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LAMPREYS (PETROMYZONTIDAE)

Caspian Lamprey *Caspiomyzon wagneri* (Petromyzontidae): A Review of Historical and Modern Data

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Abstract—Historical and modern data on the taxonomic status, external morphology, distribution features, biology, economic importance, history of fishing, conservation status, and protection measures for the Caspian lamprey *Caspiomyzon wagneri* are presented. The Caspian lamprey is an endemic species and the only anadromous lamprey in the Caspian Sea basin. The abundance of this species has declined everywhere; as a result, the species nowadays is on the verge of extinction. Being an important target of fishing in the past, the Caspian lamprey has completely lost its economic importance. It is subject to serious threats of an anthropogenic nature. Constructing of locks and dams without fish passages that prevent spawning migrations, water pollution, dredging and mining of sand and gravel leading to the destruction of habitats and spawning grounds, poaching and lack of legal protection mechanisms are the main threats for this lamprey species.

Keywords: jawless fishes, taxonomic status, morphology, distribution, biology, protection, threats
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INTRODUCTION

Lampreys occupy a special position in aquatic ecosystems. They serve as intermediate and reservoir hosts of nematodes, being the main sources of infection for freshwater and anadromous fish, which they parasitize (Butorina, 1988). Parasitic lamprey species, attacking fish, cause great damage to fish stocks,—first of all, to important commercial objects such as salmon, herring, and cod (Birman, 1950; Myagkov, 1983; Orlov et al., 2009; Orlov, 2016). This may cause major environmental catastrophes, for example, registered in the Great Lakes basin (USA) in the 1930s (Birznek, 1967). Lampreys themselves serve as a food for various animal species, such as fish, birds, marine and terrestrial mammals (Orlov et al., 2009; Orlov, 2016; Clemens et al., 2019).

Some lamprey species are of commercial interest (Almeida et al., 2021). Namely, in the first half of the XX century, lamprey fishing was well developed in the USSR, they were caught in the basins of the Baltic, White, Barents, and Caspian seas, as well as in the Amur River (Ivanova-Berg, 1932; Manteifel, 1945; Bogaevskii, 1949). In addition to their use as food products, lampreys were used to obtain vitamin, fat, protein food for cattle and poultry, and fishmeal (Close et al., 1995). Ammocoetes (lamprey larvae) are good bait for catching various fish species, they may also serve as an ideal food for rearing juvenile salmon (Scott and Crossman, 1973; Close et al., 1995). Lampreys are also of particular interest for aquaculture, both in terms of obtaining raw materials for the production of delicacy food products, and for implementing projects to restore stocks of endangered species (Robinson et al., 2002).

Lampreys are also of pharmaceutical interest as potential sources of raw materials for the production of anticoagulant medicines; the specimens that died after spawning serve as a source of biogenic elements in oligotrophic water bodies (Close et al., 1995). Due to the accumulation of heavy metals (including mercury) in lamprey organs and tissues, some species may serve as bioindicators (Shooshtari et al., 2011).

In recent decades, the abundance of many lamprey species has significantly decreased under the influence of climate change and increased anthropogenic pressure. More than half of the lamprey species are currently classified as vulnerable, endangered, or extinct, at least in some part of their range (Renaud, 1997). The Caspian lamprey *Caspiomyzon wagneri* Kessler, 1870 is one of these species; it is endemic to the Caspian Sea and the rivers of its basin (Freyhof, Kottelat, 2008). Despite the fact that its regular study has begun more than a hundred years ago, at early XX century (Pravdin, 1913a, 1913b), many issues of the life cycle of the Caspian lamprey still remain poorly understood (Lucas et al., 2020).

Meanwhile, since 2005, the Caspian lamprey has been intensively and comprehensively studied in Iranian waters (South Caspian Basin), so numerous scientific publications appeared, including two major review papers (Coad, 2016; Nazari et al., 2017). At the same time, information on the distribution and biology of the Caspian lamprey in the rest of the species range is still fragmentary and scattered, often published in local sources that are difficult to access for a wide range of specialists.

The purpose of this review is to summarize information about the distribution, biology, commercial use, and protection of the Caspian lamprey in the northern and central Caspian Sea basin.

TAXONOMIC POSITION

In accordance with recent ideas, modern lampreys belong to the ancient group of lower vertebrates of the superclass Agnatha, class Petromyzontidae, represented by single order (Petromyzontiformes). Previously, it was believed that this order included a single family, Petromyzontidae (Hardisty, 1963; Holčík, 1986; Kottelat et al., 2005). Currently, it includes three families: Petromyzontidae (8 genera and 43 species, Northern Hemisphere), Geotriidae (2 genera, 3 species, Southern Hemisphere) and Mordaciidae (1 genus, 3 species, Southern Hemisphere) (Van der Laan, Fricke, 2022). At the same time, the species diversity of lampreys remains insufficiently studied both in the world ichthyofauna (Hardisty, 1986; Renaud, 2011; Maitland et al., 2015; Potter et al., 2015; Tutman et al., 2017; Clemens et al., 2020; Riva-Rossi et al., 2020; Pereira et al., 2021) and in the waters of the Russian Federation (Levin et al., 2016). Four new lamprey species have been described in the last decade (Van der Laan and Fricke, 2022).

Representatives of the Lampetrinae subfamily, which includes six genera, inhabit the basins of the Mediterranean, Black, and Caspian seas. Representatives of four genera are found in the central part of Eastern Europe (the European part of Russia). Species of the genera *Lampetra* (the northeastern part of the Atlantic Ocean, the southern coast of the Black Sea, and the rivers of Europe) and *Lethenteron* (the basins of the White and Barents seas, the Arctic Ocean and the north Pacific Ocean) are represented by both migratory (anadromous, potamodromous) and freshwater (resident) ecological forms. The genus *Caspiomyzon* (basin of the Caspian Sea and the rivers of Greece) includes one species of anadromous lamprey *C. wagneri* and two species of residential lampreys, *C. graceus* (Renaud and Economidis, 2010) and *C. hellenicus* (Vladykov, Renaud, Kott et Economidis, 1982) living in the rivers of Greece. On the contrary, the genus *Eudontomyzon* (rivers of the basins of the Black, Azov, and Caspian seas) is currently represented only by freshwater forms (Holčík, 1986; Levin, Holčík, 2006; Renaud, 2011; Potter et al., 2015; Tsimbalov et al., 2015; Artamonova et al., 2016; Nazari et al., 2017; Zvezdin et al., 2021). Based on the results of a comparative morphological analysis, it was earlier established that the genus *Caspiomyzon* is a sister group to five other genera (*Tetrapleurodon*, *Entosphenus*, *Eudontomyzon*, *Lampetra*, and *Lethenteron*), which include both Eurasian and American species (Gill et al., 2003). This study revealed a basal polytomy and failed to determine the relationship between the families Geotriidae, Mordaciidae, and Petromyzontidae. Recent molecular genetic studies using multiloci phylogeny (Pereira et al., 2021) report that the family Petromyzontidae is monophyletic, it comprises two related groups, one of which combines the genera *Caspiomyzon*, *Ichthyomyzon*, and *Petromyzon*, and the other one, the rest of the lamprey species of the Northern Hemisphere. At the same time, the first genus in its clade occupies the most basal position, which may indicate its more ancient origin. This confirms the results of previous studies regarding the old origin of the *Caspiomyzon* genus, which has existed at least since the Miocene (Meek, 1916; Holčík, 1986; Kucheryavyi et al., 2016). According to recent genetic studies (Pereira et al., 2021), a divergence of *C. graceus* and *C. hellenicus* from *C. wagneri* occurred ~7 million years ago.

EXTERNAL MORPHOLOGY AND COLORATION

Like it is observed in all lampreys, the body of the Caspian lamprey is eel-like, scales and paired fins are absent (Fig. 1a). There are two dorsal fins, which are separated by a gap, the second dorsal fin smoothly transforms into the caudal fin. There are seven gill openings on each side of the body (Fig. 1b). The skin is covered with poisonous mucus. The mouth is a funnel-shaped sucking disc with blunt horny teeth. One small, blunt, rounded tooth locates at the place of the maxillary plate (Fig. 1c). The mandibular plate usually bears five blunt teeth. Anterior lingual plate without depression in the middle. The labial teeth are usually

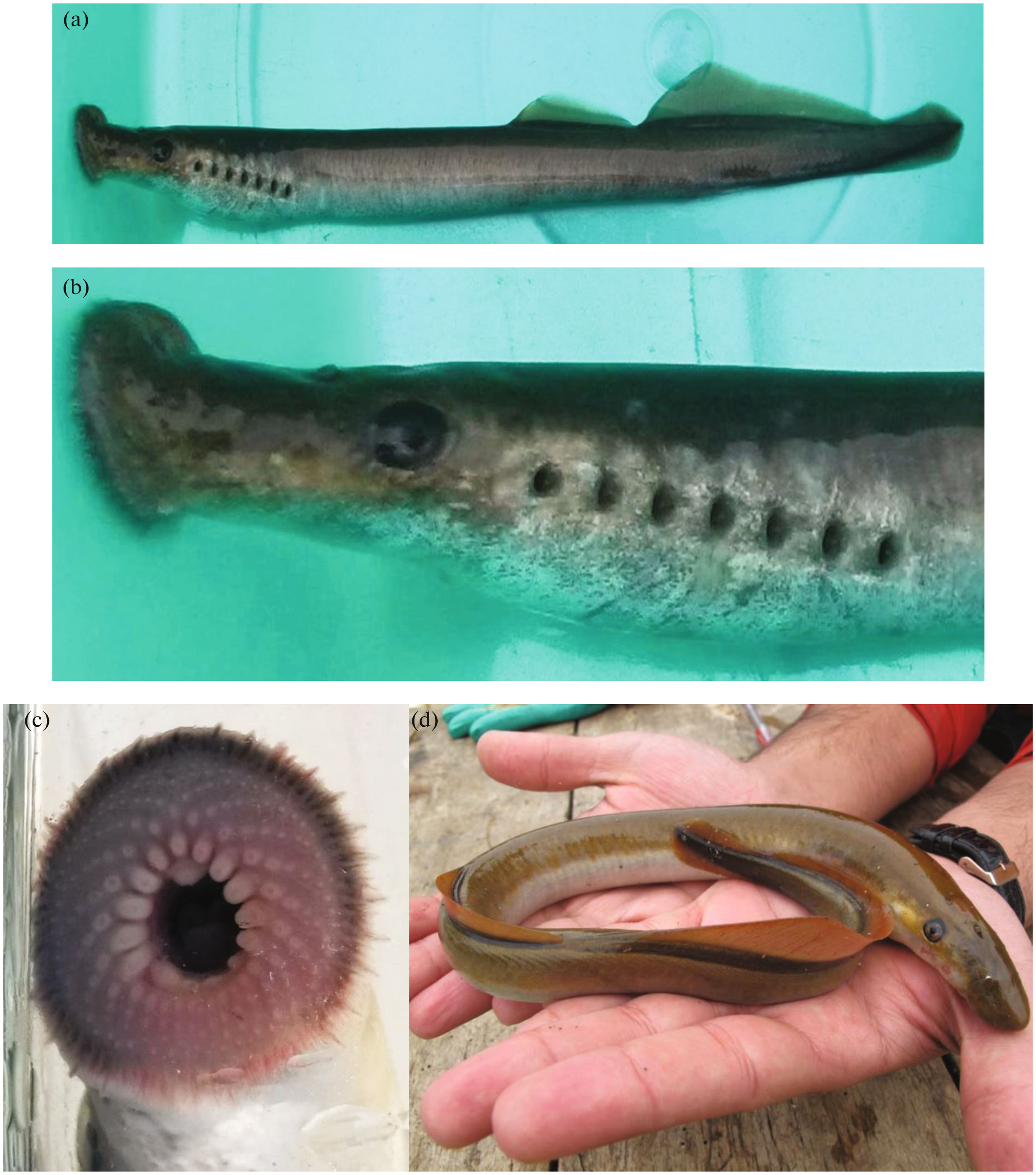

Fig. 1. The Caspian lamprey *Caspiomyzon wagneri* from the Volga River basin: (a) appearance, (b) anterior part of the body, (c) sucking disc (photo by E.V. Nikitin), (d) specimen from the Shirud River in spawning coloration (photo by H. Nazari).

arranged in radial rows. The sides of the mouth opening are bordered by 11 internal labial teeth, which are never bifid. There are three stamens directed into the pharyngeal cavity at the anterior end of the gill tube (Kazancheev, 1981; Renaud, 2011; Coad, 2016).

Females are larger than males and have a smaller urogenital papilla. During spawning migration, the lamprey undergoes certain morphological changes, which are partly related to sex; in particular, the size of the fins increases, the dorsal fins almost join at the base in males, and the body coloration changes.

Ammocoetes are pale gray to yellowish with a white belly (Ginzburg, 1936; Agamaliev, 1971b; Holčík, 1986; Renaud, 2011; Coad, 2016). Pre-spawning adults are dark gray on the back and silvery white on the sides (Agamaliev, 1971b; Holčík, 1986; Nazari, 2012). Spawning adults become black on the back and sides with a gray abdomen covered with dark oval spots, or turn golden (Pravdin, 1913a; Holčík, 1986) (Fig. 1d). Sometimes, sexually mature males with a greenish color are found at the mouth of the Shirud River (Nazari, 2012; Nazari et al., 2017).

DISTRIBUTION AND LIFESTYLE

The Caspian lamprey is endemic to the Caspian Sea and the rivers of its basin (Fig. 2), flowing into the northern, western, and southern parts of the coast in Russia, Azerbaijan, Iran, Turkmenistan, and Kazakhstan (Holčík, 1986; Freyhof, Kottelat, 2008; Zvezdin et al., 2021). There are no data indicating the existence in the past of any phylogenetically closely related forms in the basins of the Black and Azov seas, so the range of the Caspian lamprey is limited to the Caspian Sea, which is generally not typical for endemic Caspian fish (Kottelat et al., 2005; Naseka and Diripasko, 2008; Bogutskaya et al., 2013).

Previously, the Caspian lamprey entered the Volga River and its tributaries, Ural, Terek, Samur, and Kura rivers, the rivers of the Lankaran region (Azerbaijan) and further along the Iranian coast, including the Sefidrud and Babol rivers, in large numbers for breeding. Before the construction of a cascade of hydroelectric power plants (HPPs) on the Volga River (late 1930s–early 1940s), its river system was almost completely populated by the Caspian lamprey (Zvezdin et al., 2021), the spawning migrations of this species exceeded 2600 km. In the Volga River, the upstream migrations ended nearby the city of Kalinin (nowadays, Tver) and in the mouth of the Tvertsa River (left tributary of the Volga River); along the Kama River, it reached the rivers Chusovaya and Vishera, along the Oka River, the mouth of the Moskva River; along the Kura River, it reached its upper reaches (Mtskheta) and entered its tributaries (Alazan, Aragvi, Araks, and others); along the Terek River, it reached the Baksan River, and along the Ural River, the city of Orenburg (Berg, 1948; Agamaliev, 1971b; Kazancheev, 1981; Atlas..., 2002; Ivanov, Komarova, 2012). Varpakhovskii (1886, 1891) indicated the Caspian lamprey as part of the ichthyofauna of the Kazan and Nizhny Novgorod provinces in the Pyana (tributary of the Sura River), Kama, and Oka rivers. Artaev et al. (2013) noted that this species spawned up to the Kama River and in the mouth of the Vyatka River before the construction of dams on the Volga River. Magnitskii (1928) first observed the mass entry of the Caspian lamprey into the Sura River in 1926, when the spring flood reached its secular maximum. That year the lamprey has reached the areas located upstream the city of Penza in the Sura River up to the dam near the city of Kuznetsk. At the same time, it was registered in the tributaries of the Sura River (Penza, Inza, Aiva, V'yas, and Insar rivers). Migration routes in the Volga River were first blocked by dams in its upper reaches (the section between the source of the Volga River and the confluence with the Oka River, and then completely blocked after the construction of the Volga hydroelectric power station (Ginzburg, 1969, 1970; Holčík, 1986; Yakovlev et al., 2001; Atlas..., 2002). Nowadays, only single specimens of the Caspian lamprey are recorded upstream of the dam of the Volgograd Reservoir (Shashulovskii, Ermolin, 2005; Shashulovskii et al., 2016), it is absent when moving further upstream, in the Saratov Reservoir (Ermolin, 2010). Along the Kura River, lamprey migration is limited to the Mingachevir hydroelectric power station (below the Varvara dam), along the Terek River, it reaches the Baksan River (Kazancheev, 1981; Holčík, 1986; Shikhshabekov et al., 2008; Ivanov and Komarova, 2012; Orlov et al., 2021). In the tributaries of the Terek River (Sunzha, Argun, and Dzhalka rivers), the Caspian lamprey has recently been found quite often according to surveys of amateur fishermen.

The Caspian lamprey leads a migratory lifestyle, living both in the sea and in rivers, without forming freshwater populations or a freshwater resident form (Berg, 1948). However, it is assumed that there is also a purely marine form in the Caspian Sea, which spawns in the coastal zone of the western coast of the Caspian Sea and has a spotted coloration characteristic of sea lampreys (Nikitin, 2016). There is no information on the depth-dependent distribution during the marine life period, since the Caspian lamprey living near the bottom in the sea is practically inaccessible for observations.

HABITAT AND MIGRATION

The Caspian lamprey lives in rivers at the larval stage, while adults feed in the sea. The duration of the larval stage is estimated as 3 years in the Volga River and 2–4 years in the Kura River basin (Agamaliev, 1971a). Young individuals transformed in the river migrate to the sea to feed (Holčík, 1986; Kottelat and Freyhof, 2007; Renaud, 2011; Nazari et al., 2017). Lamprey larvae live in bottom sediments. Their habitats change as they grow. As the linear sizes increase, the ammocoetes, preferring earlier a substrate with fine-grained sand with a small amount of clay and detritus, seek for a substrate containing silty sand with a large amount of plant debris and macrophytes (Nazari et al., 2017; Clemens et al., 2020). In the Aldzhiganchay River (a tributary of the Kura River), the densest communities of ammocoetes on the bottom are found at the 30–85 cm depths, while in the Volga River, these are usually the depths of 6–8 m (Agamaliev, 1971a; Coad, 2016). In addition, in the Volga River, the maximum depth of ammocoetes' habitat has been recorded, 22 m from the water surface (Ginzburg, 1970). Ammocoetes prefer areas of river bends with moderate flow, where they burrow into the river substrate for 1–2 cm. They may also be found in the central part of the riverbed, in creeks, canals, and

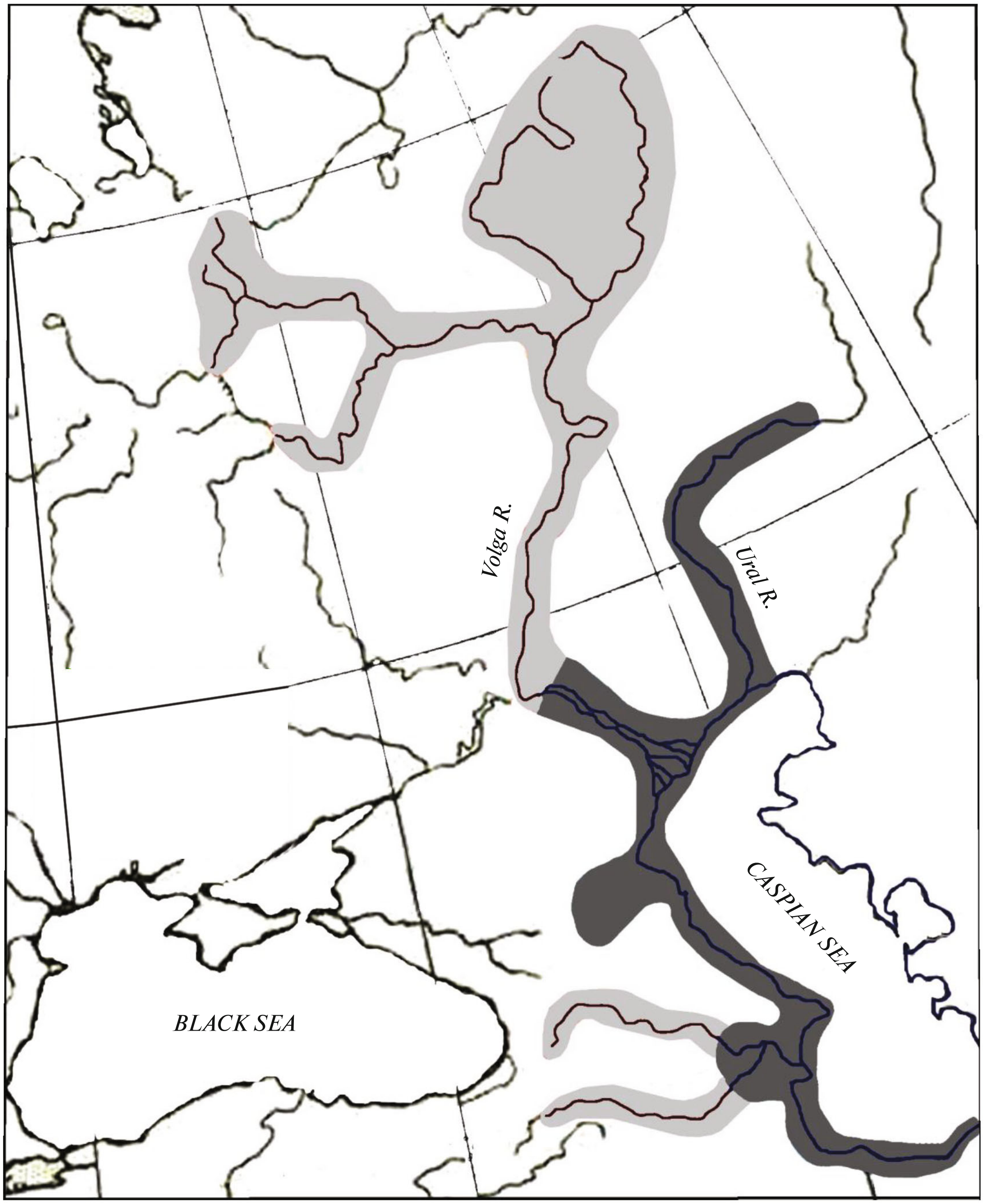

Fig. 2. Distribution map of the Caspian lamprey *Caspiomyzon wagneri:* (▫)—lost parts of the range, (▪)—modern range (according to: Berg, 1948; Kazancheev, 1981; Freyhof and Kottelat, 2008; Ivanov and Komarova, 2012).

bays. Lampreys at the stage of metamorphosis prefer the sites that locate deeper, characterized by a higher flow rate, lower water turbidity, and without macrophytes (Ginzburg, 1970; Agamaliev, 1971a; Holčík, 1986).

Most information on adults relates to the spawning migration stage; very limited data are available for other stages of the life cycle, especially the marine phase. The habitats of adults in the Caspian Sea are unknown, although some individuals were caught at depths of 600–700 m off the Iranian coast (Jolodar and Abdoli, 2004).

The spawning migration of the Caspian lamprey is predetermined by the hydrological regime of the rivers and by environmental conditions. Spawning migrations upstream the Volga River exceeded 2600 km (Berg, 1948); however, the dams prevent migrations nowadays (Moser et al., 2015). The lamprey migrates in flocks (Fig. 3). Larger lampreys are able to migrate at greater speeds and to make longer migrations. However, smaller individuals are the first to reach the river mouths, probably, they start migrating to spawning grounds earlier. The speed of lampreys varies from 1.9 to 15.9 km/day (Kazancheev, 1981; Ivanov and Komarova, 2012), although Pravdin (1965) has indicated that it can travel up to 50 km per day in the Volga River. Adults at the age of 4–6 years rise upstream for spawning to the Volga, Kura, Ural, Terek, Samur, Sefidrud, and Gorganrud rivers, as well as into small rivers of the western coast of the Caspian Sea (mainly in the spring rivers of the Karasu River system) and its southern coast. Migration takes place during two periods: in spring, from mid-March to mid-May (the most intensive run is observed in April at a water temperature of 11–15°C), and in autumn, from the end of September to mid-January (the most intensive run takes place in November–December at the water temperature of 11–16°C) (Kazancheev, 1981; Bogutskaya and Naseka, 2004; Orlov et al., 2021). At the same time, the period of spring migration is somewhat shorter comparing to autumn one. The dates of the beginning and end of the spawning migrations of the Caspian lamprey vary in accordance to different authors and for different rivers. In the Volga River, migration begins in mid-September with the peak in mid-October–mid-December and ends at the end of December. Peaks of migration are observed in late December–February near the city of Saratov and in March near the city of Kazan; in the Kura River, lamprey appears from November to February, with a peak in December–January (Pravdin, 1913b; Berg, 1948; Abdurakhmanov, 1962; Kazancheev, 1981; Holčík, 1986; Nazari, 2012; Nazari et al., 2017). In the Kura River, the Caspian lamprey often migrates attached to the Caspian trout *Salmo caspius* Kessler, 1877 in the area of gill covers (Berg, 1948; Agamaliev, 1971b; Coad, 2016), similar to other lamprey species (Tretyakov, 1949; Scott and Crossman, 1973; Orlov et al., 2007; Guidelines..., 2018). During the period of upstream migration, lampreys are inactive during the day, the intensity of migration increases at night (Pravdin, 1965; Holčík, 1986; Nazari and Abdoli, 2010). According to Nazari and Abdoli (2010), lampreys migrate most actively in the dark, with a peak observed approximately 2–3 hours after sunset. When moving along a river channel, migrating lampreys never travel along its entire width, but stay closer to the banks and the bottom, preferring coastal or midway paths and the areas with a flow velocity of 0.4–0.6 m/s (Kazancheev, 1981; Coad, 2016). Sexually mature individuals migrating in autumn–winter in rivers, overwinter in various substrates (among stones or in thickets). During winter and spring, lampreys are found curled into a ball under stones, they are almost unresponsive to external stimuli (Askerov et al., 2001).

LAMPREY SIZES

The maximum length of the Caspian lamprey ammocoete is 130 mm (Holčík, 1986; Renaud, 2011). The total length and body weight of adults within the species range vary from 190 to 553 mm and from 30 to 206 g, respectively (Holčík, 1986; Nazari et al., 2009, 2010; Nazari and Abdoli, 2010; Renaud, 2011; Nazari, 2012; Vatandoust et al., 2015; Abdoli et al., 2017; Almeida et al., 2021). The average body length and weight are 387 mm and 107 g (Lampreys..., 2015). At the Dagestan coast of the Caspian Sea, the length of a mature Caspian lamprey varies from 185 to 405 mm, weight, from 30 to 130 g (Barkhalov et al., 2012). In the southern part of the Caspian Sea, the minimum and maximum length and weight of spawning individuals are 271 and 492 mm, and 34.5 and 164.0 g, respectively, in the Shirud River; 295 and 428 mm, 54 and 133 g in the Talar River (Nazari et al., 2010). The average total length of adult lampreys is 296 mm in the Sardabrud River (Abdoli and Naderi, 2009).

Generally, females are slightly larger than males (Ghasempouri, 1993). It is noted that the average length of males and females in the Volga River is 360 and 369 mm, respectively; in the Kura River, it varies from 426 to 432 mm for males and from 436 to 440 mm for females (Smirnov, 1952; Agamaliev, 1971a, 1971b; Kazancheev, 1981). In 2000–2001, spawners in the Volga River population of the Caspian lamprey were presented by females with average length of 372 mm and a weight of 65.4 g and males with average length of 360 mm and a weight of 60.0 g (Nikitin, 2016).

AGE AND GROWTH

There are still no data on the age composition of the Caspian lamprey, since the methodology for determining its age has not been yet developed. The larval stage of anadromous lampreys is the longest stage of the entire life cycle (Dawson et al., 2015; Moser et al., 2021; Quintella et al., 2021). Since metamorphosis with transformation into an adult and migration from the river to the sea in the Caspian lamprey occurs in the fourth year of life, and the duration of the marine period is at least 1 year and 5 months, it is assumed that its age limit is 6 years (Holčík, 1986; Kottelat and Freyhof, 2007; Renaud, 2011; Ivanov and Komarova, 2012; Coad, 2016).

Information on the growth rate of the Caspian lamprey is also fragmentary and limited. Three age groups of larvae with an average length of 31, 62, and 101 mm have been recorded in the Volga River (Ginzburg, 1970); in Kura River, 2–4 age groups (Holčík, 1986; Coad 2016). The marine life span of the Caspian lamprey is 17 months or slightly exceeds it (Holčík, 1986; Kottelat and Freyhof, 2007; Renaud, 2011). Ammocoetes and adults are characterized by allometric growth (Holčík, 1986). Negative allometric growth of lampreys migrating upstream of the Shirud and Talar riv-

Fig. 3. Spawning run of the Caspian lamprey *Caspiomyzon wagneri* in the Shirud River (a–c) and sampling of the specimens (d) (photo by H. Nazari).

ers was noted (Nazari et al., 2010). After metamorphosis, there is a gradual reduction in the total length of lampreys by an average of 22.3% within 5–6 months (Renaud, 1982; Holčík, 1986). The total length and weight of adult Caspian lampreys in the Shirud River decrease in males and females by 6.8 and 18.8%, and by 13.6 and 26.2%, respectively (Nazari et al., 2017), which is noticeably less compared to other lamprey species, such as the Pacific lamprey *Entosphenus tridentatus* (Richardson, 1837), which loses up to 30% of the body length (Clemens et al., 2010). During the pre-spawning and spawning periods, the length and weight of the Caspian lamprey gradually decrease, while the condition factor increases (Fig. 4), indicating that the rates of growth of body length and weight during this period differ, especially in females (Holčík, 1986; Nazari et al., 2010). Factors determining condition factor include the size of the individuals, the maturity state, and the geographic location of the river (Holčík, 1986). For example, the condition factor of

Fig. 4. The Caspian lamprey *Caspiomyzon wagneri* from the Volga River basin in a state of maximum fatness (photo by E.V. Nikitin).

the Caspian lamprey from the Volga River varies from 0.13 to 0.14, remaining stable from December to April, but in May and June it increases up to 0.16 (Ginzburg, 1969; Holčík, 1986). In the Kura River, it ranges as 0.133–0.293 in females (Smirnov, 1953), in the Shirud River, 0.095–0.347 (Nazari et al., 2010; Nazari, 2012). At the same time, the condition factor is higher in individuals migrating in autumn comparing to those migrating in spring. Since the condition factor depends on the gonad maturity state, autumn migrants entering the river look more mature than the individuals of the spring group (Nazari, 2012). It should be noted that the condition factor of the Caspian lamprey falls within similar limits of other lamprey species, for example, the Arctic lamprey *Lethenteron camchaticus* (Tilesius, 1811) and the Pacific lamprey; the latter species is also characterized by maximum values of this parameter in the spring-summer period (Orlov et al., 2008, 2014).

REPRODUCTIVE BIOLOGY

Lampreys are characterized by a complex life cycle. The Caspian lamprey can live up to 4 years in fresh water before migrating to the Caspian Sea where it spends the next 1.5 years. Throughout its life, the Caspian lamprey performs regular migrations, which may be divided into four types (Holčík, 1986): (1) spawning migration of adults from the sea to rivers; (2) feeding migration of ammocoetes; (3) migration of ammocoetes preparing for metamorphosis; (4) feeding migration of ammocoetes, which undergone metamorphosis, to the sea.

Pre-spawning individuals begin their migration to rivers in autumn and winter, depending on hydrological and meteorological conditions, such as temperature, flow velocity, water level in the river, water quality and turbidity, illumination and the phase of the lunar cycle (Holčík, 1986; Nazari and Abdoli, 2010). At the beginning of spawning migration, the Caspian lamprey is characterized by a very high fat content (30–34%), which reduces greatly down to 2.0–3.5% as the individuals reach the spawning grounds. During spawning migration, when the gonads mature, lampreys do not feed, and the development of the gonads, especially the ovaries, depends on the accumulated energy reserves during this period. During the period of natural starvation, the Caspian lamprey undergoes a sharp body transformation, which uses the reserves of fat and protein, accumulated mainly in the muscles and skin, for the gonad development. During the spawning period, the appearance of the lamprey changes; in particular, its body shortens, the teeth become blunt, the size of the fins increases, the dorsal fins become higher and closer, the coloration changes, the urogenital papilla is formed near the anus, reaching an average length of 1.2–4.8 mm in males and 0.6–1.5 mm in females (Renaud, 1982; Nazari and Abdoli, 2010; Coad, 2016). Spawning takes place from March through June in shallow waters with a moderate water flow and a sandy-pebbly bottom.

In the rivers of the central and northern Caspian Sea, migration is most intense at the water temperature of 6–11°C (Pravdin, 1913b; Abdurakhmanov, 1962; Ginzburg, 1969, 1970; Agamaliev, 1971b; Kazancheev, 1981; Ivanov and Komarova, 2012). In the Shirud River, mass migration of the Caspian lamprey begins at a water temperature of 16°C and ends when it reaches 21°C; individuals need 208–470 degree-days to reach sexual maturity after they have started upstream migration (Pravdin, 1965; Nazari and Abdoli, 2010; Farrokhnejad et al., 2014; Nazari et al., 2017).

On the spawning grounds, the males or the individuals of both sexes build oval-shaped nests, moving gravel and small stones with sucking discs using wave-like movements of the body (Abdurakhmanov, 1962; Maitland et al., 1994); as a result, a shallow depression ~0.5–1.0 m in diameter is formed at the bottom. According to Nikitin (2016), lampreys can also use artificial pebble spawning grounds of other anadromous fish, such as sheefish *Stenodus leucichthys*

Table 1. Fecundity of the Caspian lamprey of the Volga population depending on body weight (according to: Nikitin, 2016)

Body weight, g	Absolute fecundity, thousand eggs		Relative fecundity, thousand eggs/g of body weight	
	min–max	*M*	min–max	*M*
46–50	19.0–26.0	22.6	0.400–0.540	0.460
51–55	16.0–24.0	20.7	0.290–0.460	0.380
56–60	20.0–38.0	26.4	0.350–0.630	0.450
61-65	20.0–31.0	25.0	0.300–0.500	0.360
66–70	–	25.0	–	0.360
71–75	28.0–30.0	29.0	0.390–0.400	0.390
76–80	–	36.0	–	0.460

Min–max—limits of indicator, *M*—mean. Here and in Table. 2: "–"—no data.

(Güldenstädt, 1772) and the representatives of the family Acipenseridae, in the areas with depths of down to 2 m, flow velocity of 0.8 m/s, and dissolved oxygen content of 8–12 mg/L.

Most authors note the predominance of females over males in the lamprey populations, the males to females ratio varies from 0.62: 1.00 to 1.00: 2.92 (Pravdin, 1913a, 1913b; Dyuzhikov, 1956; Ginzburg, 1969; Holčík, 1986; Nazari and Abdoli, 2010; Ahmadi et al., 2011; Nazari, 2012; Nazari et al., 2017). Although, some authors report about the dominance of males at the spawning grounds in a ratio of 2.2 : 1.0 (Ghasempouri, 1993). Probably, these contradictions are due to different observation periods, since males usually predominate at the beginning of spawning as they mature earlier than females (Farrokhnejad et al., 2014), but during the entire spawning period, the ratio of males and females is more or less close to 1 : 1 (Smirnov, 1953; Nazari and Abdoli, 2010). Lampreys often spawn in groups, when there are several males per female. During mating, males attach their sucking discs to the female's head and wrap their bodies around the female body (Coad, 2016). The Caspian lamprey is characterized by one-time spawning (Kazancheev, 1981; Ivanov and Komarova, 2012; Nazari et al., 2017; Orlov et al., 2021). During the release of reproductive products, the tails of individuals of both sexes tremble, eggs and sperm are released simultaneously (Coad, 2016). The spawning process takes several days, since the female lays only a few sticky eggs, colored from white to yellow, at a time (Coad, 2016; Nazari et al., 2017). The egg diameter is 0.60–1.15 mm in the Caspian lamprey of the Volga River population (Pravdin, 1913a, 1913b; Berg, 1948; Smirnov, 1953; Ginzburg, 1969, 1970; Holcik, 1986). For Iranian waters, similar values are reported: 0.78–1.15 (average 0.92 ± 0.08) mm (Nazari and Abdoli, 2010; Lampreys..., 2015).

Since lampreys do not feed during the upstream migration, females die of starvation immediately after spawning, but males remain alive for several more days or weeks until spermatogenesis stops (Smirnov, 1952, 1953; Larsen, 1980; Kazancheev, 1981; Holčík, 1986; Ghasempouri, 1993; Coad, 2016; Nazari et al., 2017). Nevertheless, some authors suggest that nowadays some individuals may remain alive after the first spawning and participate in spawning in the new spawning season after feeding in the sea due to the reduction in migration routes (Ivanov and Komarova, 2012; Coad, 2016; Orlov et al., 2021). Cases of repeated spawning are also known in other lamprey species (Michael, 1980).

The absolute fecundity of the Caspian lamprey of the Volga River population is 16–43 (average 21–36) thousand eggs (Table 1), of the Kura population, 14–38 (average 24) thousand eggs (Pravdin, 1913a, 1913b; Kazancheev, 1981; Holčík, 1986; Nikitin, 2016). In Iranian waters, the absolute individual fecundity of the Caspian lamprey is noticeably higher, reaching 32–51 (41.9 ± 5.4, on average) thousand eggs in the individuals migrating in spring (Nazari and Abdoli, 2010; Lampreys ..., 2015).

In the Caspian lamprey, absolute fecundity depends significantly on the body size and weight (Holčík, 1986; Ahmadi et al., 2011; Nikitin, 2016). According to Nikitin (2016), in the Volga River, the minimum absolute fecundity (20.7–22.6 thousand eggs) is observed in lampreys weighing 46–55 g, the maximum (29.0–36.0 thousand eggs), in the individuals weighing 71–80 g (Table 1).

The relative fecundity of the Caspian lamprey of the Volga River population varies within 290–630 eggs per 1 g of body weight (Table 1), the maximum values are typical for specimens weighing 46–50 g and 76–80 g (Nikitin, 2016). In the waters of Iran, the relative fecundity of the Caspian lamprey is characterized by similar values, amounting 260.8–677.4 (average 397.6 ± 93) eggs per 1 g of body weight or 80.3–148.1 (107.2 ± 15.1) eggs per 1 mm of body length (Nazari and Abdoli, 2010; Lampreys..., 2015).

The gonadosomatic index (GSI) in females varies from 2.67 in the Volga River to 35.12 in the Shirud River (Table 2). At the same time, the average GSI value of the lamprey population in spring is somewhat higher than in autumn, when maximum values are noted in April–May (Ghasempouri, 1993). During the spawning period, the GSI reaches its maximum values, while both in spring and autumn migrating lampreys, the gonads are at maturity stage IV. The hepato-somatic index averages 0.85 and 1.02 in maturing females and males, respectively, while that of mature ones is 1.310 and 0.975, which indicates starvation during this period and the expenditure of energy reserves accumulated in the liver for the development of gonads (Ahmadi et al., 2011; Coad, 2016).

After 9–11 days at a water temperature of 15–22°C, the fertilized eggs hatch into worm-shaped larvae (ammocoetes) with a body length of 3.3–4.2 mm. They have no teeth, a mouth hood, eyes covered with skin, and a light-sensitive area near the tail. Ammocoetes burrow into bottom sediments consisting of fine-grained sand with a small amount of silt and detritus, and a large amount of plant debris, macrophytes, and submerged wood (Coad, 2016; Nazari et al., 2017). These transparent, blind, and poorly swimming larvae are carried downstream from the spawning grounds (nests) to the areas with the deposits of sand, silt, and detritus, where they later spend most of their lives (2–4 years), feeding on microorganisms by filtration. In the northern part of their range, ammocoetes live in the river until they reach a length of 10–12 cm, after which they undergo metamorphosis. The latter usually takes place from July to December (Holčík, 1986), in the rivers of the Iranian coast, in October, when a total body length of ammocoetes reaches 8–11 cm (Renaud, 1982, 2011). During metamorphosis, they do not feed. After metamorphosis, lampreys migrate to the Caspian Sea, where they fatten before returning to fresh water to spawn (Holčík, 1986).

FEEDING AND TROPHIC RELATIONSHIPS

Almost nothing is known about the feeding of the Caspian lamprey in the sea, which contributed to different ideas (Quintella et al., 2021). Sabaneev (1892) reported that individuals of this species fed on organic matter and silt, but most of all, on the flesh of living and dead fish. Based on observations by Kessler (1870) and Kavraiskii (1897), the Caspian lamprey attacked the Caspian trout; Hubbs and Potter (1971) and Lelek (1987) came to the conclusion that individuals of this species parasitized on fish; Abakumov (1965) believed that they attacked the Caspian trout. However, Kavraiskii (1897) pointed out that the Caspian lamprey used the Caspian trout only for transportation to the spawning grounds. The Caspian salmon *Salmo ciscaucasicus* Dorofeeva, 1967 is another fish species, on which the traces of the sucking disc of the Caspian lamprey have been found. However, similar to the Caspian trout, the Caspian lamprey attaches to the opercular area and uses salmon as a transport species during spawning migrations (Quintella et al., 2021). The idea of a non-parasitic way of life of this species is supported by Holčík (1986) and Agamaliev (1971b), reporting that the teeth of the Caspian lamprey are already blunt during the transformation period, and this completely excludes the possibility of parasitism on other fish. Vladykov and Kott (1979) suggested that the Caspian lamprey could feed on the eggs of benthic fish or on some invertebrates. Renaud (1982) found juvenile acanthocephalans (*Corynosoma* sp.) in the Caspian lamprey intestines and suggested that it fed on amphipods, since the latter served as an intermediate host of these parasites. However, Holčík (1986) speculated that these acanthocephalans could have been consumed by lampreys with the infected decaying fish. Renaud et al. (2009) considered the Caspian lamprey to be a scavenger, but he noted the presence of well-developed buccal glands that could compensate for its blunt teeth and allowed it to feed on fish. In general, most authors tend to believe that the Caspian lamprey cannot parasitize on fish and is classified as a scavenger by the type of food based on the findings of algae and detritus in its intestines and the presence of blunt teeth (Abdurakhmanov, 1962; Kazancheev, 1981; Shooshtari et al., 2011; Ivanov and Komarova, 2012; Bogutskaya et al., 2013; Quintella et al., 2021; Orlov et al., 2021). However, even now the considered species is classified by some authors as a parasitic lamprey, which is supported by direct observations (Lampreys..., 2015). Nikitina and Salnikov (2000) found traces of lamprey sucking disc in the tail part of the sterlet *Acipenser ruthenus* Linnaeus, 1758 (45-cm long), caught in the Volga River near the village of Nikolsky. A cavity measuring 100 × 40 × 20 mm with uneven edges was eaten out inside the sterlet's body, while the wound was filled with blood and mucus. Contradictory data on the type of feeding of adults indicate a rather high trophic plasticity of the Caspian lamprey.

Table 2. Some characteristics of the Caspian lamprey females during the reproductive period and the sex ratio (males : females) in the spawning part of populations

River (period, year)	Body length, mm	Body weight, g	Gonad weight, g	Gonadosomatic index	Fecundity, eggs	Sex ratio	Source
Volga	305–530	47.0–180.0	4.60–7.90	2.67–11.10	25.000–43.000	1.13–1.94 : 1.00	Pravdin, 1913a, 1913b; Holčík, 1986
Volga (2000–2001)	320–410	46.0–80.5	7.30–9.40	7.20–11.30	24.770–39.020	1.00 : 1.00	Nikitin, 2016
Kura	388–447	88.0–124.0	3.89–10.30	–	–	–	Smirnov, 1953; Holčík, 1986
Kura	330–530	46.0–192.0	3.89–10.30	3.38–11.70	14.000–38.000	–	Agamaliev, 1971b; Kazancheev, 1981
Shirud (autumn 2011)	293–443	55.4–168.6	9.12–23.68	6.38–25.38	17.514–64.425	0.62–0. 94 : 1.00	Nazari et al., 201 7
Shirud (spring of 2006 and 2012)	330–369	74.1–91.4	19.8 0 –32.1 0	9.51–35.12	45.793–51.198	0.87–1.07 : 1.00	Nazari, Abdoli, 2010; Farrokhnejad et al., 2014

Fig. 5. Individuals of the Caspian lamprey *Caspiomyzon wagneri,* found in stomach of the northern pike *Esox lucius,* caught in the Volga River (photo from the site https://kaspyinfo.ru/news/gorod/54314).

During the period of spawning migration, both in the lower reaches of the Volga River and in the rivers of the Iranian coast, blue-green algae are found in the intestines of the Caspian lamprey, which are accidentally sucked together with water (Nikitina and Salnikov, 2000), or enter the digestive tract from a solid substrate, to which lampreys attach themselves (Nazari et al., 2010). Large numbers of crustaceans parasitizing on the amphipods *Monoporeia affinis* (Lindström, 1855) are also found, which may indicate that lampreys feed on the latter during the marine period of life (Nikitina and Salnikov, 2000).

Ammocoetes are filter feeders, consuming diatoms and detritus. Migrating, metamorphosing and spawning lampreys do not feed. The intestinal diameter decreases from 2.7 mm in pre-spawning lampreys down to 1.4 mm in spawning specimens (Renaud, 1982). Benam et al. (2016), examining the gastrointestinal tract of maturing and mature lampreys in the Shirud River, have found that their intestines are empty, confirming the fact that lampreys stop feeding when migrating to the river. In addition, these authors report that the lamprey's digestive tract and associated organs (liver and pancreas) have undergone degeneration (especially in females).

Lampreys play a vital role in freshwater and marine ecosystems, serving as food for fish and other vertebrates (Orlov et al., 2007; Maitland et al., 2015; Guidelines..., 2018). Predatory fish such as the northern pike *Esox lucius* Linnaeus, 1758 feed on the Caspian lamprey (Fig. 5)[1], as well as wels catfish *Silurus glanis* Linnaeus, 1758, burbot *Lota lota* (Linnaeus, 1758), zander *Sander lucioperca* (Linnaeus, 1758) and beluga *Huso huso* (Linnaeus, 1758) (Coad, 2016). The Eurasian otter *Lutra lutra* (Linnaeus, 1758) and near-water birds (Nazari et al., 2010; Coad, 2016) hunt of the lamprey as well.

PARASITES AND DISEASES

Little is known about the parasites and diseases of the Caspian lamprey. Pravdin (1913a) and Zekhnov (1958) reported on finding the acanthocephalan *Echinorhynchus* sp. in the body cavity of pre-spawning individuals in the Volga River and in the Caspian Sea. Juveniles of the acanthocephalan *Corynosoma* sp. were found in migrating lamprey in the upper reaches of the Kama River and in the Iranian rivers Shirud and Talar (Zakhvatkin, 1936; Zekhnov, 1958; Renaud, 1982; Nazari and Abdoli, 2010; Nazari et al., 2010). Parasitic

[1] https://kaspyinfo.ru/news/gorod/54314; assessed December 2021.

larvae of bivalve mollusks (glochidia) were also found on the gills of pre-spawning lampreys (Zakhvatkin, 1936). Abnormalities in the development of the caudal and anal fins and various infections have been noted in some lampreys migrating upstream the Shirud River (Abdoli et al., 2017; Nazari et al., 2017).

INTRASPECIFIC STRUCTURE

Berg (Berg, 1931, 1948) reported that the Caspian lamprey had two adult forms: a typical form with a body length of 370–553 mm and a dwarf form (praecox) with a body length of 190–310 mm.

When comparing the lampreys caught in the Volga and Kura rivers, no significant differences in their morphology were found (Smirnov, 1952, 1953). Nazari and co-authors (2009) found significant differences in morphometric characters of lampreys from the Shirud and Talar rivers and the absence of statistically significant differences between them in meristic characters. Comparison of lampreys sampled from two other Iranian rivers of the southern Caspian (Babolrod and Kheyrod) revealed significant differences between a number of morphometric features (Vatandoust et al., 2015). This allowed the authors to conclude that the Caspian lamprey in the southern Caspian was represented by at least two morphological forms, and there was an independent population in each of the studied rivers. A different point of view was proposed by Kucheryavyi and co-authors (2016), who suggested that the Caspian lamprey was a homogeneous metapopulation consisting of mixing individuals during their sea period of life in the Caspian Sea.

NUTRITIONAL VALUE, ECONOMIC AND SOCIO-ECONOMIC IMPORTANCE

The Caspian lamprey was of great economic importance in the Caspian Sea basin in the past (Berg, 1948; Kazancheev, 1981; Kottelat and Freyhof, 2007; Renaud, 2011), which is currently true to a certain extent only for the waters of Iran (Imanpoor and Abdollahi, 2011). In terms of nutritional value, it is almost unique, being a valuable delicacy product (Kazancheev, 1981). Lamprey flesh contains up to 29.0–30.3 fat, 11.8–13.2 proteins, 1.9 mineral salts, 1.4 ash, and 55.1–57.5% moisture, the energy value is 324 kcal per 100 g of wet weight (Chemical composition..., 1987). Lamprey fat contains a lot of iodine, a full set of essential amino acids, vitamins A, B, B_{12}, C, D_1, E and others; it is very useful and palatable (Hajibababekov, 1939; Holčík, 1986; Askerov et al., 2001). However, Coad (1979, 2016) states that Caspian lamprey meat is toxic, and intoxication occurs within a few hours after eating it. Contact with lamprey mucus may cause skin irritation. Therefore, to prevent the described phenomena, lamprey must be soaked in brine before use.

In the past, the Caspian lamprey was dried and used as candles or for fat, and also caught by man for consumption (Berg, 1948; Kazancheev, 1981; Kottelat and Freyhof, 2007; Renaud, 2011). In Russia, the Caspian lamprey was used for food and for lighting by the non-Muslim population of the Caucasus, while the Muslims used it exclusively for making candles (Almeida et al., 2021). In the XX century, the Caspian lamprey in Russia began to be cooked fried and pickled (Orlov et al., 2021). In Turkmenistan, the Caspian lamprey is believed to be useful as a remedy for hemorrhoids and asthma. In Iran, this species has no commercial value and is practically not eaten for religious reasons due to the lack of scales. Nevertheless, it is still fished, for example, in the Gorganrud River, and is used to treat health problems, and is also eaten smoked or aged in brine (Coad, 2016; Nazari et al., 2017; Shirood Mirzaie et al., 2017).

POPULATION DYNAMICS AND LIMITING FACTORS

The abundance of the Caspian lamprey may only be judged by the changes in its catches. In the past, its numbers were quite high, being of great commercial importance. At the lower reaches of the Volga River, the annual catch amounted to 552 tons in 1875–1884, increasing up to 2478 tons in 1900–1915, and the maximum annual catch was recorded in 1903, when 4440.7 tons of lamprey were fished in the Volga River delta (Mitropol'skii, 1916; Strubalin, 1989; Nikitina, 1998). Subsequently, its catches decreased sharply. In 1932–1937, they averaged 30–80 tons (Kazancheev, 1981). According to other sources, they decreased from 640 to 150 tons from 1925 to 1942 (Nikitin, 2016).

In the Kura River, in 1891–1935, the minimum five-year catch was recorded in 1891–1895, when only 11 thousand lampreys were caught, while the five-year catch peaked at 612000 individuals in 1911–1915. After 1935, 213000 lampreys were caught in 1936, and a catch of 304000 lampreys was reported in 1937. The annual catch in the Chur River varied from 10 to 269 tons in 1930–1963 (Berg, 1948; Holčík, 1986; Renaud, 2011).

Since the middle of the XX century, due to the construction of the dams at the Mingachevir and Volga hydroelectric power stations, the numbers of the Caspian lamprey began to decline; its annual catches in the Volga and Kura rivers have decreased from 150 to 10 tons in 1951–1960 (Kazancheev, 1981; Nikitin, 2016). In the middle and in the end of the XX century,

Fig. 6. Catch of the Caspian lamprey *Caspiomyzon wagneri* in the Shirud River during the autumn migration (photo by H. Nazari).

lamprey was fished mainly in the Astrakhan region nearby the Nikol'skoe village (230–300 km upstream the city of Astrakhan), where the main spawning grounds of the species were located. Here, the average annual catches of lamprey were about 0.8 tons in 1966–1987, 5.6 tons were caught in 1992 (Nikitina, 1995, 1998; Nikitin, 2016).

On the Iranian coast of the Caspian Sea, the number of lampreys remains relatively high; during the spawning migration in some rivers, up to several hundred kilograms of Caspian lamprey may be caught within an hour (Fig. 6) (Coad, 2016). However, the abundance of this species in Iran has noticeably decreased in recent years (Nazari et al., 2017).

The main reasons for the sharp decline in the number of populations of the Caspian lamprey are associated with the regulation of river flow by dams and locks, the construction of hydraulic structures, a decrease in spawning areas, water pollution due to human activities, climate change towards aridity, water intake for irrigation, dredging and sand mining, which destroys spawning grounds and habitats of ammocoetes (Nazari et al., 2017; Orlov et al., 2021). Lack of public awareness of the characteristics of the biology of the Caspian lamprey (people still believe that it harms fish stocks) stimulates a barbaric opinion and fishing, when caught individuals are killed or not returned to their natural habitat (Nazari et al., 2017; Orlov et al., 2021). In the Terek River, dredging operations to remove sand from the bottom nearby the villages of Chervlenaya and Azamat-Yurt led to the death of many ammocoetes, thereby reducing the number of recruits (Orlov et al., 2021). In addition, intense winter water releases from the Volga HPP, observed in recent years, affect the flow velocity, the state of the spawning grounds of the Caspian lamprey, and its spawning process. In some areas, illegal lamprey fishing (poaching) is possible, but it probably has a lesser impact on the state of stocks (Nikitin, 2016).

FISHING

The history of the Russian fishery of the Caspian lamprey has ~300 years (Almeida et al., 2021). Until 1997, it was classified as a valuable commercial object in the Russian Federation (the lower reaches of the Volga River) and Azerbaijan (the Kura River) (Nikitin, 2016). At present, it has completely lost its commercial value (Almeida et al., 2021; Orlov et al., 2021).

In the XIX century, lamprey was probably not in a great demand for the population of the lower reaches of the Volga River. In the request of the Chernoyarsk fish merchants for the "Permission of lamprey fat burning", sent to Tsar Alexander II in May 1877, it was reported that ordinary people do not eat lamprey, disgusted by it because of the serpentine body shape. Lampreys were used at that time mainly for rendering

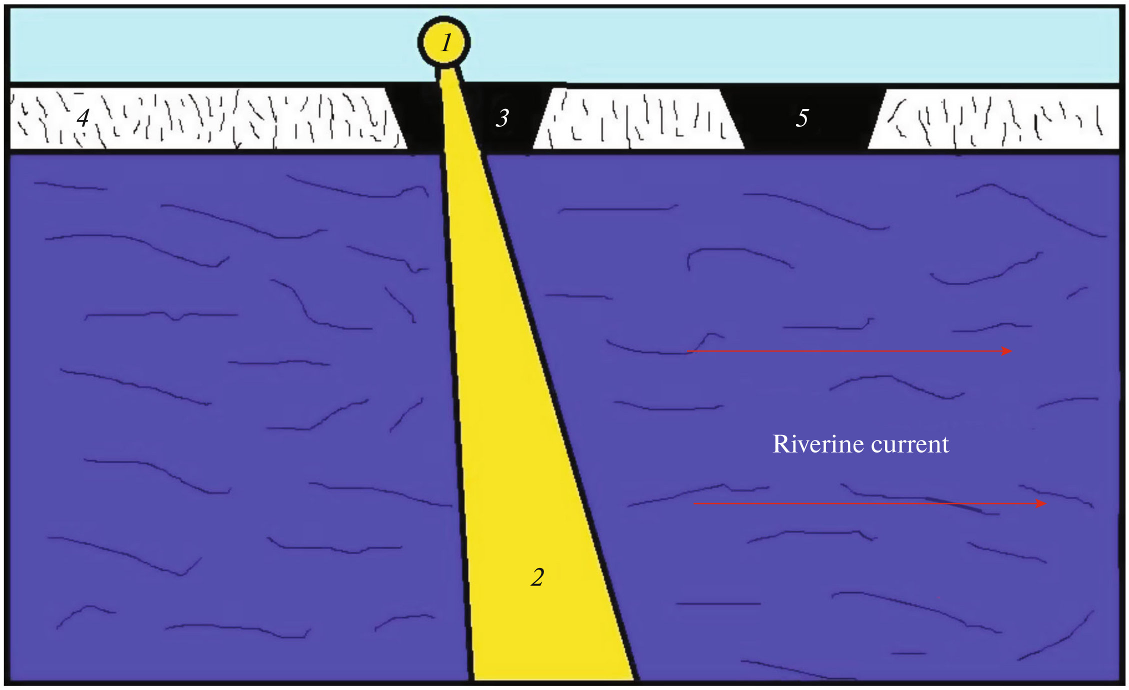

Fig. 7. Scheme of ice fishing for the Caspian lamprey *Caspiomyzon wagneri* in the Volga River with the use of light (according to: Pravdin, 1965, with modifications): 1—light source (lantern); 2—water column illuminated by a beam of light rays; 3—ice hole with a lantern, 4—ice surface, 5—ice hole where fishing takes place; (→)—flow direction.

fat and for lighting (dried lampreys were burned instead of candles). They caught lampreys with special traps of the "fish top" type (local name "neredy"), which were woven from thin brushwood or wood twigs (most often willow) and were usually installed near the shore. In winter, local residents caught lampreys in holes with their hands and with the help of nets (Pallas, 1788). Here is how Pravdin (1965, p. 60) describes ice fishing for the Caspian lamprey: "In those days, on the Volga [River], lampreys were caught with a "lantern", believing that it was striving for light. On the ice, above the fast [water], usually not very deep, where the densest run of the lamprey was assumed, a brightly burning lantern was placed near the hole, and at some distance from it, several more holes were punched, in which they scooped lamprey by "saks" [fishing nets], believing that it [lamprey] "swirls" around illuminated strip of water. Indeed, the lamprey gathers near the illuminated strip, but this is not due to the fact that the fish strives for the light, but because, on the contrary, it avoids it. The lamprey, moving all the time in the dark towards the fast-flowing stream, runs into the light and, hiding from it, rises up into a darker space, where it falls into the "sak" hold by fisherman" (Fig. 7). Lampreys were fished in the summer to obtain fat, caught in the winter, they were salted and delivered to the markets of the cities of Moscow, Riga, Nizhny Novgorod, Smolensk, and Kiev (Minkh, 1902).

CONSERVATION STATUS AND CONSERVATION MEASURES

The population of the Caspian lamprey has declined sharply in recent decades, mainly due to destruction and degradation of habitats and spawning grounds (Renaud, 1997; Clemens et al., 2013). The Caspian lamprey was first proposed to be listed in the Red Data Book of the USSR in 1985 (Pavlov et al., 1985). It is listed as "vulnerable" in Europe (Lelek, 1987; Maitland, 1991). Due to the scarcity of the Caspian lamprey, it is included in the IUCN Red List (Freyhof and Kottelat, 2008), category "Near threatened" (NT), and in the Appendix 3 of the Bern Convention (The Bern Convention..., 1979). It is listed in the Red List of the Russian Federation (category and status 2, species declining in numbers and/or distribution) (Kucheryavyi, 2021) and the Red Lists of a number of its regions: the Republic of Dagestan (category and status 2) (Abdusamadov and Barkhalov, 2020), the Republic of Kalmykia (2) (Poznyak, 2013), the Republic of Chechnya (2) (Batkhiev and Kaimov, 2020), the Republic of North Ossetia-Alania (category and status 1, endangered species) (Sokhno, 1999), the Republic of Mordovia (category and status 0, probably an extinct species) (Vechkanov, 2005), the Republic of Chuvashia (0) (Alyushin et al., 2010), Astrakhan Oblast (1) (Red List..., 2014), Saratov Oblast (1) (Shlyakhtin et al., 2021), Volgograd Oblast (2) (Boldyrev, and

Yakovlev, 2017), Ivanovo Oblast (0) (Barinov, 2007), Nizhny Novgorod Oblast (0) (Anufriev et al., 2014), Orenburg Oblast (category and status 4, species with insufficiently clarified distribution and abundance) (Chibilev, 2019), and Stavropol Territory (0) (Mishvelov, 2013).

In Iran, the Caspian lamprey was previously considered endangered due to the loss of major spawning grounds and a sharp decline in numbers (Kiabi et al., 1999). Currently, its status is set to NT (Clemens et al., 2020). It is also included in the list of vulnerable species of the Republic of Kazakhstan (category 2, species rapidly reducing its numbers within the range) as a result of disturbance of habitats and spawning grounds caused by the construction of hydroelectric power plants (Red List..., 2006); it is currently considered in the category "Vulnerable" (VU) (Clemens et al., 2020). In Turkey (Fricke et al., 2007) and Azerbaijan (Clemens et al., 2020), this species has been assigned the status of "Extinct" (EX), however, in the waters of Azerbaijan, an increase in its abundance has been noted in recent years (Yusifov and Ahmadov, 2021). In Turkmenistan, the Caspian lamprey is considered in the status of "Data Deficient" (DD) (Nazari et al., 2017; Clemens et al., 2020).

Most of the conservation efforts in the Caspian Sea basin are focused on high-value commercial fish such as sturgeon and Caspian trout. Unfortunately, the Caspian lamprey is not added to this list, so it does not receive legal protection. Despite the different conservation status of the species in different countries and even within the same country, three common features may be distinguished for its conservation (Clemens et al., 2020): (1) international or local protection measures have not been developed; (2) there is a high level of anthropogenic threats within the range; 3) the degree of knowledge remains insufficient regardless of the country. The lack of complete information about the ecology and distribution of the Caspian lamprey in many parts of its vast range makes it difficult to develop appropriate conservation measures.

The most serious threats to the Caspian lamprey are the following: (1) dams and locks that prevent lampreys from accessing spawning grounds (Holčík, 1986; Coad, 2016; Nazari et al., 2017; Orlov et al., 2021); (2) climate aridization, causing disturbance of habitats as a result of shallowing and drying of spawning grounds and areas inhabited by ammocoetes (Abdoli et al., 2017; Coad, 2016; Nazari et al., 2017; Clemens et al., 2020); (3) water withdrawal for irrigation, which leads to a deterioration of spawning grounds and disturbance of lamprey habitats (Rabazanov et al., 2017; Rabazanov et al., 2019); (4) pollution of rivers by industrial and household effluents, which have a negative impact on the survival of lampreys at different stages of ontogenesis and their reproductive ability (Nasrollah Pourmoghadam et al., 2015; Eagderi et al., 2017); (5) dredging and sand mining destroying spawning grounds and habitats of ammocoetes (Nazari et al., 2017; Clemens et al., 2020; Orlov et al., 2021); (6) illegal (poaching) fishing, reducing the population already low in numbers (Nikitin, 2016; Nazari et al., 2017; Clemens et al., 2020); and (7) insufficient awareness of the local population about the state of the environment and the conservation status of rare and endangered species (Nazari et al., 2017).

Pollution is one of the key factors that have a negative impact on the state of the stocks of the Caspian lamprey. Recent studies on the Iranian coast of the southern Caspian evidence that lamprey sperm motility and morphology, and ultimately reproductive success, may be adversely affected by the increased concentrations of heavy metals (Shooshtari et al., 2011; Eagderi et al., 2017). Concentrations of heavy metals in the aquatic environment have been increasing in recent years, especially in areas where industrial, agricultural, and mining activities are widely carried out. At the Iranian coast of the Caspian Sea, the concentration of mercury in the muscles of the adult Caspian lamprey is 10 times lower than in ammocoetes (Shooshtari et al., 2011). It is assumed that the increased content of mercury in the ovaries may adversely affect the reproductive ability of females (Shooshtari et al. 2011).

It is believed that the illegal fishing of the Caspian lamprey does not have such a negative impact on its stocks as other factors (Nikitin, 2016). However, in Iranian waters it is recognized as a rather serious type of anthropogenic impact (Nazari et al., 2017; Clemens et al., 2020). Iranian fishermen kill lampreys or leave them to dry on the shore, believing that the lampreys parasitize important commercial fish species. This is partly due to the poor awareness of the local population about the ecological characteristics of the Caspian lamprey, as well as the lack of effective measures for its conservation.

Currently, there are no special measures for the protection of the Caspian lamprey (Almeida et al., 2021; Clemens et al., 2020; Orlov et al., 2021). In order to preserve and restore the population of the Caspian lamprey in modern conditions, it is necessary to carry out regular monitoring studies and conservation and regulatory measures aimed at improving the conditions for natural reproduction. In this regard, the experience of restoring the abundance of some species of anadromous lamprey species from the North Pacific (Clemens et al., 2020), including the removal of barriers to spawning migration routes, equipping dams and locks with fish passes to allow breeders to

Fig. 8. The Caspian lamprey *Caspiomyzon wagneri* accidentally caught in the Volga River and returning to habitat (photo by E.V. Nikitin).

spawn, restoration of river habitats and their regular monitoring, and control of pollutant content in rivers. It is necessary to conduct research in order to determine the damage to the stocks of the Caspian lamprey from the operation of water intake facilities with the direction of the funds received for its artificial reproduction and the release of reared juveniles (ammocoetes) into natural reservoirs (Nikitin, 2016). There is an experience in the artificial reproduction of the Caspian lamprey experimenting on catching and long-term keeping of producers, obtaining mature sexual products, fertilizing eggs and incubating them in Weiss apparatus (Nikitina and Salnikov, 1996; Nikitina, 1998). In particular, in the experiments performed in 1989–1991, they managed to bring the incubation to the stage of isolation of the anterior part of the embryo, but the attempts to obtain viable offspring under artificial conditions did not produce results.

Along with these measures, raising the public awareness of the state of the environment, ecology, and conservation status of rare and endangered species is an important element of the management of aquatic biological resources (Clemens et al., 2020). Efforts in this direction will help improve the environmental awareness of the population, will eradicate the barbaric opinion and activities on accidentally caught specimens of the Caspian lamprey, and will contribute to their return to their natural habitat (Fig. 8).

GAPS IN KNOWLEDGE AND MAIN DIRECTIONS FOR FUTURE RESEARCH

There are huge gaps in many areas of knowledge regarding the Caspian lamprey (Lucas et al., 2020) compared to other species, especially sea lamprey *Petromyzon marinus* Linnaeus, 1758 and the Pacific lamprey. These include, for example, threats and factors limiting its distribution and abundance; habitats of adults and ammocoetes, population structure, location of spawning grounds, length of migration routes, sea period of life of adults, and peculiarities of their feeding in the sea (Renaud, 2011; Nazari et al., 2017; Renaud and Cochran, 2019; Quintella et al., 2021). This species is poorly studied, especially in the northern and western parts of the Caspian Sea basin. After a rapid decline of its abundance in the basins of the Volga and Kura rivers, the studies of the current distribution and state of stocks have not been carried out. On the contrary, in the southern part of the Caspian Sea basin (in the waters of Iran), a significant number of studies have been carried out to assess the distribution and structure of populations of the Caspian lamprey, basic biological information has been obtained, the locations of spawning grounds and ammocoete habitats have been determined in recent years (Jolodar and Abdoli, 2004; Nazari, Abdoli, 2010; Nazari et al., 2010; Ahmadi et al., 2011; Coad, 2016; Nazari et al., 2017). All these measures are the first and most important steps towards the conservation of biologically, socio-economically, commercially, culturally, and historically important species, which is endemic to the Caspian Sea basin.

In the coming years, the research efforts should be focused on studying the feeding ecology, identifying the localization of modern spawning grounds (Ahmadi et al., 2011) and habitats of the Caspian lamprey during the sea period of life cycle (Holčík, 1986; Renaud, 2011; Nazari et al., 2017; Quintella et al., 2021), which may be facilitated by analyzing the environmental DNA (aquaDNA) in the water samples (Nikiforov et al., 2018). Physiology (Imanpoor, Abdollahi, 2011) and population structure (Quintella et al., 2021) of the considered species are still poorly studied. It seems relevant to compare samples from different parts of the range by molecular genetic methods using different markers; this is especially important for the Caspian lamprey from the northern and southern parts of the Caspian basin, since different results have been obtained regarding the intraspecific structure of the Caspian lamprey (Smirnov, 1952, 1953; Nazari et al., 2009; Vatandoust et al., 2015; Kucheryavyi et al., 2016). The issue of age determination remains very relevant; it is intractable for all lamprey species, since traditional methods of age determination using calcified structures (statoliths) are poorly applicable to lampreys due to the complex life cycle with metamorphosis. Isotope method of age determination currently being developed on eye lens of the Pacific lamprey seems to be very promising (Pelekai, 2021).

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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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