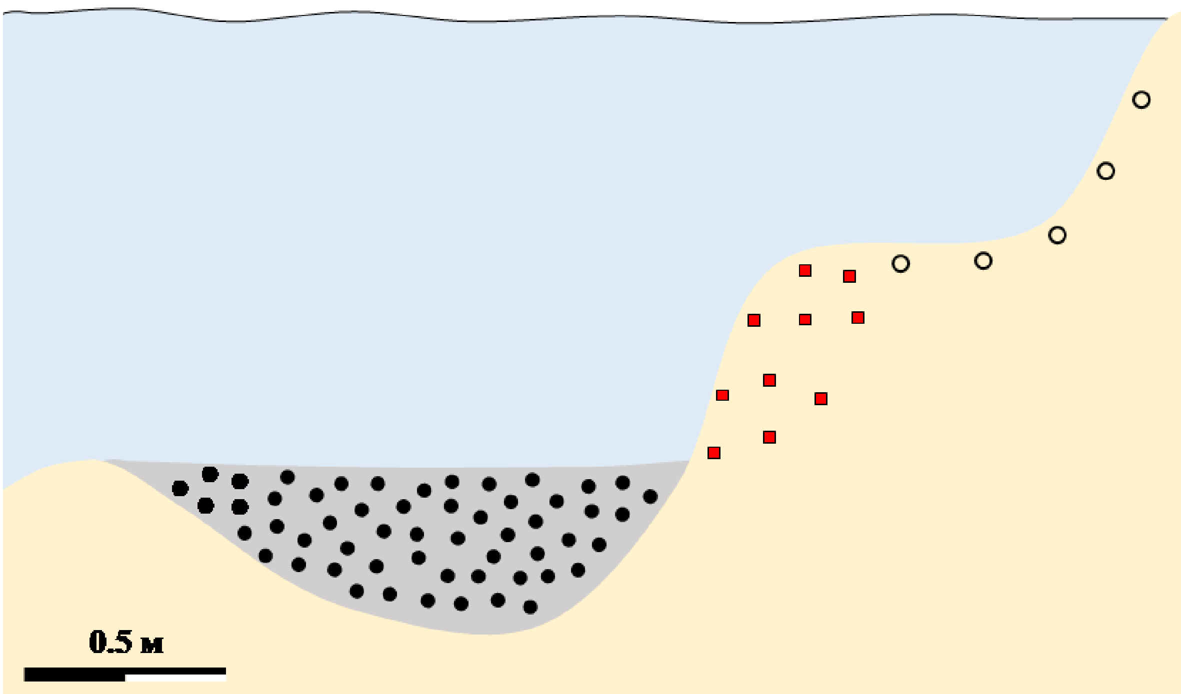

Fig. 6. Habitat of *Eudontomyzon* sp. ammocoetes in Lake Baklanovskoe. Designations: ▭ – debris; ▭ – coarse sand; relative abundance of the ammocoetes is indicated by density of black dots in swale, and by red squares in swale wall; empty dots – no ammocoetes.

In the studied lakes ammocoetes were documented either in loose organic deposits or in loose large sand, both substrates that retain water circulation. Dense substrates, like the fine sand areas next to vegetated masses, were avoided by lampreys. A similar situation was observed in *Lampetra fluviatilis* substrate preference experiments (Zvezdin et al., 2017). Under non-flowing conditions, sand was the least favoured substrate type relative to soft mud, debris, and pebbles. In addition to water circulation, the preferred substrate must be conducive to larval burrowing. That is why in Lake Baklanovskoe the abundance of ammocoetes in the sandy sides of the swales was almost three times smaller than in ammocoetes bed sedimented with debris in the swale itself (Table 3, Fig. 5).

Reid & Goodman (2017) found that *Typha* sp. roots were more likely to have no ammocoetes, though in rare cases they may reached a density of 6 specimens/m^2 in these habitats. In the dense beds of other aquatic plants, the picture was similar, i.e. usually abundance ranged from 0–4 specimens/m^2. The lakebeds that we studied were extensively covered with submerged vegetation, though we did not document ammocoete settlement in these areas. Fodale et al. (2003) noted that aquatic vegetation (*Potamogeton* spp.) can play a role in the accumulation of soft sandy soils that would be used for ammocoetes.

In habitats occupied by ammocoetes in the Smolenskoye Poozerye National Park and in the Hamilton Pond system, the release of gas bubbles from the ground was low or absent. In contrast, in Lake Dgo and Lake Sapsho, where no ammocoetes were found, there were many gas bubbles. This indicates that larvae avoid areas where organic residues are intensively degraded. Organic decay considerably alters the hydrochemical conditions at microscale levels, which in turn degrades the ecological characteristics of habitats. For example, it is performed through the promotion of sediment anoxia and decreasing the number of available food items for ammocoetes, which determines the habitat suitability as ammocoetes beds (Sutton & Bowen, 1994; Beamish & Lowartz, 1996; Moser et al., 2007; Smith, 2009; Limm & Power, 2011).

The absence of direct currents in the lake areas considered and the known depths preferred for ammocoete habitation (0.35–1.30 m in Lake Baklanovskoe and Lake Petrovskoe and 0.30–1.82 m in Hamilton Ponds) also correspond to the preferences of larvae for lotic ecosystems. Thus, it can be concluded that the identified lake habitats were similar to the sedimentary areas of riverbanks, i.e. stretched pools or streams with low water exchange. According to the classification of Nazarov et al. (2016), the habitat of swales can be attributed to deltas at the mouth of a stream and to channel formation between sandbars, riverbanks, and mid-channel sandbars. The classification of Slade et al. (2003) for river conditions identifies three habitat types: preferred (Type I); acceptable but not preferred (Type II); and unacceptable (Type III). The swale habitats identified in Lake Baklanovskoe and Lake Petrovskoe can be attributed to Type I ammocoete habitat, and the sandy sloping sides of the swales to Type II.

Settlement of lamprey larvae in lakes

It is believed that the primary distribution of larvae from the spawning grounds in rivers occurs during downstream migrations (Quintella et al., 2005; Pavlov et al., 2014) until ammocoetes find a substrate suitable for further habitation, the ammocoete bed (White & Harvey, 2003; Brumo, 2006; Brumo et al., 2009). This settlement mechanism has been documented for both anadromous and resident forms of *L. fluviatilis* (Zvezdin et al., 2017). Relocation of larvae of various lamprey species of older ages also occurs mainly downstream (Lucas & Bracken, 2010). Therefore, there is reason to believe that the same mechanism occurs in the movements of *Eudontomyzon* sp. larvae.

In the watersheds we studied, due to migratory activity, the primary distribution and redistribution of larvae may result in their entering a lake, where they settle in swales with suitable habitats. The systems of the River Senokositsa and Lake Baklanovskoe, the nameless creek and Lake Petrovskoe are all similar in their hydrological structure. Larvae can enter lakes both during floods and between hydrologic stages, as the distances from spawning sites and streams to lakes are not long. The movement of ammocoetes into lakes during lower flow periods in summer may be stimulated by deteriorating conditions in the streams, such as falling water levels (Kelly & King, 2001), reduced velocity (Jażdżewski et al., 2016), growing degree of shading along a stream, which may make small, shallow, and narrow streams into heterotrophic (Minshall, 1978) or eutrophication resulting in algal blooms reducing light penetration, water clarity, changing water chemistry (Wade et al., 2015). Any of these external stimuli but, more likely, a complex of factors (Stone & Barndt, 2005) can lead to a highly aggregative non-random spatial distribution of ammocoetes in more suitable environmental conditions, which is preceded by the exit of specimens from the grounds and moving eventually downstream. In some of the studied cases ammocoetes avoiding sub-optimal or non-optimal conditions appeared in the lentic habitats (Lake Sapsho).

In our opinion, the larvae absence in Lake Dgo and the River Ilzhitsa systems relates in part to the fact that known spawning grounds are located far from the lake source of the river that we studied. Adults most likely do not reach the lake during spawning, and while the distribution of larvae upstream is possible, it is less frequent and not widespread (Quintella et al., 2005; Dawson et al., 2015). In the Hamilton Ponds system, the abundances of larvae were higher at the inflow to the ponds than at their outflow (Reid & Goodman, 2017). An additional barrier to the lamprey settlement during the study was formed by the marshlands and overgrown vegetation in the lower reach of the River Sapshanka and in the source of the River Ilzhitsa. The lamprey redistribution was also blocked, on one hand by physical passage barriers to potential migrants, and on the other hand, by unsuitable habitat conditions, with the stagnant nature of these sites contributing to the massive decay of organic material on the bottom.

During earlier observations by the authors in 1994–2001, lamprey larvae were documented in Lake Sapsho, near the mouth of the River Sapshanka. Results of hydrochemical comparison of surface waters in Lake Sapsho and Lake Baklanovskoe do not identity any significant differences (Khokhryakov & Antonova, 2021). Therefore, we believe the decomposition process occurring in substrates may cause these habitats to be unsuitable for lamprey larvae. Much of the development of these processes may be related to the exchange of water masses and the influx of freshwater. In the littoral area of Lake Baklanovskoe and Lake Petrovskoe, where free flow of water occurred and decay was not observed, ammocoetes were documented. No ammocoetes were found in Lake Dgo and Lake Sapsho, where abundant vegetation slowed water exchange and organic material was considerably degraded. The key importance of river-water inflow underscores the comparison of well-known Petromyzontiformes lentic habitats: they are either ponds characterised by flow, or lake bays where wind and run-off flows are present.

The larvae distribution in lakes is probably not limited to swale habitats. In September 2020, there was no debris layer in the swale in Lake Baklanovskoe, where ammocoetes were found a month earlier. It can be assumed that the contents of this layer were washed away by the flow of water from the River Senokositsa, for example, because of a flash flood. A similar mechanism is shown for ammocoetes in Lake Superior, where floods flush ammocoetes (abundant in the mouth areas of the lake tributaries) to the littoral area of the lake (Lee & Weise, 1989). In the lakes we studied and in Lake Superior, a «migration of biotopes» occurs, i.e. movement of ammocoetes beds along with larvae and other inhabitants. These movements can be attributed to involuntary passive migrations of aquatic organisms together with habitats, as described by Nezdoly & Pavlov (2019) for water bodies in tropical zones.

The larvae, once flushed from the swale habitat, could be distributed further into the lake, and reach depths of up to 7 m, which is not critical to their survival. It should be noted that in Lake Baklanovskoe larvae of all sizes were captured (except the young-of-year larvae, which may be related to the selectivity of the fishing gear), as well as metamorphic individuals. That is, the larvae may mature to adulthood in the lake, and during spawning migrations enter both their native stream and other streams connected to Lake Baklanovskoe.

Conclusions

Ammocoetes of the genus *Eudontomyzon* were recorded in lakes of the Smolenskoye Poozerye National Park. Their habitats were studied for the first time in the littoral zone of small lakes in the Smolenskoye Poozerye National Park. Suitable habitats in the lake and the absence of passage barriers to migrants are prerequisites for the settlement of littoral areas. The known littoral habitats of ammocoetes were associated with the mouths of tributaries, where a portion of their life cycle occurs. Redistribution of larvae through lakes can likely continue both through escaping from the littoral zones along with the habitat, and through active movement of larvae, metamorphic, and adult individuals. In the described lakes, biotic and abiotic habitat characteristics can thus provide suitable conditions for development of several stages of the life cycle of resident lampreys, except for the spawning stage, although we cannot exclude the possibility of spawning in lakes, as there are observations on spawning of *Entosphenus minimus* in Miller Lake itself (Bond & Kan, 1973). The primary habitat constraints on ammocoetes appear to be suitable flow conditions, fine grained sediments and absence of excessive organic decomposition (indicated by gas release), in dense fluviolacustrine systems, the habitation of lakes by lamprey larvae is a potentially common but poorly understood phenomenon. However, it is crucial to our understanding of benthic communities and their ecology in the lakes, the recognition of the role played by larvae in substrate processes, and the conservation of these species.

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ОБНАРУЖЕНИЕ ЛИЧИНОК *EUDONTOMYZON* SP. (PETROMYZONTIDAE) В ОЗЕРАХ И ХАРАКТЕРИСТИКА ИХ МЕСТООБИТАНИЙ

А. О. Звездин[1,*], Н. В. Полякова[1], А. В. Кучерявый[1], В. Р. Хохряков[2], А. В. Колотей[1], Д. С. Павлов[1]

[1]*Институт проблем экологии и эволюции имени А.Н. Северцова РАН, Россия*
[2]*Национальный парк «Смоленское Поозерье», Россия*
**e-mail: a.o.zvezdin@gmail.com*

Продолжительный пресноводный период жизни личинок Petromyzontiformes (далее – пескоройки) реализуется, главным образом, в лотических местообитаниях и хорошо изучен. Данные об обитании пескороек в лентических местообитаниях крайне ограничены сведениями о находках особей в прудах или крупных озерах. Для территории национального парка «Смоленское Поозерье» характерна развитая сеть озер и рек, водотоки которой обильно населены личинками миног родов *Lampetra* и *Eudontomyzon*. В настоящей работе мы рассматриваем заселенность пескоройками озер, принадлежащих к этой системе, а также механизмы проникновения в них миног. Были проведены поиск личиночных местообитаний и их описание (анализ структуры личиночного ложа, в том числе фракционного состава грунтов, биотических и абиотических характеристик), что позволило впервые задокументировать личинок и метаморфных особей *Eudontomyzon* sp. в литоральных частях малых озер. Пескоройки были обнаружены в пограничных биотопах между устьями рек и озерами. Отличительной особенностью обнаруженных местообитаний от типичных речных является отсутствие выраженного течения. В них происходит рассеивание воды, которая постоянно перемешивается в изученных биотопах. В исследованных озерах биотопы, предпочитаемые *Eudontomyzon* sp., состоят из желобов, заполненных растительным мусором, вынесенным из впадающих водотоков и осевшем при уменьшении направленного тока. Пескоройки из личиночных лож этого типа находятся в благоприятных с точки зрения обеспеченности пищей условиях. Подобные местообитания могут быть как постоянными, так и временными, что связано с изменением уровня воды в притоках. Возрастающий во время паводков расход воды может смывать растительный мусор и пескороек дальше в озеро. Выраженных процессов гниения в местах обитания пескороек не обнаружено. Результаты исследования показывают, что личинки могут быть обычными обитателями в лентических биотопах.

Ключевые слова: личиночное ложе, механизм перераспределения, механизм расселения, миграция, миноги, озерное местообитание, пескоройки