# LAMPREYS (PETROMYZONTIDAE)

# Morphobiological Characteristic of the Arctic Lamprey Lethenteron camtchaticum (Petromyzontidae) in the Basins of Large Rivers of the Arkhangelsk Region, Russia

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Abstract—Data have been presented on the morphobiological parameters of the anadromous Arctic lamprey Lethenteron camtschaticum (Tilesius, 1811) in spawning stocks of large river basins of the Arkhangelsk region — Onega, Severodvinsk and Mezen. The clinal variability of linear-weight parameters, absolute fecundity, and a number of plastic characters was revealed, according to which the lamprey population from the Northern Dvina River occupies an intermediate position between the lampreys of the Onega and Mezen rivers. Higher average values of biological indicators (length, body weight, fecundity) were noted in European lamprey populations compared to those in individuals from the Far Eastern part of the range.

**Keywords:** Arctic lamprey, ecology, morphology, biology, large river basins, European North **DOI:** 10.1134/S0032945222070049

# **INTRODUCTION**

Arctic lamprey Lethenteron camtschaticum (Tilesius, 1811) is an anadromous predatory cyclostome species (Cyclostomata) with a discontinuous range; it is widespread in the Arctic and north Pacific Ocean. Its modern habitat covers the waters of the Arctic seas from the Varangerfjorden in the Barents Sea to the Beaufort Sea, in the North Pacific, from the Bering Strait to the southern part of the Korean Peninsula (the Sea of Japan) and the central part of Honshu Island along the Asian coast in the east to Kenai Peninsula to the Gulf of Alaska along the American coast in the west (Mecklenburg et al., 2002; Fedorov et al., 2003; Renaud, 2011; Orlov and Baitalyuk, 2015). In Russia, the European part of the range extends from the Kola Peninsula (basins of the Pasvik and Tuloma rivers) in the west to the basin of the Kara River and the western coast of the Yamal Peninsula in the east. The Arctic lamprey has been also reported for the basin of the Ob River: Tobol, Tura, Irtysh, and Tom' rivers (Berg, 1948). The Asian part of the range covers the eastern Pacific coast, where the species reappears in the Anadyr River basin and further southwards to the rivers of Korea.

Within the European North of Russia, the Arctic lamprey is found in the basins of the White Sea, the southeastern Barents Sea, and the Kara Sea (southwestern, occurring in significant numbers on the Kanin Banks, in the Cheshskaya Bay and in the river. Pechora. Recorded in the rivers Onega, Severnaya

Dvina, Vyg, Mezen and other rivers of the region (Berg, 1948; Zvereva et al., 1953; Ostroumov, 1954; Novoselov, 1992; Boznak et al., 1995; Stasenkova and Novoselov, 2007: Kudersky, 2011). In the Kara Sea, it occurs in its southern part along the coast. The species is recorded in the Baydaratskaya Bay, the Gulf of Ob, the Khalmyer (Gydan) Bay, and the Yenisei Gulf (Dolgov et al., 2018). In the regions adjacent to the Gulf of Ob, the Arctic lamprey has been known only westwards (the Pechora Sea). In August 1935, a single specimen of the Arctic lamprey has been caught in the northern Gulf of Ob, during the wintering at the Cape Drovyanoy; it was a young specimen 17.1-cm long weighting 5 g (Burmakin, 1940). Recent information on the Arctic lamprey was presented for the Gulf of Ob and the Taz Estuary of the Kara Sea (Matkovskii, 2006). According to oral communications with the Nenets, lampreys were accidentally caught in the Tambey River (Burmakin, 1940). Target fishing for lampreys was not carried out in the Gulf of Ob (Burmakin, 1940), it is currently absent as well.

The lamprey is distinguished by its serpentine body, which has two dorsal fins, separated in immature specimens and connected in adults. The anterior dorsal fin is lower than the posterior one. The caudal fin connects to the dorsal and anal fins. There are seven gill openings in the anterior part of the body on its sides, as a result, the lamprey has the local name "seven holes". The general coloration of the body is

Fig. 1. Oral funnel of Arctic lamprey Lethenteron camtschaticum from the Mezen River (photo by A.P. Novoselov).

dark, the upperparts are often grayish, the underparts are white (Berg, 1948; Nikolskii, 1971; Ryby..., 2010).

Up-to-date, lamprey taxonomy is very complex as that of whitefish (genus Coregonus) and of Arctic char (Salvelinus alpinus); this causes certain difficulties even when applying modern methods of genetic analysis (Lang et al., 2009; Artamonova et al., 2011, 2015). Previously, the anadromous Arctic lamprey was presented in Russian publications as L. japonicum; however, according to the priority rule, it was re-assigned with the original name L. camtschaticum. The number of myomers and the dental formula on the mouth funnel are main systematic features of lampreys. In the Arctic lamprey, the number of trunk myomers varies from 65 to 77. The dentition of the mouth funnel is well developed: all teeth are sharp outside the spawning season. The lower labial teeth form one row; they are well-developed. There are two teeth on the maxillary plate, and six or seven teeth, on the mandibular plate (Fig. 1).

Lateral labial teeth are bifid, three on each side. The number of teeth on the maxillary plate vary individually, but in narrow range; for the most specimens, there are two. The number of teeth on the lower jaw plate varies much greatly; both single-ended and bifid teeth are found. There are up to 18 small teeth on the anterior lingual plate (Martynov, 2002).

Information about the marine period of lamprey life in the White Sea is limited to single publications (Novikov and Kharlamova, 2018). At the same time, within the range boundaries, it prefers shallow waters near the river mouths (Atlas..., 2003). After the riverine larval period, lampreys migrate seawards, where they lead a predatory lifestyle, sucking to the fish body and feeding on their blood and muscle tissue (Berg, 1948; Nikolskii, 1971; Stasenkova, Novoselov, 2007; Orlov and Pelenev, 2009; Pelenev et al., 2010; Orlov,

2012; Mateus et al., 2021). In summer, in the Dvina Bay of the White Sea, lampreys can cause some damage to fisheries, since they suck the fish entangled in nets (Kuderskii, 1998).

In the Far Eastern part of the range, the Arctic lamprey has been studied relatively in detail. Its biology, morphology, intraspecific structure, behavioral features, and variations of life strategy have been described (Mecklenburg et al., 2002; Fedorov et al., 2003; Kucheryavyi et al., 2007a, 2007b; Kucheryavyi, 2008, 2014; Nazarov et al., 2011; Orlov and Baitalyuk, 2015). The current state of its populations in the European part of Russia (the western part of the range) is not sufficiently covered in the scientific literature. A general description of cyclostomes in water bodies of the European North-East of Russia is given (Boznak et al., 1995). There is fragmentary information about the morphology of the Arctic lamprey in the Vashka River, the tributary of the Mezen River (Martynov, 2002), about the biology of the species and its fishery in the Severnava Dvina River (Kozmin, 2011a, 2011b), as well as brief description on its distribution in the water bodies of the Arkhangelsk Region (Stasenkova and Novoselov, 2007).

In this regard, the obtained materials on the morphobiological characteristics of the Arctic lamprey in the European part of its range are of scientific interest and relevant. In this paper, comparative analysis is performed for morphological data and biological characteristics of the spawning stocks of the Arctic lamprev from the three largest rivers of the Arkhangelsk Region and clinal variability of some plastic features is revealed for the first time.

The study aims to summarize information about the morphobiological parameters of the anadromous Arctic lamprey from the western part of its range: the Onega, Severnaya Dvina, and Mezen rivers.

#### MATERIALS AND METHODS

The material was collected in 2000–2019 during the autumn-winter spawning migration of the Arctic lamprey (January-March) from commercial and amateur catches in the Onega River (101 specimens), the Severnaya Dvina River (28), and the Mezen River (45). Lampreys were caught with fyke hoop nets in the main channel of the river during anadromous migration. The systematic status of the species is presented in accordance with modern taxonomic concepts (Renaud, 2011; Nelson et al., 2016). Laboratory processing has been carried out on freshly caught specimens according to the standard method (Pravdin, 1966). Lamprey morphometry was measured with a vernier caliper with a 0.1-mm accuracy; individuals were weighed on household scales with a 1.0-g accuracy.

Absolute fecundity was determined by the weight method (Anokhina, 1969): the number of eggs were

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counted and recalculated subsequently for the weight of the entire ovary. Individual relative fecundity was calculated per 1 g of body weight. Statistical processing of the results was performed in the SPSS program. When assessing the differences in the plastic signs of the lampreys of the Onega, Severnaya Dvina, and Mezen rivers' basins, the Student's *t*-test was used for independent samples checked firstly by the Levene test for equality of variances (Ivanter and Korosov, 2003); statistically significant differences were set at p < 0.05 (Ivanter and Korosov, 2003).

# RESULTS

The smallest Arctic lampreys of the spawning stock in terms of body size and weight are found in the population from the Onega River; somewhat larger migrating individuals are caught in the Severnaya Dvina River. The largest lampreys are registered in the Mezen River, their absolute length varies from 34.3 to 51.1 cm, body weight, from 43 to 193 g. Thus, there is an increasing trend of both the linear and weight indicators of the Arctic lamprey in spawning stocks eastwards (the Onega River—the Severnaya Dvina River the Mezen River). The results of measurements of analyzed specimens are presented in Table 1.

Pairwise statistical analysis of samples obtained from different river basins evidences that only two signs out of 18 analyzed (snout length and distance between the eye and gill apparatus) have no significant differences between the spawning stocks of the Arctic lamprey populations in the analyzed river basins. For all other signs, there are differences in various combinations.

In the western cluster of adjacent river basins "the Onega River—the Severnaya Dvina River", eleven plastic signs differ significantly (Tables 1, 2). In the Onega River, the lamprey spawning stock is characterized by greater distances between the first and second dorsal fins, the height of these fins, the length of the dorsal part of the caudal fin, and the distance from the snout tip to the first gill opening. For the lampreys from the Severnaya Dvina River, the length of the base of the dorsal fins, the distance from the anus to the end of the caudal fin, head height, as well as the length of the gill apparatus, and the diameter of the oral disc are significantly greater.

When comparing lamprey populations of the Severnaya Dvina River and Mezen River, located to the east, significant differences are found for 12 out of 18 traits. The lampreys from the Severnaya Dvina River have significantly greater values. Only three signs (the greatest body height, the distance between the dorsal fins, and the length of the gill apparatus) are higher for the lampreys from the Mezen River compared to those from the Severnaya Dvina River (Tables 1, 2).

When comparing lamprey populations of the rivers most distant from each other, the Onega River (to the west) and the Mezen River (to the east), the differences are significant similarly to the cluster "the Onega River—the Severnaya Dvina River" in eleven studied signs, but in other variations. For the lampreys from the Onega River, antedorsal and anteanal distances, the length of the dorsal part of the caudal fin, the distance from the snout tip to the gill apparatus, the eye horizontal diameter, and the oral disc diameter are greater (Tables 1, 2).

The lowest absolute fecundity is noted for the Arctic lamprey from the Onega River, 17.3–50.1 (average 38.6) thousand eggs. Slightly higher absolute fecundity is found in the lampreys from the Severnaya Dvina River, 22.6–49.2 (40.4) thousand eggs. The maximum values, 34.3–67.1 (58.2) thousand eggs, are recorded for the lampreys of the Mezen River (Table 3). Therefore, there is a certain trend of increasing the absolute fecundity of the Arctic lamprey eastwards in the rivers of the northeastern European Russia.

No linear dependence has been found for the relative fecundity on the geographical location of the rivers, but the opposite trend is observed (Table 3), since the lowest relative fecundity is observed in the easternmost lamprey population from the Mezen River (464.1 eggs per 1 g of body weight). The highest value of this indicator is registered for the lampreys from the Severnaya Dvina River (603.9 eggs per 1 g body weight). A slightly lower relative fecundity is noted for the lampreys from the Onega River (577.0 eggs per 1 g of body weight).

#### DISCUSSION

According to the data published earlier (Berg, 1948; *Atlas...*, 2003), the absolute length of a mature lamprey varies from 11.0 to 62.5 cm, weight, from 150 to 200 g. Adult anadromous lampreys reach a length of 62 cm and a weight of 240 g; the body length of resident lampreys is up to 18–35 cm (Martynov, 2002). The lifespan of anadromous lampreys is up to seven years; resident forms live less. In the Mezen River basin, the absolute length of males and females averages 42 cm, body weight, 110 g. The sex ratio in the spawning stock is close to 1 : 1. The coefficient of gonad maturity in females averages 6.6%, in males, 3.3% (Martynov, 2002).

There are only scarce morphological data on the Arctic lamprey of the study area. This is the description of the lamprey morphometry from the Onega River (Kuderskii, 2011), some measurements are given for the populations inhabiting the water bodies of the European North-East of Russia (Boznak et al., 1995). According to plastic signs, the females from the Vashka River are larger than males, but the males have higher head index values (from the snout tip to the first gill opening) and higher relative tail length. In males, the horizontal eye diameter is also significantly higher. At the same time, these sex differences are pro-

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$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		Body weight, g	19.0-125.0	$50.59 \pm 2.096$	21.064	443.692	21.0-139.0	+1	27.382	749.774	43.0-193.0	$127.02 \pm 5.172$	34.701	1204.159	
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$ \begin{array}{llllllllllllllllllllllllllllllllllll$		aa	58.50-76.92	$73.30 \pm 0.215$	2.155	4.644	70.78-75.78	$73.38 \pm 0.272$	1.437	2.065		$72.30\pm0.181$	1.216	1.479	
ID1 $ 0.54- 6.06$ $ 4.05\pm0.114$ $ 1.42$ $ 1.36-1.36$ $ 1.36-1.78$ $ 1.95- 6.22$ $ 1.39\pm0.134$ $ 1.41-1.91$ $ 1.52\pm0.026$ HD1 $ 1.36-2.78$ $2.00\pm0.028$ $0.284$ $0.081$ $ 1.32-2.73$ $ 1.80\pm0.047$ $0.247$ $0.061$ $ 1.4-1.91$ $ 1.52\pm0.026$ LD2 $ 1.84-2.669$ $2.261\pm0.132$ $ 1.329$ $ 1.766$ $ 1.82-1.751$ $2.332\pm0.354$ $ 1.873$ $3.508$ $ 9.92-26.98$ $22.56\pm0.224$ LD2 $ 1.84-2.512$ $3.95\pm0.045$ $0.455$ $0.207$ $3.00-4.86$ $3.60\pm0.072$ $0.379$ $0.144$ $2.94-3.91$ $3.43\pm0.039$ LC $ 1.32-12.21$ $9.68\pm0.095$ $0.954$ $0.910$ $7.36-1101$ $0.908\pm0.174$ $0.919$ $0.845$ $6.42-10.36$ $8.67\pm0.142$ LC $ 1.33-22.09$ $ 8.30\pm0.170$ $ 1.612$ $ 1.612$ $ 1.261$ $ 1.161$ $ 1.264\pm0.181$ Act $ 1.33-22.09$ $ 8.30\pm0.170$ $ 1.709$ $2.924\pm0.201$ $ 1.201$ $ 1.264\pm0.181$ ace $ 1.33-22.09$ $ 8.30\pm0.170$ $ 1.692$ $3.694$ $ 0.247$ $ 1.612$ $ 1.264\pm0.132$ ace $ 1.33-22.09$ $ 8.30\pm0.170$ $ 1.570$ $ 1.692-21.88$ $ 9.72\pm0.241$ $ 1.201$ $ 1.26+2.132$ ace $ 1.33-22.09$ $ 8.30\pm0.170$ $ 1.692$ $ 1.692-21.88$ $ 9.72\pm0.241$ $ 1.201$ $ 1.26+2.132$ ace $ 1.33-22.09$ $ 8.30\pm0.161$ $ 1.692-21.88$ $ 9.72\pm0.241$ $ 1.201$ $ 1.271$ $ 1.26+2.132$ ace $ $		D1 - D2	2.08-6.62	$4.01 \pm 0.093$	0.932	0.869	0.89-4.07	$2.79 \pm 0.170$	0.886	0.785	1.70 - 6.85	$4.49\pm0.168$	1.126	1.268	
HD1 $1.36-2.78$ $2.00\pm0.028$ $0.284$ $0.081$ $1.33-2.43$ $1.80\pm0.047$ $0.247$ $0.061$ $1.14-1.91$ $1.52\pm0.026$ LD2 $18.43-26.69$ $2.261\pm0.132$ $1.329$ $1.766$ $18.21-27.51$ $23.32\pm0.354$ $1.873$ $3.508$ $19.92-26.98$ $22.56\pm0.224$ HD2 $2.88-51.2$ $3.95\pm0.045$ $0.455$ $0.207$ $3.00-4.86$ $3.69\pm0.072$ $0.379$ $0.144$ $2.94-391$ $1.343\pm0.039$ <i>IC</i> $7.02-12.21$ $9.68\pm0.095$ $0.954$ $0.207$ $3.00-4.86$ $3.69\pm0.072$ $0.845$ $6.42-10.36$ $8.67\pm0.142$ <i>DA</i> $23.98-30.68$ $26.96\pm0.126$ $1.770$ $1.613$ $26.17-30.72$ $28.24\pm0.201$ $1.061$ $1.126$ $24.89-30.96$ $27.46\pm0.181$ <i>CH</i> $13.33-22.09$ $18.30\pm0.170$ $1.770$ $1.613$ $20.24\pm0.247$ $1.961$ $1.744$ $2.94-30.96$ $27.46\pm0.181$ <i>cH</i> $13.33-22.09$ $18.30\pm0.170$ $1.709$ $2.921$ $10.61$ $1.701$ $1.764$ $24.89-30.96$ $27.46\pm0.181$ <i>cH</i> $13.33-22.00$ $18.30\pm0.170$ $1.702$ $26.91$ $1.061$ $1.271$ $1.661$ $21.74\pm0.269$ <i>cH</i> $13.33-22.00$ $18.30\pm0.170$ $1.702$ $2.921$ $16.92-26.92$ $50.54\pm0.720$ $50.54\pm0.726$ <i>ace</i> $48.44-57.14$ $52.74\pm0.191$ $1.922$ $3.690-55.74$ $51.92\pm0.247$ $1.271$ $1.612$ $21.74\pm0.269$ <i>ace</i> $48.44-57.14$ $52.74\pm0.1616$ $1.922$ $3.043-34.$		<i>ID</i> 1	10.54-16.96	$14.05\pm0.114$	1.142	1.304	13.64-16.82	$14.96\pm0.162$	0.855	0.731	11.95-16.22	$13.99 \pm 0.134$	0.899	0.808	
LD2 $18, 43 - 26, 69$ $22.61 \pm 0.132$ $1.329$ $1.766$ $18, 21 - 27.51$ $23.32 \pm 0.354$ $1.873$ $3.508$ $19.92 - 26.98$ $22.56 \pm 0.224$ HD2 $2.88 - 5.12$ $3.95 \pm 0.045$ $0.455$ $0.207$ $3.00 - 4.86$ $3.69 \pm 0.072$ $0.379$ $0.144$ $2.94 - 3.91$ $3.43 \pm 0.039$ $10$ IC $7.02 - 12.21$ $9.68 \pm 0.095$ $0.910$ $7.36 - 11.01$ $9.08 \pm 0.174$ $0.919$ $0.845$ $6.42 - 10.36$ $8.67 \pm 0.142$ $10$ IC $7.02 - 12.21$ $9.68 \pm 0.095$ $0.910$ $7.36 - 11.01$ $9.08 \pm 0.174$ $0.919$ $0.845$ $6.42 - 10.36$ $8.67 \pm 0.142$ $10$ IC $7.02 - 12.21$ $9.68 \pm 0.0126$ $1.270$ $1.611$ $10.61$ $1.126$ $24.89 - 30.96$ $27.46 \pm 0.181$ IC $1.333 - 22.09$ $18.30 \pm 0.170$ $1.709$ $2.921$ $81.972 \pm 0.244$ $1.061$ $1.126$ $24.89 - 30.96$ $27.46 \pm 0.181$ ace $48.44 - 57.14$ $52.74 \pm 0.191$ $1.709$ $2.921$ $81.972 \pm 0.244$ $1.305$ $1.771$ $1.615$ $24.89 - 30.96$ $27.46 \pm 0.181$ ace $48.44 - 57.14$ $52.74 \pm 0.191$ $1.702$ $2.924$ $51.92 \pm 0.244$ $1.703$ $33.33 - 56.72$ $50.84 \pm 0.269$ ace $43.44 - 57.14$ $52.74 \pm 0.101$ $1.702$ $16.92 - 2.128$ $19.72 \pm 0.244$ $1.703$ $32.74 \pm 0.470$ ace $43.33 - 52.108$ $1.771$ $1.772$ $24.92 - 3.034$ $20.723$ $20.742$ $20.742$ $20.742$ <		1 <i>D</i> 1	1.36 - 2.78	$2.00\pm0.028$	0.284	0.081	1.33-2.43	$1.80\pm0.047$	0.247	0.061	1.14-1.91	$1.52\pm0.026$	0.176	0.031	
HD2 $2.88-5.12$ $3.95\pm0.045$ $0.455$ $0.207$ $3.00-4.86$ $3.69\pm0.072$ $0.379$ $0.144$ $2.94-3.91$ $3.43\pm0.039$ $0$ IC $7.02-12.21$ $9.68\pm0.095$ $0.954$ $0.910$ $7.36-11.01$ $9.08\pm0.174$ $0.919$ $0.845$ $6.42-10.36$ $8.67\pm0.142$ $1$ $pA$ $23.98-30.68$ $26.96\pm0.126$ $1.270$ $1.613$ $26.17-30.72$ $28.24\pm0.201$ $1.061$ $1.126$ $24.89-30.96$ $27.46\pm0.181$ $pA$ $23.398-30.68$ $26.96\pm0.126$ $1.770$ $1.613$ $28.24\pm0.201$ $1.061$ $1.126$ $24.89-30.96$ $27.46\pm0.181$ $ee$ $48.44-57.14$ $52.74\pm0.191$ $1.922$ $3.694$ $50.0-55.74$ $51.92\pm0.247$ $1.270$ $24.89-30.96$ $27.46\pm0.181$ $ae$ $48.44-57.14$ $52.74\pm0.191$ $1.922$ $3.694$ $50.0-55.74$ $51.92\pm0.247$ $1.270$ $1.615$ $18.29-24.73$ $21.47\pm0.269$ $ae$ $48.44-57.14$ $52.74\pm0.191$ $1.922$ $3.694$ $50.0-55.74$ $51.92\pm0.247$ $1.703$ $32.33-56.72$ $50.54\pm0.470$ $ae$ $48.44-57.14$ $52.74\pm0.161$ $1.922$ $3.694$ $50.0-55.74$ $51.92\pm0.247$ $1.703$ $32.33-56.72$ $50.54\pm0.470$ $ae$ $48.44-57.14$ $52.74\pm0.163$ $1.972$ $2.941$ $3.042$ $47.78-55.29$ $50.84\pm0.269$ $ae$ $48.44-57.14$ $52.74\pm0.163$ $1.972$ $2.942$ $3.042$ $2.947\pm0.238$ $50.64\pm0.238$ $ae$ $62.7-0.181$ $7$		LD2	18.43-26.69	$22.61 \pm 0.132$	1.329	1.766	18.21–27.51	$23.32 \pm 0.354$	1.873	3.508	19.92-26.98	$22.56 \pm 0.224$	1.504	2.262	
IC $7.02-12.21$ $9.68\pm0.095$ $0.954$ $0.910$ $7.36-11.01$ $9.08\pm0.174$ $0.919$ $0.845$ $6.42-10.36$ $8.67\pm0.142$ $1.61$ $pA$ $23.98-30.68$ $26.96\pm0.126$ $1.270$ $1.613$ $26.17-30.72$ $28.24\pm0.201$ $1.061$ $1.126$ $24.89-30.96$ $27.46\pm0.181$ $cH$ $13.33-22.09$ $18.30\pm0.170$ $1.709$ $2.921$ $16.92-21.88$ $19.72\pm0.240$ $1.271$ $1.615$ $18.29-24.73$ $21.47\pm0.269$ $ae$ $48.44-57.14$ $52.74\pm0.191$ $1.922$ $3.694$ $50.00-55.74$ $51.92\pm0.247$ $1.305$ $1.703$ $21.47\pm0.269$ $ae$ $48.44-57.14$ $52.74\pm0.191$ $1.922$ $3.694$ $50.00-55.74$ $51.92\pm0.247$ $1.305$ $1.771$ $2.64\pm0.470$ $ae$ $48.44-57.14$ $52.74\pm0.191$ $1.709$ $2.941$ $30.43-34.43$ $32.35\pm0.239$ $29.4\pm0.203$ $ae$ $48.44-57.14$ $52.74\pm0.191$ $1.715$ $2.941$ $30.43-24.23$ $21.742-55.29$ $50.84\pm0.285$ $ae$ $48.47-57.10$ $32.77\pm0.171$ $1.715$ $2.944$ $30.42-0.247$ $1.305$ $1.744$ $30.23$ $29.4\pm0.470$ $ae$ $6.25-10.81$ $7.78\pm0.095$ $0.916$ $5.63-9.84$ $7.70\pm0.160$ $0.849$ $0.721$ $50.72-9.38$ $6.96\pm0.122$ $ae$ $6.25-10.81$ $7.79\pm0.096$ $0.916$ $5.63-9.84$ $7.70\pm0.160$ $0.849$ $0.721$ $5.26-9.38$ $6.96\pm0.122$ $ae$ $9.23-16.22$ $1.200\pm0.130$ $1.549$ <td< td=""><td>101</td><td>HD2</td><td>2.88-5.12</td><td><math display="block">3.95\pm0.045</math></td><td>0.455</td><td>0.207</td><td>3.00-4.86</td><td><math>3.69 \pm 0.072</math></td><td>0.379</td><td>0.144</td><td>2.94-3.91</td><td><math display="block">3.43\pm0.039</math></td><td>0.259</td><td>0.067</td></td<>	101	HD2	2.88-5.12	$3.95\pm0.045$	0.455	0.207	3.00-4.86	$3.69 \pm 0.072$	0.379	0.144	2.94-3.91	$3.43\pm0.039$	0.259	0.067	
$p_A$ $23.98-30.68$ $26.96 \pm 0.126$ $1.270$ $1.613$ $26.17-30.72$ $28.24 \pm 0.201$ $1.061$ $1.126$ $24.89-30.96$ $27.46 \pm 0.181$ $cH$ $13.33-22.09$ $18.30 \pm 0.170$ $1.709$ $2.921$ $16.92-21.88$ $19.72 \pm 0.247$ $1.205$ $18.29-24.73$ $21.47 \pm 0.269$ $ae$ $48.44-57.14$ $52.74 \pm 0.191$ $1.922$ $3.694$ $50.00-55.74$ $51.92 \pm 0.247$ $1.305$ $1.703$ $33.33-56.72$ $50.84 \pm 0.470$ $ae$ $48.44-57.14$ $52.74 \pm 0.191$ $1.922$ $3.694$ $50.00-55.74$ $51.92 \pm 0.247$ $1.305$ $1.703$ $33.33-56.72$ $50.54 \pm 0.470$ $ae$ $43.33-52.00$ $48.17 \pm 0.165$ $1.655$ $2.739$ $45.90-54.29$ $49.32 \pm 0.234$ $1.714$ $3.042$ $44.78-55.29$ $50.84 \pm 0.285$ $ao$ $28.79-37.10$ $32.77 \pm 0.171$ $1.715$ $2.941$ $30.43-34.43$ $32.35 \pm 0.234$ $1.703$ $29.17-35.82$ $32.93 \pm 0.233$ $ao$ $6.25-10.81$ $7.98 \pm 0.095$ $0.916$ $5.63-9.84$ $7.70 \pm 0.160$ $0.849$ $0.721$ $5.26-9.38$ $6.96 \pm 0.121$ $ao$ $6.25-10.81$ $7.98 \pm 0.095$ $0.916$ $5.63-9.84$ $7.70 \pm 0.160$ $0.849$ $0.721$ $5.26-9.38$ $6.96 \pm 0.122$ $ao$ $6.25-10.81$ $1.711$ $1.771$ $10.77-13.79$ $12.11 \pm 0.153$ $0.810$ $0.656$ $10.22.52$ $21.56 \pm 0.192$ $ao$ $9.23-16.22$ $1.549$ $2.399$ $2.940 \pm 2.540$ $22.40 \pm 0.230$ $12.11$		<i>IC</i>	7.02-12.21	$9.68\pm0.095$	0.954	0.910	7.36-11.01	$9.08 \pm 0.174$	0.919	0.845	6.42-10.36	$8.67\pm0.142$	0.949	0.901	
In % of head lengthcH <th l<="" light="" td=""><td></td><td>pA</td><td>23.98-30.68</td><td><math>26.96 \pm 0.126</math></td><td>1.270</td><td>1.613</td><td>26.17-30.72</td><td><math>28.24 \pm 0.201</math></td><td>1.061</td><td>1.126</td><td>24.89-30.96</td><td><math>27.46 \pm 0.181</math></td><td>1.212</td><td>1.469</td></th>	<td></td> <td>pA</td> <td>23.98-30.68</td> <td><math>26.96 \pm 0.126</math></td> <td>1.270</td> <td>1.613</td> <td>26.17-30.72</td> <td><math>28.24 \pm 0.201</math></td> <td>1.061</td> <td>1.126</td> <td>24.89-30.96</td> <td><math>27.46 \pm 0.181</math></td> <td>1.212</td> <td>1.469</td>		pA	23.98-30.68	$26.96 \pm 0.126$	1.270	1.613	26.17-30.72	$28.24 \pm 0.201$	1.061	1.126	24.89-30.96	$27.46 \pm 0.181$	1.212	1.469
$cH$ $13.33-22.09$ $18.30\pm0.170$ $1.709$ $2.921$ $16.92-21.88$ $19.72\pm0.247$ $1.271$ $1.615$ $18.29-24.73$ $21.47\pm0.269$ $ae$ $48.44-57.14$ $52.74\pm0.191$ $1.922$ $3.694$ $50.00-55.74$ $51.92\pm0.247$ $1.305$ $1.703$ $33.33-56.72$ $50.54\pm0.470$ $eo$ $48.47-57.10$ $32.77\pm0.161$ $1.655$ $2.739$ $45.90-54.29$ $49.32\pm0.330$ $1.744$ $3.042$ $44.78-55.29$ $50.84\pm0.285$ $ao$ $28.79-37.10$ $32.77\pm0.171$ $1.715$ $2.941$ $30.43-34.43$ $32.36\pm0.204$ $1.081$ $1.169$ $29.17-35.82$ $32.93\pm0.233$ $ao$ $6.25-10.81$ $7.98\pm0.095$ $0.957$ $0.916$ $5.63-9.84$ $7.70\pm0.160$ $0.849$ $0.721$ $5.26-9.38$ $6.96\pm0.121$ $o$ $6.25-10.81$ $7.98\pm0.095$ $0.957$ $0.916$ $5.63-9.84$ $7.70\pm0.160$ $0.849$ $0.721$ $5.26-9.38$ $6.96\pm0.121$ $o$ $6.25-10.81$ $7.98\pm0.095$ $0.957$ $0.916$ $5.63-9.84$ $7.70\pm0.160$ $0.849$ $0.721$ $5.26-9.38$ $6.96\pm0.121$ $o$ $6.25-10.81$ $7.98\pm0.0957$ $0.916$ $5.63-9.84$ $7.70\pm0.160$ $0.849$ $0.721$ $5.26-9.38$ $6.96\pm0.122$ $o$ $6.25-10.81$ $7.98\pm0.0957$ $0.916$ $5.63-9.84$ $7.70\pm0.160$ $0.849$ $0.721$ $6.96\pm0.126$ $o$ $9.23-16.22$ $12.00\pm0.130$ $1.711$ $10.77-13.79$ $12.11\pm0.153$ $0.810$ $0.656$ $10.65-14.63$ <	0 F 1		_	-	_	-	In % of h	nead length	-	_	_	-	-		
ae $48.44-57.14$ $52.74\pm0.191$ $1.922$ $3.694$ $50.00-55.74$ $51.92\pm0.247$ $1.305$ $1.703$ $33.33-56.72$ $50.54\pm0.470$ eo $43.33-52.00$ $48.17\pm0.165$ $1.655$ $2.739$ $45.90-54.29$ $49.32\pm0.330$ $1.744$ $3.042$ $44.78-55.29$ $50.84\pm0.285$ ao $28.79-37.10$ $32.77\pm0.171$ $1.715$ $2.941$ $30.43-34.43$ $32.36\pm0.204$ $1.081$ $1.169$ $29.17-35.82$ $32.93\pm0.233$ o $6.25-10.81$ $7.98\pm0.095$ $0.957$ $0.916$ $5.63-9.84$ $7.70\pm0.160$ $0.849$ $0.721$ $5.26-9.38$ $6.96\pm0.121$ o $9.23-16.22$ $12.00\pm0.130$ $1.308$ $1.711$ $10.77-13.79$ $12.11\pm0.153$ $0.810$ $0.656$ $10.59-14.63$ $12.21\pm0.122$ ik $20.00-26.87$ $23.52\pm0.159$ $1.549$ $2.399$ $20.48-25.40$ $22.40\pm0.230$ $1.219$ $1.466\pm0.163$ $12.21\pm0.122$ ik $10.53-17.14$ $13.66\pm0.155$ $1.542$ $2.392$ $12.11\pm0.153$ $0.810$ $0.656$ $10.25.37$ $21.56\pm0.192$ o $0.23-17.14$ $13.66\pm0.155$ $1.542$ $2.394$ $12.11\pm0.123$ $12.19$ $12.16$ $12.00-16.84$ $14.69\pm0.172$	CUI	cH	13.33-22.09	$18.30 \pm 0.170$	1.709	2.921	16.92-21.88	$19.72 \pm 0.240$	1.271	1.615		$21.47 \pm 0.269$	1.806	3.262	
$eo$ $43.33-52.00$ $48.17\pm0.165$ $1.655$ $2.739$ $45.90-54.29$ $49.32\pm0.330$ $1.744$ $3.042$ $44.78-55.29$ $50.84\pm0.285$ $ao$ $28.79-37.10$ $32.77\pm0.171$ $1.715$ $2.941$ $30.43-34.43$ $32.36\pm0.204$ $1.081$ $1.169$ $29.17-35.82$ $32.93\pm0.233$ $o$ $6.25-10.81$ $7.98\pm0.095$ $0.957$ $0.916$ $5.63-9.84$ $7.70\pm0.160$ $0.849$ $0.721$ $5.26-9.38$ $6.96\pm0.121$ $o$ $9.23-16.22$ $12.00\pm0.130$ $1.308$ $1.711$ $10.77-13.79$ $12.11\pm0.153$ $0.810$ $0.656$ $10.59-14.63$ $12.21\pm0.122$ $o$ $9.23-16.22$ $12.00\pm0.130$ $1.308$ $1.711$ $10.77-13.79$ $12.11\pm0.153$ $0.810$ $0.656$ $10.59-14.63$ $12.21\pm0.122$ $ik$ $20.00-26.87$ $23.52\pm0.159$ $1.549$ $2.399$ $20.48-25.40$ $22.40\pm0.230$ $1.219$ $1.486$ $19.10-25.37$ $21.56\pm0.192$ $cw$ $10.53-17.14$ $13.66\pm0.155$ $1.557$ $2.424$ $13.11-17.74$ $15.40\pm0.208$ $1.098$ $1.200-16.84$ $14.69\pm0.174$	<b>FI IX</b> /	ae	48.44-57.14	$52.74 \pm 0.191$	1.922	3.694	50.00-55.74	$51.92 \pm 0.247$	1.305	1.703	33.33-56.72	$50.54 \pm 0.470$	3.152	9.935	
ao $28.79-37.10$ $32.77\pm0.171$ $1.715$ $2.941$ $30.43-34.43$ $32.36\pm0.204$ $1.081$ $1.169$ $29.17-35.82$ $32.93\pm0.233$ o $6.25-10.81$ $7.98\pm0.095$ $0.957$ $0.916$ $5.63-9.84$ $7.70\pm0.160$ $0.849$ $0.721$ $5.26-9.38$ $6.96\pm0.121$ $0.0$ oe $9.23-16.22$ $12.00\pm0.130$ $1.308$ $1.711$ $10.77-13.79$ $12.11\pm0.153$ $0.810$ $0.656$ $10.59-14.63$ $12.21\pm0.122$ $1$ ik $20.00-26.87$ $23.52\pm0.159$ $1.549$ $2.399$ $20.48-25.40$ $22.40\pm0.230$ $1.219$ $1.486$ $19.10-25.37$ $21.56\pm0.192$ cw $10.53-17.14$ $13.66\pm0.155$ $1.557$ $2.424$ $13.11-17.74$ $15.40\pm0.208$ $1.098$ $1.200-16.84$ $14.69\pm0.174$		60	43.33–52.00	$48.17 \pm 0.165$	1.655	2.739	45.90-54.29	$49.32 \pm 0.330$	1.744	3.042		$50.84\pm0.285$	1.908	3.640	
o $6.25-10.81$ $7.98\pm0.095$ $0.957$ $0.916$ $5.63-9.84$ $7.70\pm0.160$ $0.849$ $0.721$ $5.26-9.38$ $6.96\pm0.121$ $10.121$ oe $9.23-16.22$ $12.00\pm0.130$ $1.308$ $1.711$ $10.77-13.79$ $12.11\pm0.153$ $0.810$ $0.656$ $10.59-14.63$ $12.21\pm0.122$ $10.122$ ik $20.00-26.87$ $23.52\pm0.159$ $1.549$ $2.399$ $20.48-25.40$ $22.40\pm0.230$ $1.219$ $1.486$ $19.10-25.37$ $21.56\pm0.192$ cw $10.53-17.14$ $13.66\pm0.155$ $1.557$ $2.424$ $13.11-17.74$ $15.40\pm0.208$ $1.006$ $12.00-16.84$ $14.69\pm0.174$		<i>ao</i>	28.79-37.10	$32.77 \pm 0.171$	1.715	2.941	30.43-34.43	$32.36 \pm 0.204$	1.081	1.169	29.17-35.82	$32.93\pm0.233$	1.560	2.434	
oe $9.23-16.22$ $12.00 \pm 0.130$ $1.308$ $1.711$ $10.77-13.79$ $12.11 \pm 0.153$ $0.810$ $0.656$ $10.59-14.63$ $12.21 \pm 0.122$ $0.122$ ik $20.00-26.87$ $23.52 \pm 0.159$ $1.549$ $2.399$ $20.48-25.40$ $22.40 \pm 0.230$ $1.219$ $1.486$ $19.10-25.37$ $21.56 \pm 0.192$ $0.002$ cw $10.53-17.14$ $13.66 \pm 0.155$ $1.557$ $2.424$ $13.11-17.74$ $15.40 \pm 0.208$ $1.206$ $10.20-16.84$ $14.69 \pm 0.174$	V	0	6.25-10.81	$7.98 \pm 0.095$	0.957	0.916	5.63-9.84	$7.70 \pm 0.160$	0.849	0.721	5.26-9.38	$6.96 \pm 0.121$	0.809	0.654	
$ik \qquad 20.00-26.87 \qquad 23.52 \pm 0.159 \qquad 1.549 \qquad 2.399 \qquad 20.48-25.40 \qquad 22.40 \pm 0.230 \qquad 1.219 \qquad 1.486 \qquad 19.10-25.37 \qquad 21.56 \pm 0.192 \qquad cw \qquad 10.53-17.14 \qquad 13.66 \pm 0.155 \qquad 1.557 \qquad 2.424 \qquad 13.11-17.74 \qquad 15.40 \pm 0.208 \qquad 1.098 \qquad 1.206  12.00-16.84 \qquad 14.69 \pm 0.174 \qquad 12.06 \qquad 12.00-16.84 \qquad 14.69 \pm 0.174 \qquad 12.00 $		<i>oe</i>	9.23-16.22	$12.00\pm0.130$	1.308	1.711	10.77-13.79	$12.11 \pm 0.153$	0.810	0.656		$12.21 \pm 0.122$	0.816	0.666	
$cw \qquad \qquad 10.53 - 17.14 \qquad 13.66 \pm 0.155 \qquad 1.557 \qquad 2.424 \qquad 13.11 - 17.74 \qquad 15.40 \pm 0.208 \qquad 1.098 \qquad 1.206  12.00 - 16.84 \qquad 14.69 \pm 0.174 \qquad 12.00 + 10.008 \qquad 10$		ik	20.00-26.87	$23.52 \pm 0.159$	1.549	2.399	20.48-25.40	$22.40 \pm 0.230$	1.219	1.486		$21.56\pm0.192$	1.289	1.662	
	No.	CW	10.53-17.14	$13.66 \pm 0.155$	1.557	2.424	13.11-17.74	$15.40 \pm 0.208$	1.098	1.206		$14.69\pm0.174$	1.169	1.367	

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NOVOSELOV, IMANT

Sign	Onega–Severnaya Dvina		Severnaya Dy	vina-Mezen	Onega-Mezen					
Sigii	t	р	t	t p		р				
	In % of <i>TL</i>									
Η	—	_	3.645	0.001	14.022	0.000				
aD	_	_	_	—	-3.735	0.000				
aa	_	_	-3.565	0.001	-2.917	0.004				
D1-D2	6.067	0.000	6.674	0.000	2.701	0.008				
<i>lD</i> 1	-3.917	0.000	-4.583	0.000	_	_				
HD1	3.399	0.001	-5.666	0.000	_	_				
LD2	-2.293	0.023	_	_	_	_				
HD2	2.767	0.006	-3.609	0.001	_	_				
lC	2.972	0.004	_	_	-5.906	0.000				
pА	-4.888	0.000	-2.812	0.006	2.226	0.028				
In % of head length										
cH	-4.084	0.000	-	_	10.174	0.000				
ae	2.124	0.036	-2.205	0.031	-5.198	0.000				
0	_	_	-3.764	0.000	-6.270	0.000				
ео	-3.249	0.001	3.393	0.001	8.582	0.000				
ik	3.528	0.001	-2.733	0.008	-7.343	0.000				
СW	_	_	- 2. 574	0.012	—	—				

**Table 2.** Statistically significant differences in the plastic signs of the Arctic lamprey Lethenteron camtschaticum from the largest rivers of the Arkhangelsk Region Russia

t—Student's t-test, p—probability of the null hypothesis according to Student's t-test, "—"—Student's t-test was not applied according to the Levene test for equality of variances (Ivanter and Korosov, 2003).

**Table 3.** Fecundity of the Arctic lamprey Lethenteron camtschaticum within the range according to the literature and original data

	Eu	ropean Nor	Far East			
Fecundity	Severnaya Dv	vina River	Onega River	Mezen River	Chukotka rivers	Kol River (Western Kamchatka)
	Kozmin, 2011a		Our data		Chereshnev, 1996	Nazarov et al., 2011
Absolute, thousand eggs	$\frac{21.5-56.2}{34.4}$	$\frac{22.6-49.2}{40.4}$	$\frac{17.3-50.1}{38.6}$	$\frac{34.3-67.1}{58.2}$	$\frac{12.3-34.6}{23.5}$	$\frac{24.1-31.1}{27.8}$
Relative, the number of eggs per 1 g of body weight	585.8	603.9	577.0	464.1		
Number of individuals, ind.	20	12	43	22		

Values above the line are the limits of variation of the indicator, below the line, the mean.

nounced slightly, so it is impossible to determine visually the sex of an individual. No significant sex differences are found in the Arctic lamprey in terms of meristic signs (Martynov, 2002).

In the pre-spawning period (from July to September), the lampreys concentrate in the pre- estuary sections of the rivers, then they start the extended spawning migration upstream the rivers, both along the main watercourses of large river basins and in the smaller rivers along the entire coast of the northern seas. The

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migration rate in the lower reaches of the rivers is from 3 to 5 km per day; upstream, it increases up to 10–15 km per day (Kozmin, 2011b). In the Severnaya Dvina River basin, lampreys migrate upstream the river and its tributaries up to the Kotlas town, and then up to the rivers Vychegda, Sukhona, and Yug; they enter the Vaga River tributary as well. The maximum length of spawning migration is registered in the Vychegda River (750 km), it may reach up 400 km in the Severnaya Dvina River and up to 200 km in the Onega



Fig. 2. The female of the Arctic lamprey *Lethenteron camtschaticum* its ovary, the Severnaya Dvina River (after: Kozmin, 2011a). The scale is presented in centimeters.

River. In the Mezen River basin, it is found in the Vashka River; in the Pechora River, it is observed almost along the entire watercourse. The migration to the rivers, where this species hibernates, lasts throughout the winter; but the migration peak takes 10–20 days (Stasenkova and Novoselov, 2007).

In January, the gametes of lamprey females are at maturity stages III, III–IV (Kozmin, 2011a). The eggs are light-yellow, quite large, their diameter is 0.5-0.8 mm. The ovary occupies more than half of the body cavity (Fig. 2). In the Severnaya Dvina River, the gonad maturity coefficient in females averages  $16.08 \pm 0.11\%$ , in males,  $3.85 \pm 0.20\%$ , the gonadosomatic index,  $22.87 \pm 0.10$  and  $4.85 \pm 0.22\%$ , respectively. The minimum absolute fecundity is 21.5 thousand eggs, the maximum, 56.2 thousand eggs, the average, 34.4 thousand eggs. Relative fecundity averages 586 eggs per 1 g of body weight (Table 3).

In our study, both absolute and relative fecundity observed for the Arctic lamprey the Severnaya Dvina River do not differ significantly when comparing to those presented earlier (Kozmin, 2011a), but confirm them again (Table 3). At the same time, a linear increasing trend for absolute fecundity eastwards (the Onega River—the Severnaya Dvina River—the Mezen River) is registered for the first time when comparing our data to other rivers of the Arkhangelsk Region analyzed earlier. In general, relative fecundity decreases eastwards, but no clearly pronounced linear dependence is found.

When analyzing the indicators of natural reproduction throughout the vast (but geographically fragmented) range of the Arctic lamprey, the absolute fecundity in the Far Eastern part of the range is significantly lower compared to that in the European populations. For example, absolute fecundity varies from 24.1 to 31.1 thousand eggs, averaging 27.8 thousand eggs, in the Kol River, Western Kamchatka (Nazarov et al., 2011). It is even lower in the Arctic lampreys from the rivers of Chukotka, 12.3–34.6 (average 23.5) thousand eggs (Chereshnev, 1996).

#### CONCLUSIONS

Average values of the size-weight parameters of spawners of the anadromous Arctic lamprey tend to increase eastwards in the rivers of the Arkhangelsk Region, Russia. The lowest length and weight are found for the lampreys in the Onega River, the highest, in the Mezen River. Anadromous individuals from the Severnaya Dvina River are characterized by intermediate values. The same trend is noted for the average absolute fecundity. Higher average values of biological parameters (length, body weight, and fecundity) of the Arctic lamprey populations are found at the western part of the range comparing to those from the Far Eastern part of the range.

According to the morphological parameters, the body height of the Arctic lamprey spawners, inhabiting the most western rivers of the study area (the Onega River), is lower; these specimens have smaller distances between the dorsal fins and from the anus to the end of the caudal fin, as well as lower head height, gill apparatus length, and forehead width. In turn, the lampreys from the Mezen River are characterized by smaller antedorsal distance, smaller distance from the snout tip to the anus, lower length of the dorsal part of the caudal fin, smaller horizontal eye diameter, and smaller oral disc. When compared with individuals of a more western population (the Onega River) and a more eastern one (the Mezen River), anadromous lampreys from the Severnaya Dvina River occupies an intermediate position in regard to the distance between the dorsal fins, the distance between the snout tip and the gill apparatus, as well as in the gill apparatus length and the oral disk diameter, but they have a maximum distance from the anus to the end of the caudal fin.

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## COMPLIANCE WITH ETHICAL STANDARDS

*Conflict of interests.* The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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