

Mollusks of the Aral Sea

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Abstract—Based on published data and studies carried out by the authors over more than 30 years, an analysis of the mollusk fauna of the Aral Sea is made. The species composition of mollusks that lived in the sea during the Holocene is considered and clarified. The main reason for changes in the species composition of this group is shown to have been a decrease or increase in the salinity of the environment associated with changes in the sea level. Long-term changes in the salinity of water, in our opinion, could have become the main reason for the scarcity of the mollusk fauna of the Aral Sea. We assume that the transfer of juvenile mollusks by birds might have played an important role in the replenishment of the fauna with new species. This is probably true for mollusks of the family *Cardiidae* and *Ecrobia grimmi*. Another source of replenishment of the fauna of the Aral Sea must have been due to species inhabiting the rivers flowing into the Aral Sea and the surrounding lakes. The process of faunal changes during the last regression of the sea is discussed in detail. The availability of data on the salinity at which the mollusks became extinct makes possible a retrospective evaluation of the estimates of limits of salinity tolerance for the existence of the same species obtained by different methods. The future of the fauna of the mollusks of the Aral Sea is considered in the implementation of different scenarios of sea rehabilitation.

Keywords: Aral Sea, mollusks, salinity, fauna

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INTRODUCTION

The Aral Sea is a large drainless saltwater lake in the desert zone of Central Asia on the territory of Kazakhstan and Uzbekistan; it is the terminal reservoir of the Syr Darya River in the northeast and the Amu Darya River in the south (Fig. 1). In the Aral Sea, two main parts are distinguished: the northern one is the Small Sea, or the Small Aral, and the southern one is the Large Sea, or the Large Aral, separated by Kok-Aral Island. The Large Aral Sea includes a deep-water western depression, a vast eastern part, and Tshchebas Bay (Bortnik and Chistyayeva, 1990). Due to this, when the level of the Aral Sea drops, it breaks up into residual water bodies.

Prior to the modern regression, the Aral Sea was brackish with an average salinity of 10.3‰. In the southern and southwestern parts of the Great Sea, salinity was reduced due to the freshening effect of the Amu Darya. In the Small Aral, the freshened zone is located in front of the mouth of the Syr Darya (Bortnik and Chistyayeva, 1990). Due to intensive evaporation and difficult water exchange, the salinity in shallow waters, in the bays of the eastern coast and in the water area of the Akpetki (Karabayli) archipelago, was increased and reached 50‰ or more (Dengina, 1959; Khusainova, 1960).

The Aral Sea within the limits closest to the Holocene time, formed in the Late Pleistocene (about 17600 years ago) at the boundary of the maximum of the last glaciation and the early Dryas, most likely due to the melt waters of the glacial massifs of the Tien Shan, Pamir, and smaller nearby mountain systems (Burr et al., 2019). The resulting large drainless reservoir was already at this time characterized by significant salinity, as evidenced by finds of foraminifera *Ammonia beccarii* and *Retroelphidium littorale*, as well as marine ostracods, mainly *Cyprideis torosa* in the Late Pleistocene bottom sediments.

Since the 20th century, native fauna of free-living invertebrates of the Aral Sea, i.e., fauna without taking into account the invasive species, in comparison with the fauna of the largest continental saline water body, the Caspian Sea, has been distinguished by scarcity caused by human activity. The Late Holocene Aral lacked a number of taxa of invertebrates present in the native fauna of the Caspian. There were no sponges (Porifera) or polychaetes (Polychaeta), while one sponge species and five polychaeta species were present in Caspian. Out of the higher crustaceans (Malacostraca), representatives of orders such as Mysida, Cumacea, Isopoda, and Decapoda were completely absent (Mordukhai-Boltovskoi, 1974), while in the aboriginal fauna of the Caspian, these groups include 5,

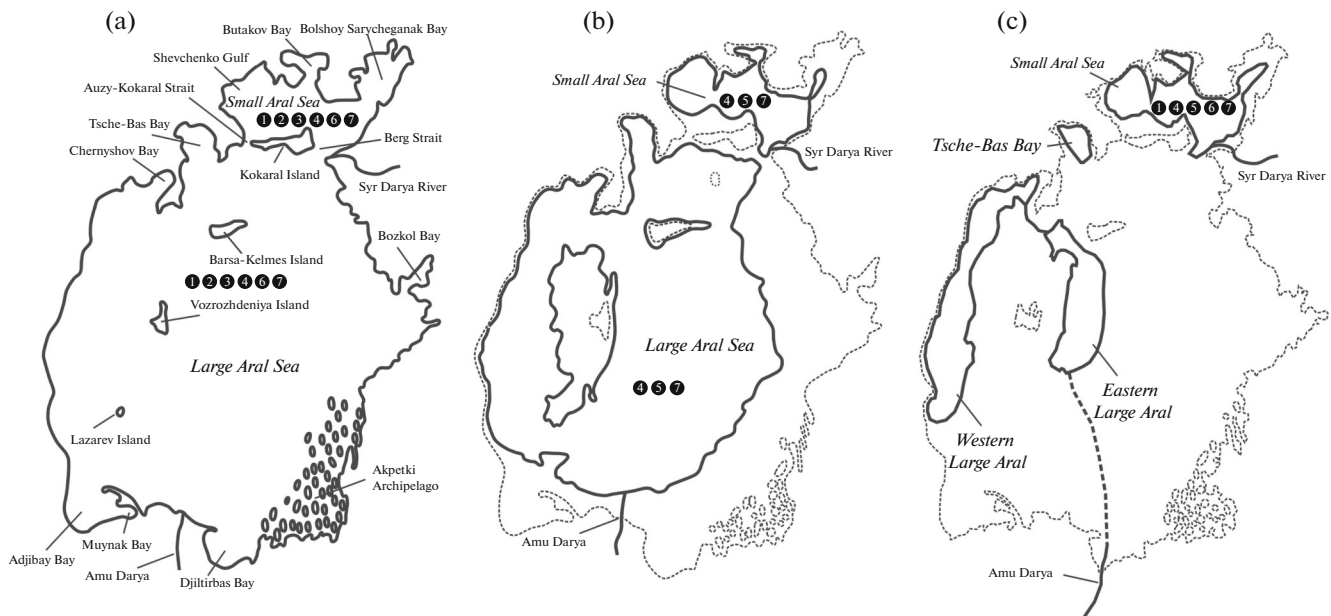


Fig. 1. Aral Sea: (a) before the beginning of the modern regression; (b) after separation; (c) currently. The composition of the mollusk fauna: 1, *Dreissena polymorpha aralensis*; 2, *D. p. obtusecarinata* and *D. caspia*; 3, *Adacna* spp.; 4, *Cerastoderma* spp.; 5, *Abra segmentum*; 6, *Theodoxus pallasi*; 7, *Ecrobia grimmi*.

22, 18, 2, and 2 species, respectively (Birshtein et al., 1968; Kijashko, 2013).

With regard to the malacofauna: out of the bivalve mollusks (Bivalvia) of the Cardiidae family, only five species common with the Caspian were revealed, while in the Caspian 24 species were detected. Among the gastropods (Gastropoda) in the Aral Sea, genera such as *Pyrgula* (38 species in the Caspian), *Caspia* (five species in the Caspian), *Andrusovia* (four species in the Caspian), *Pseudoamnicola* (four species in the Caspian), and *Tenellia* (one species in the Caspian) were completely absent (Birshtein et al., 1968; Mor-dukhai-Boltovskoi, 1974; Kijashko, 2013).

The purpose of this study was to identify the reasons for the scarcity of the mollusk fauna of the Aral Sea and to trace the changes in the fauna during its existence. This article uses both published data and data obtained by the authors during research in the Aral Sea and in a series of laboratory experiments in the period of 1980–2011.

HISTORY OF THE STUDY OF MOLLUSKS OF THE ARAL SEA

The first information on the mollusk fauna of the Aral Sea was obtained during the processing of the material collected during an expedition in 1874, which was organized by the Imperial Russian Geographical Society and the St. Petersburg Society of Naturalists. The zoologist V.D. Alenitsyn collected flora and fauna samples from various biotopes. O.A. Grimm processed this material and in 1881 published a note on

the history of the Aral Sea, based on the composition of the fauna. He summarized the information available at that time on the species composition of the invertebrate fauna of the Aral Sea and indicated seven species of mollusks of this fauna (five species were indicated based on the findings of living specimens and two species were indicated based on the findings of empty shells).

Later, new information about the flora and fauna (including mollusks) of the Aral Sea was obtained as a result of the studies of L.S. Berg. The malacological materials collected by him at the turn of the 19th–20th centuries were processed by A.A. Ostroumov (Berg, 1908). As a result, a monograph by Berg (1908) provided information on the following species and subspecies of mollusks¹: *Dreissena polymorpha* Pallas 1771 [*D. polymorpha* var. *obtusecarinata* (Andrusov 1897), *D. polymorpha* var. *aralensis* (Andrusov 1897)], *D. caspia* Eichwald 1855, *D. caspia pallasi* (Andrusov 1897) [*D. pallasi*], *Adacna minima minima* Ostroumov 1907 [*Adacna minima*], *Cerastoderma rhomboides* (Lamarck 1819) [*Cardium edule* var. *lamarcki* Reeve 1843], *Caspihydrobia eichwaldiana* (Golikov et Starobogatov 1966) [*Hydrobia pusilla* (Eichwald 1838)], and *Neritina liturata* (Eichwald 1855).

A scientific and fishing expedition to the Aral Sea was organized in 1920–1921. Collections of mollusks obtained in the Aral Sea in 1920–1921 were processed by S.A. Sidorov (1929), who indicated 37 species for

¹ The names of taxa indicated by L.S. Berg different from the valid names are shown in square brackets.

the sea. He included in the composition of the sea fauna freshwater mollusks, which were found only in the most freshened areas. Among marine and brackish mollusks, he indicated *Dreissensia caspia*, *D. caspia pallasii* [*D. pallasii*], *D. polymorpha* [*D. polymorpha* var. *aralensis*, *D. polymorpha* var. *obtuscarinata*], *D. rostriformis* (Deshayes in Verneuil et Deshayes 1838), *Adacna vitrea* (Eichwald 1829), *Adacna minima minima* Ostroumoff 1907 [*Adacna minima*], *Cerastoderma rhomboides* (Lamarck 1819) [*Cardium edule* Linnaeus 1758, *Cardium edule* var. *lamarcki*], *Theodoxus pallasii* Lindholm 1924 [*Neritina liturata* Eichwald 1838], *Turricaspia spica* (Eichwald 1855) [*Micromelania spica*], and *Caspiohydrobia eichwaldiana* (Golikov et Starobogatov 1966) [*Hydrobia pusilla*].² An important result of the study by Sidorov (1929) is the mention of fairly rich freshwater fauna in the estuarine areas of the sea, where the salinity of the Aral Sea was especially low. The freshwater species of mollusks mentioned by this author are quite common in the Syr Darya and Amu Darya rivers and the lakes surrounding the Aral Sea. However, a number of identifications of the mollusk species made by Sidorov are questionable. Thus, freshwater bivalves in the estuarine areas of the Aral Sea, identified by Sidorov as *Anodonta piscinalis* Nilsson 1822 were most likely some other species. According to Zhadin (1952), *A. piscinalis* does not occur in the Aral Sea region. Another disadvantage of the study of Sidorov is the inclusion of a number of species in the fauna of the Aral Sea based on the finds of empty shells. Thus, assignment of *Turricaspia spica* to recent species was based on the fact that, in the samples obtained by Sidorov, the shells of this species were remarkably well preserved. Meanwhile, as we know from subsequent studies and our own collections, this species did not inhabit the Aral Sea in the 20th century.

For the Aral Sea, in the book of V.I. Zhadin (1952) in the section "Ecology," the following bivalves are indicated: *Dreissena polymorpha* [*D. polymorpha* var. *aralensis*, *D. polymorpha* var. *obtuscarinata*], *D. caspia*, *D. caspia pallasii* [*D. pallasii*], *Adacna vitrea*, *Cerastoderma rhomboides* (Lamarck 1819) [*Cardium edule*] and three species of gastropods: *Ecrobia grimmi* (Clessin in Dybowski, 1887) [*Hydrobia grimmi*], *Turricaspia spica* [*Micromelania spica*], and *Theodoxus pallasii*.³ However, the indication of *Turricaspia spica*, as a species characteristic of the Aral Sea in the 20th century, is apparently erroneous, since in the part of the book relating to the identification keys, this species is indicated only for the Caspian Sea. It is interesting that Zhadin's book (1952) indicates the periodic disappearance or significant reduction in the water area inhabited by freshwater fauna in the estuarine areas, depending on changes in the salinity of the sea. Zhadin definitely

did not consider freshwater species of mollusks related to the Aral fauna.

In the 1960s the list of mollusks of the Aral Sea was replenished with a bivalve mollusk *Abra segmentum* (Récluz 1843). This species was imported and introduced into the Aral Sea from Taganrog Bay and the Berdyansk limans of the Sea of Azov three times, in 1960, 1961, and 1963. The first attempt (1960) at the introduction of *A. segmentum* into the freshened Dzhida Bay of the Small Aral Sea was unsuccessful. Most likely, the first batch perished, since no mollusks were later found in this area. In 1961 and 1963, these mollusks were also released in the Small Sea in Bolshoy Sarycheganak Bay with a salinity of 10.2‰, and this time their acclimatization and naturalization were successful. They were first recorded in samples of zoobenthos in 1967, in 1970 they penetrated into the Large Aral Sea, and by 1973 they had already settled throughout the Aral Sea (Fig. 2) (Kortunova, 1970; Karpevich, 1975; Andreeva, 1978).

The data on the mollusk fauna of the Aral Sea available by the early 1970s were summarized by Starobogatov (1974). In the *Atlas of Invertebrates of the Aral Sea*, he indicated nine species and subspecies of bivalves and three species of gastropod mollusks for the Aral Sea, "peculiar to the Aral Sea itself": *Dreissena polymorpha aralensis* (Andr.), *D. polymorpha obtuscarinata* (Andr.), *D. caspia pallasii* (Andr.), *Cerastoderma lamarcki* (Reeve), *C. unbonatum* (Wood), *Hypanis vitrea bergi* Starobogatov, *H. minima sidorovi* Starobogatov, *H. minima minima* (Ostr.), *Abra ovata* (Phil.), *Theodoxus pallasii* Lindholm, *Caspiohydrobia conica* (Logv. et Star.), and *C. husainovae* Starobogatov.

After the description by Ya.I. Starobogatov of the new genus *Caspiohydrobia* (Starobogatov, 1970), further taxonomic studies led to a subsequent significant expansion of the list of gastropod species in the fauna of the Aral Sea. At first Starobogatov (1974) indicated for the Aral Sea two species from this genus, then subsequently their number increased dramatically. According to S.I. Andreeva (1989), this genus of gastropods is represented in the Aral Sea by 23 species: *Caspiohydrobia chrysopsis* (Kolesnikov 1947), *C. conica* (Logvinenko et Starobogatov 1968), *C. convexa* (Logvinenko et Starobogatov in Golikov et Starobogatov, 1966), *C. curta* (Logvinenko et Starobogatov 1968), *C. cylindrica* (Logvinenko et Starobogatov 1968), *C. dubia* (Logvinenko et Starobogatov 1968), *C. gemmata* (Kolesnikov 1947), *C. grimmi* (Clessin et W. Dybowski in W. Dybowski, 1888), *C. oviformis* (Logvinenko et Starobogatov 1968), *C. parva* (Logvinenko et Starobogatov 1968), *C. subconvexa* (Logvinenko et Starobogatov 1968), *C. aralensis* Starobogatov and Andreeva 1981, *C. behningi* Starobogatov and Andreeva 1981, *C. bergi* Starobogatov and Andreeva 1981, *C. husainovae* Starobogatov 1974, *C. kazakhstanica* Starobogatov and Andreeva 1981, *C. nikitinsky* Starobogatov and Andreeva 1981,

² The names of taxa indicated by S.A. Sidorov different from the valid names are shown in square brackets.

³ The names of taxa indicated by V.I. Zhadin different from the valid names are shown in square brackets.

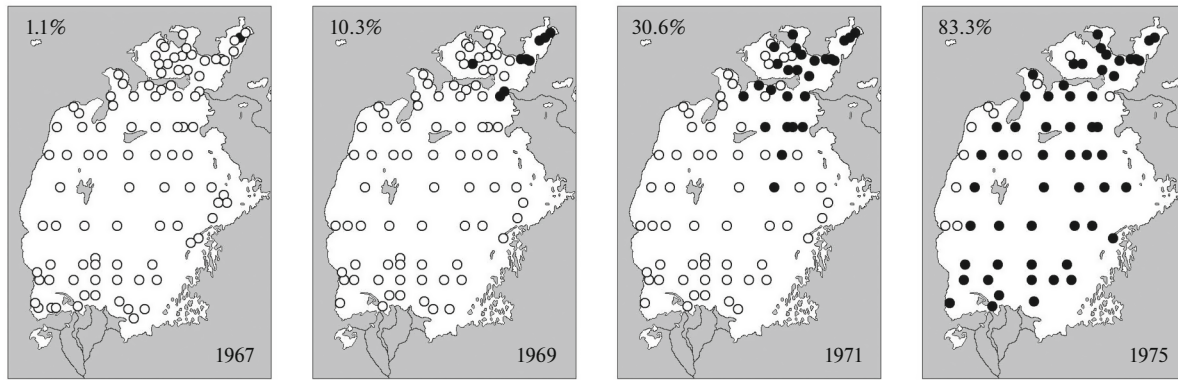


Fig. 2. Distribution of *Abra segmentum*. ● Standard grid stations where the mollusk was found; ○ stations where the object was not found. The frequency is indicated, %.

C. nikolskii Starobogatov and Andreeva 1981, *C. obrutchevi* Starobogatov and Andreeva 1981, *C. pavlovskii* Starobogatov and Izzatullaev 1974, *C. sidorovi* Starobogatov and Andreeva 1981, *C. sogdiana* Starobogatov and Izzatullaev 1974, and *C. tajikistanica* Starobogatov et Izzatullaev 1974.

It should be noted that now many authors consider the genus *Caspiohydrobia* invalid and consider the existence of one extremely morphologically variable species *Ecrobia grimmeri* (Clessin in Dybowski 1887) to be real (Filippov and Riedel, 2009; Haase et al., 2010; Wesselingh et al., 2019).

Since the end of the 1970s, due to the progressive salinization of the sea, some species have become extinct.

SPECIES COMPOSITION OF MOLLUSKS IN THE ARAL SEA

Class Bivalvia

Order Veneroida

Family Cardiidae Lamarck 1809

Genus Cerastoderma Poli 1795

Fossil known from the Oligocene (Keen, 1969). The divergence of this genus is usually associated with the isolation of the Mediterranean Sea from the Atlantic Ocean at the end of the Miocene (Hummel et al., 1994). In the Soviet Union, the opinion that the systematics of the genus includes five species was dominant: *Cerastoderma glaucum* Poiret 1789, *C. rhomboides* Lamarck 1819, *C. lamarcki* (Reeve 1845), *C. umbonatum* Wood 1850, and *C. clodiense* Brocchi 1814 (Skarlato and Starobogatov, 1972). Subsequently Kafanov (1980) proposed a refined system of four species: *C. glaucum*, *C. rhomboides*, *C. clodiense*, and *C. isthmicum* Issel 1869 (= *C. umbonatum*). Now, the genus includes three valid species: *C. glaucum*, *C. edule*, and *C. rhomboides* ([http://mussel-project.uwsp.edu/fmu-](http://mussel-project.uwsp.edu/fmu-otwaolcb/validgen_1647.html)

[otwaolcb/validgen_1647.html](http://mussel-project.uwsp.edu/fmu-otwaolcb/validgen_1647.html)), and probably another undescribed species (Wesselingh et al., 2019).

At the beginning of the Holocene, mollusks of the genus *Cerastoderma* were neither in the Caspian nor in the Aral Sea. The earliest shell deposits of *Cerastoderma* in the Caspian are dated to the middle of the Holocene, i.e., around 6000 BC, with colonization believed to have been associated with the Khvalyn transgression, which may have coincided with the Black Sea transgression and with the earliest post-glacial dates of *C. glaucum* from this basin 9000–8500 BC (Mamedov, 1997).

Species of the genus *Cerastoderma* appeared in the Aral Sea about 5000 years ago, after they entered the Caspian Sea from the Black Sea. If they could have penetrated into the Black Sea naturally, they could enter the Caspian and, even more so, the Aral Sea only through invasion. Currently, there are two points of view on how the invasion occurred. According to the first of them, the settling of *Cerastoderma* occurred with the participation of man (Fedorov, 1978; Yanina, 2009). Numerous authors of the study: “Mollusk species from the Pontocaspian region: an expert opinion list” have recently agreed with this point of view (Wesselingh et al., 2019). Another point of view attributes a major role in the invasion of *Cerastoderma* spp. to birds. The fact that birds are involved in the distribution of this species has been shown by many authors (Boyden and Russell, 1972; Rose, 1972; Spenser and Patchett, 1997). Adult mollusks can attach to the legs of birds, spat can be carried by birds in their plumage, and spat and juveniles can be carried by birds along with plants.

Even if we agree that, in the salt lakes along the Manych depression, *Cerastoderma* was spread on the boats of ancient man, which were moved along the rivers from the sea to the lake (Yanina, 2009; Yanina et al., 2011), it still remains unclear how mollusks could have moved from the Caspian to the Aral Sea, since the flow of the Amu Darya that existed at that time according to Uzboy was not saline enough for

their survival. Most likely, in this case, the distribution of *Cerastoderma* occurred with the participation of birds. It is known that numerous endorheic lakes were in the Caspian deserts during times with a humid climate (Mamedov and Trofimov, 1986). These lakes were oligohaline, polyhaline, and hyperhaline. For *C. glaucum* it was shown that the median lethal survival time of juveniles out of the water ranges from 80 to 43 hours depending on the ambient temperature (Tarnowska et al., 2012). This time is sufficient for their distribution along the chain of polyhaline lakes up to the Aral Sea.

The mode of life of bivalve mollusks of the genus *Cerastoderma* is benthic; they are endobionts, burrowing into the surface layer of the ground. According to the feeding type, they are filter feeders, mobile santonophages. Disturbing the surface layer of the ground with a current of water from the exhalant siphon, they draw in light particles used for food by an inhalant siphon (Nevesskaya, 1965). Reproduction takes place during the warm season. Development occurs through the planktonic larval stage.

Due to the salinization of the Aral Sea, which led to the extinction of the *Dreissena*, the emergence of *Cerastoderma* in the ground became possible. As a result of natural selection, mollusks *C. glaucum* in the late 1980s were represented in the Aral Sea by three life forms: (1) typical, living in sandy ground; (2) with a flattened shell that lives in liquid silty ground (by 1989 it had become extinct due to a sharp change in the nature of the ground); (3) living on the surface of sandy–silty or silty–shell ground and filtering, like *Dreissena*, from the water column (Andreeva, 2000; Andreeva and Andreev, 2003).

***Cerastoderma* sp. A [non *C. rhomboides*
(Lamarck 1819)] (Fig. 3a)**

Initially, these mollusks from the Aral Sea were considered *Cardium edule* var. *lamarcki* Reeve 1843 (Berg, 1908). Subsequently, they (Starobogatov, 1974) were assigned to the species *C. lamarcki* (Reeve 1845) as a subspecies *C. l. lamarcki* (Reeve 1845), but then they were reidentified (Andreeva, 1989, 2000) as *C. rhomboides rhomboides* (Lamarck 1819). According to Wesselingh et al. (2019), neither *C. lamarcki* nor *C. rhomboides* were present in the Aral Sea.

The length of the shell is usually up to 30 mm (Starobogatov, 1974).

Prior to the salinization of the Aral Sea, this species inhabited its entire water area, except for highly saline areas. Currently, it does not occur in the Aral Sea, since it had become extinct by 1976 due to salinization (Andreeva, 1989, 2000).

***Cerastoderma glaucum* Bruguière 1789 (Fig. 3b)**

Synonyms: *Cardium rusticum* Eichwald 1829; *Cardium rusticum* Eichwald 1829, non Linnaeus 1758; *Cardium edule* var. *umbonatum* Wood 1850; *Cardium glaucum* Poiret 1789; *Cerastoderma umbonatum* Wood 1850; *Cerastoderma isthmicum* Issel 1869.

The length of the shell is usually up to 30 mm (Starobogatov, 1974).

Distribution. Mediterranean–Atlantic marine species; also inhabits in the Caspian and Aral Seas (Starobogatov, 1970). In the Aral Sea, it was initially found only in its salinized areas (kultuks of the eastern coast), but with the increase in salinity of the main water area, it is distributed throughout the sea (Andreeva, 1989, 2000).

During the salinization of the Large Aral Sea, the species became extinct in the second half of the 1990s at salinity exceeding 60‰, but not yet approaching the upper limit of the salinity tolerance range of adult specimens. At this salinity, the reproduction of these mollusks was no longer possible, as evidenced by the absence of their larvae in plankton (Stuge, 2002), and the remaining bivalves gradually died out. In the Small Aral Sea, this species remained among the main representatives of the benthic fauna (Filippov, 1994; Grishaeva, 2010). A significant decrease in the salinity of the Small Aral Sea, apparently, has now become unfavorable, which has now led to a significant decrease in its abundance (Toman et al., 2015; Plotnikov et al., 2016). With further freshening of the sea, it may become extinct.

Genus *Adacna* Eichwald 1838

An endobiont that burrows into the surface layer of the ground and exposes long fused siphons. According to the feeding type, they are filter feeders, mobile santonophages. It consumes unicellular algae and relatively large diatoms. Reproduction occurs during the warm season. There is a planktonic larval stage.

At present, no *Adacna* species are found in the Aral Sea. Due to salinization, they became extinct by the end of the 1970s (Andreeva, 1989).

***Adacna minima minima* Ostroumov 1907 (Fig. 3c)**

Synonym: *Hypanis minima minima* Ostroumov 1907.

The length of the shell is up to 20 mm (Starobogatov, 1974).

An endemic Aral subspecies of the species *Adacna minima* Ostroumov 1907 is also present in the Caspian. It was distributed throughout the Aral Sea (Starobogatov, 1974).

***Adacna minima sidorovi* (Starobogatov 1974)**

Synonym: *Hypanis minima sidorovi* Starobogatov 1974.

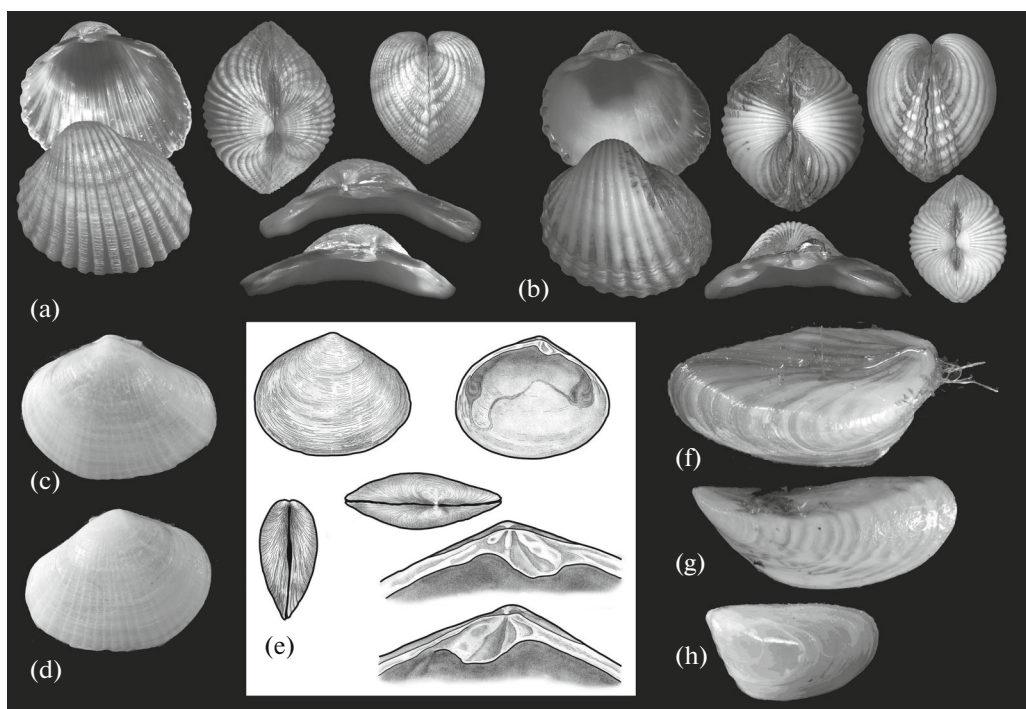


Fig. 3. Bivalves: (a) *Cerastoderma* sp. A; (b) *Cerastoderma glaucum* (photo by P.V. Kijashko); (c) *Adacna minima minima*; (d) *Adacna (Adacna) vitrea bergi* (photo by P.V. Kijashko and A.O. Smurov); (e) *Abra segmentum* (drawing by P.V. Kijashko); (f) *Dreissena polymorpha aralensis* (photo by P.V. Kijashko); (g) *Dreissena polymorpha obtusecarinata*; (h) *Dreissena caspia pallasii* (photo by P.V. Kijashko and A.O. Smurov).

The length of the shell is up to 20 mm (Starobogatov, 1974).

An endemic Aral subspecies of the species *Adacna minima* is also present in the Caspian. It inhabits the coastal area to a depth of 10 m (Starobogatov, 1974). Recently, doubts about the reality of the existence of this subspecies have been expressed (Wesselingh et al., 2019).

Adacna (Adacna) vitrea bergi
(Starobogatov 1974) (Fig. 3d)

Synonym: *Hypanis vitrea bergi* Starobogatov 1974.

The length of the shell is up to 20 mm (Starobogatov, 1974).

An endemic Aral subspecies of the species *Adacna vitrea* (Eichwald 1829) is also present in the Caspian. It is known based on single records (Starobogatov, 1974). At present, there are doubts (Wesselingh et al., 2019) about the validity of the identification of the Aral *A. vitrea* into a separate subspecies.

Family Semelidae Stoliczka 1870

Genus *Abra* Lamarck 1818

***Abra segmentum* Récluz 1843 (Fig. 3e)**

Synonyms: *Erycina ovata* Philippi 1836 non Gray 1825; *Amphidesma lactea* Krynicky 1837; *Syndesmya apelina* Récluz 1843; *Abra segmentina* H. et A. Adams 1856; *Scrobicularia fabula* Brusina 1865; *Syndesmya*

segmentum var. *brevis* Fischer 1867; *Syndesmya segmentum* var. *incrassata* Fischer 1867; *Syndesmya segmentum* var. *subrostrata* Fischer 1867; *Syndesmya cailaudii* Fischer 1867.

The length of the shell is up to 25 mm (Starobogatov, 1974).

Distribution. Atlantic coast of Europe (north to England), Mediterranean and Black seas, Sea of Azov, acclimatized in the Caspian Sea (Kijashko, 2013). It was introduced into the Aral Sea in 1960–1963. Lifestyle is benthic. Representative of the infauna; burrows into the ground, exposing long siphons. According to the feeding type, it is a detritophage (Karpevich, 1962; Neveeskaya, 1965). Mollusks capture detritus particles from the bottom with an inhalant siphon. Reproduction occurs in the warm season. Development occurs with the pelagic larval stage.

Order Myida

Family Dreissenidae J.E. Gray 1840

Genus *Dreissena* Van Beneden 1835

Dreissena polymorpha aralensis
(Andrusov 1897) (Fig. 3f)

Distribution. Aral Sea basin, endemic Aral subspecies *Dreissena polymorpha* (Pallas 1771). The length of the shell is up to 25 mm. The mollusk inhabits the lower reaches of the Syr Darya and Amu Darya rivers

and the lakes associated with them; in the sea, it was found only in freshened water areas near river mouths (Starobogatov, 1974; Andreeva, 1989).

Due to salinization, it became extinct in the 1970s (Andreeva, 1989), but was preserved in rivers and lakes associated with them (Grishaeva, 2010).

Now, due to a significant decrease in the salinity of the Small Aral Sea, there exist the necessary conditions for the return of this mollusk from the Syr Darya River in the freshened zone near its delta. Therefore, this mollusk is now returning (Fig. 1c) from the Syr Darya River into the freshened zone near its delta (Toman et al., 2015; Plotnikov et al., 2016).

Dreissena polymorpha obtusecarinata
(Andrusov 1897) (Fig. 3g)

Distribution. This endemic Aral subspecies *Dreissena polymorpha* inhabited the open sea in its coastal zone in the thickets. The length of the shell is up to 17 mm (Starobogatov, 1974).

Due to increased salinity, this subspecies became extinct in the Aral Sea in the 1970s. (Andreeva, 1989). Apparently, it should be considered extinct.

Dreissena caspia pallasii Andrusov 1897 (Fig. 3h)

Two subspecies of *Dreissena caspia* are known: the Caspian subspecies *D. caspia caspia* Eichwald 1855 and the Aral subspecies *D. caspia pallasii* Andrusov 1897.

The length of the shell is up to 8–10 mm. Distribution. The Aral subspecies of *Dreissena caspia* Eichwald 1855 is endemic to the Caspian and Aral seas. It was distributed on soft grounds throughout the Aral Sea (Starobogatov, 1974).

In the Aral Sea, this species ceased to exist by the end of the 1980s (Andreeva, 1989). Most likely, it should be considered extinct due to salinization. It should be noted that in the Caspian Sea *D. caspia* was displaced by *Mytilaster lineatus* (Gmelin 1791) and is considered extinct (Kijashko, 2013).

Class *Gastropoda*

Subclass *Caenogastropoda*

Order *Littorinimorpha*

Family *Hydrobiidae* Stimpson 1865

Ecrobia grimmi (Clessin in Dybowski 1887) (Fig. 4a)

Synonyms: *Hydrobia grimmi* Clessin in W. Dybowski 1888; *Caspiohydrobia grimmi* (Clessin et W. Dybowski in W. Dybowski 1888).

The height of the shell is up to 4 mm (Starobogatov, 1974).

In the past, Aral *Hydrobia* were attributed to various species of the genus *Hydrobia* W. Hartmann 1821

(Berg, 1908; Dengina, 1959): *H. stagnalis* Baster, *H. pusilla* Eichwald, *H. ventrosa* (Montagu). After the study of Starobogatov and Logvinenko (1966), the Aral and Caspian species of mollusks, previously assigned to the genus *Hydrobia*, were considered to be members of the genus *Caspiohydrobia*. Now, a number of researchers believe that all Caspian species of this genus are morphotypes of the same species (Filippov and Riedel, 2009; <http://www.marinespecies.org/aphia.php?p=taxdetails&id=575789>; Neubauer et al., 2018), *Ecrobia grimmi*. However, adherents of the former point of view remain: there is a genus *Caspiohydrobia* represented by numerous species (Andreeva et al., 2020). Recently, after the appearance of molecular genetic methods, it became clear that this species can be reliably identified only using these methods (Haase et al., 2010). However, molecular genetic studies of the Caspian and Aral Hydrobiidae have not been carried out thus far. Nevertheless, after the publication of data by Filippov and Riedel (Filippov and Riedel, 2009), we believe that it is *E. grimmi*.

Ponto-Caspian *Ecrobia grimmi* is widespread throughout Central Asia and occurs in brackish waters from the mountains of the Central Urals in the north to the Persian Gulf in the south and Issyk-Kul Lake in the east (Vandendorpe et al., 2019). Lifestyle is benthic. Herbivorous species.

Turricaspia spica (Eichwald 1855) (Fig. 4b)

Synonyms: *Micromelania spica* (Eichwald 1855); *Hydrobia pusilla* (Eichwald 1838); *Paludina pusilla* Eichwald 1838.

In the *Atlas of Invertebrates of the Aral Sea* (1974), in the section devoted to mollusks, Starobogatov (1974) stated that the empty shells of this species found in the lake were washed out from Quaternary or Upper Pliocene sediments. However, there is another point of view on when *Turricaspia spica* inhabited the Aral Sea. Thus, according to Filippov and Riedel (Filippov and Riedel, 2009), it probably died out in the Aral Sea around 1300–1350 AD. During this period, according to the data on the carbon and oxygen isotopes in the corresponding sections of the core, significant freshening of the central water area of the Aral Sea occurred.

Turricaspia spica was found at a depth of 0–30 m in the western and northern parts of the Central Caspian (Logvinenko and Starobogatov, 1968), which indicates that it was associated with brackish water. It is now endemic to the Caspian Sea.

Subclass *Neritimorpha*

Order *Cycloneretida*

Family *Neritidae* Rafinesque 1815

Theodoxus pallasii Lindholm 1924 (Fig. 4c)

Neritina pallasii Lindholm, 1924c: 34 (nom. n. pro *Neritina liturata* Eichwald 1838 non Schultze 1826).

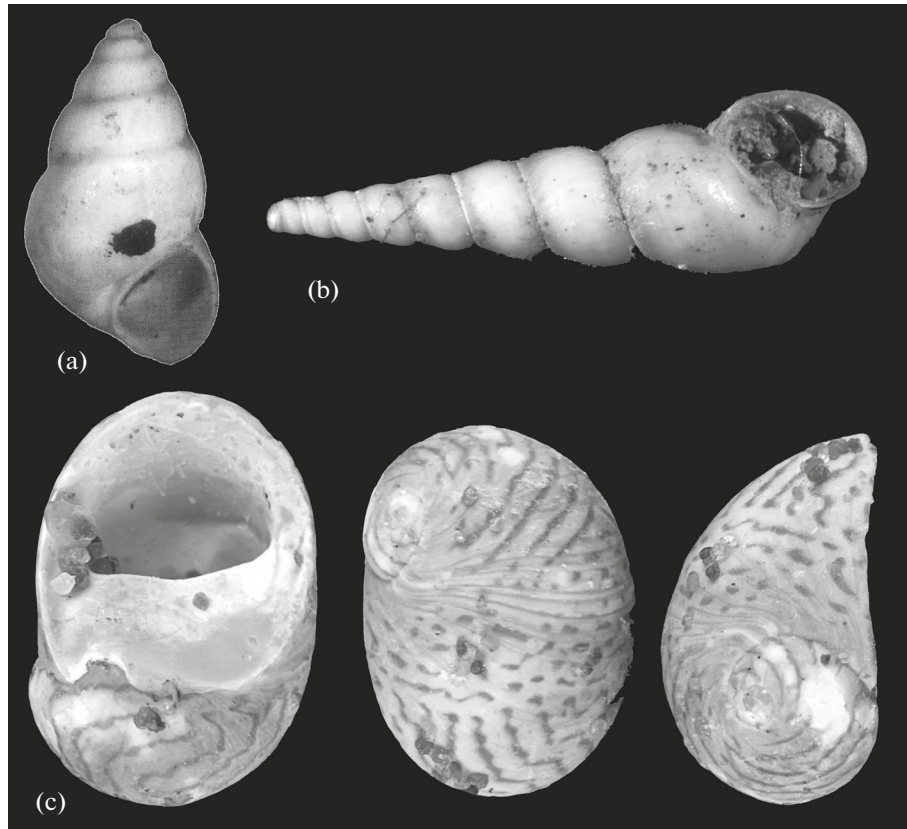


Fig. 4. Gastropods: (a) *Ecrobia grimmi*; (b) *Turricaspia spica*; (c) *Theodoxus pallasi* (photo by P.V. Kijashko).

Synonyms *Nerita pupa* Pallas 1771, non Linnaeus 1758; *Neritina liturata* Eichwald 1838, non Schultze 1826; *Neritina schirazensis* var. *major* Issel 1865; *Theodoxus pallasi* var. *aralensis* Sidorov 1929; *Theodoxus astrachanicus* Starobogatov 1994.

The height of the shell is up to 8.5 mm, the width of the shell is up to 7.5 mm (Starobogatov, 1974).

Distribution. Caspian, Black, and Aral seas, Sea of Azov, penetrates into rivers. In the Aral Sea, it was a common species in the coastal zone down to depths of 5–10 m (Starobogatov, 1974). Lifestyle is benthic. Herbivorous species. The mollusks are dioecious; after fertilization, the females deposit eggs in the form of small capsules, and the egg deposition is attached to the substrate.

Due to salinity, *Theodoxus pallasi* disappeared from the Aral Sea in the 1980s (Fig. 1b, 5). Since the mollusk inhabits the lower reaches of the Syr Darya River and related lakes (Grishaeva, 2010), with a decrease in the salinity of the Small Aral Sea, its return back to the Small Aral Sea became possible (Fig. 1c). It entered the freshened zone of this residual reservoir no later than 2001, where it is now found in small numbers (Aladin and Plotnikov, 2008; Krupa et al., 2019; Krupa and Grishaeva, 2019).

EXPERIMENTAL INVESTIGATIONS OF THE LIMITS OF THE SALINITY TOLERANCE OF THE EXISTENCE OF MOLLUSKS IN THE ARAL SEA

Researchers of salinity adaptations of hydrobionts of the Aral Sea were primarily interested in the range of changes in this indicator of sea water, in which the existence of certain species is possible. Such a range, which is limited by “the phenotypic adaptation, outlining the genotypically determined reaction rate,” according to V.V. Khlebovich (1981), was proposed to be called the potential tolerant range (Filippov, 1995).

The assessment of potential salinity tolerance in different species of aquatic organisms and its comparison is difficult since now there are no generally accepted methods for determining this indicator. Over the past 30 years, a large number of articles have been published on the determination of the salinity potential tolerance of multicellular organisms. According to A.A. Filippov (1998), who conducted a critical analysis of the methodology of these studies, several main methods can be distinguished: direct transfer, physiological adaptation, stepwise acclimation, and an express method based on studying the salt tolerance of isolated tissues. We can point out another method that is widely used by foreign researchers in the study of

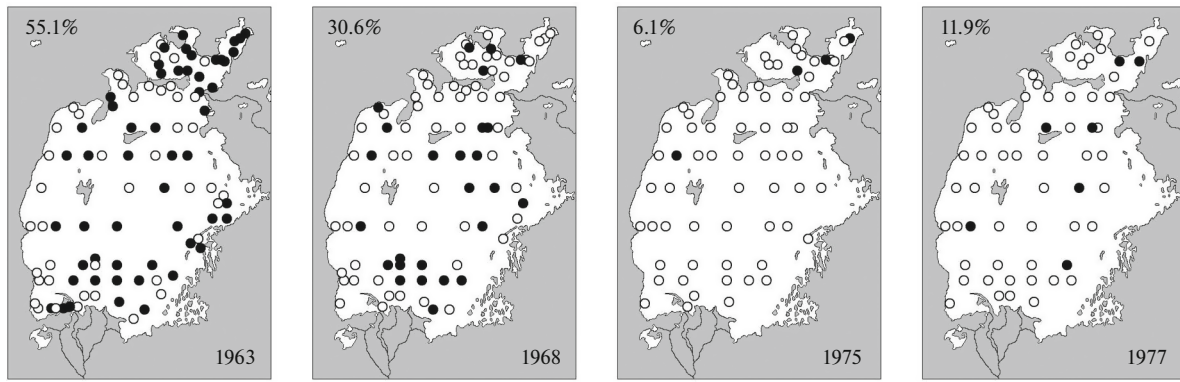


Fig. 5. Distribution of *Theodoxus pallasi*. (Symbols as in Fig. 2.)

temperature adaptations, i.e., the construction of a tolerance polygon, which is a graph of the dependence of tolerance limits on the salinity of the habitat. This method was not used for investigation of the limits of salinity tolerance for the existence of Aral mollusks.

A feature of all methods, except for the last one, is that the researcher is ultimately interested in only two values: the values of the upper and lower potential limits, upon reaching which the organisms of the population studied die. Changes in the limits of salinity tolerance during the experiment are not taken into account.

The direct transfer method consists of a sharp change in salinity in experimental aquariums with experimental organisms. The state of animals under different salinity conditions is assessed by the percentage of mortality, functional activity, and other indicators. The methods of processing the data obtained in this way and the final result do not differ from the data obtained using similar methods for assessing tolerance. Accordingly, this method is poorly suited for assessing potential tolerance, but it has advantages. Under field conditions, it allows a quick understand of whether the species studied can exist under conditions with a certain indicator of the water salinity.

It was shown by the direct transfer method that *Dreissena polymorpha aralensis* and *D. polymorpha obtusecarinata* can survive up to 14–15‰, while *D. caspia*, *Adacna* spp., and *Theodoxus pallasi* can survive at a salinity of more than 20‰ (Table 1). A salinity tolerance of not higher than 45‰ was determined for *Cerastoderma glaucum*, *Abra segmentum*, and *Ecrobia grimmeri* using this method (Andreev, 1999).

Another advantage of the direct transfer method is that it is the only one suitable for estimating the limits of salinity tolerance at which reproductive products are shed and metamorphoses occur. According to our observations, even a slight change in the salinity (about 5–7‰ within the tolerance range) of water containing adults of the White Sea mollusks can significantly shift the timing of spawning and affect the

viability of gametes. An assessment of the limits of salinity tolerance at which spawning is possible was made for *Dreissena polymorpha aralensis* and *Adacna* spp. The salinity values at which spawning was possible turned out to be significantly lower than the salinity at which adults survived. Subsequently, in the process of salinization of the Aral Sea, the data of the experiments were confirmed by nature: *Dreissena* and *Adacna* stopped reproduction before they disappeared from the sea.

The physiological adaptation method is based on the observation that many physiological processes in the body are stabilized by small changes in the salinity within two days. It was proposed to change the salinity by 2‰ every two days (Karpevich, 1947). The results obtained using this method showed that the range of salinity is much wider than that obtained by the direct transfer method (Karpevich, 1953, 1958; Bekmurzaev, 1970, 1971). This method was used to obtain the potential limits of salinity tolerance for both bivalves and gastropods. *Dreissena polymorpha aralensis*, *D. caspia*, *Cerastoderma glaucum*, *Abra segmentum*, *Adacna* spp., *Ecrobia grimmeri*, and *Theodoxus pallasi* were investigated (Table 1). At the same time, the physiological adaptation method provided much more accurate results in assessing the salinity at which the above species should have disappeared from the Aral Sea. Thus, we can state that the results of experiments were accurate for *Dreissena* spp. and *Adacna* spp. At the same time, the estimates of the limits of salinity tolerance for *Abra segmentum*, *T. pallasi*, and *E. grimmeri* were quite different from the real values.

A significant disadvantage of this method is the assertion that two days are required to complete acclimation. Later studies have repeatedly shown that the required period is usually longer (Khlebovich and Kondratenkov, 1971; Khlebovich, 1981; Filippov, 1995; etc.).

The most modern method for assessing the potential tolerance was developed in the early 1970s. This is **stepwise acclimation** (Khlebovich and Kondratenkov,

1971, 1973). Over the course of stepwise acclimation, the duration of acclimation to each subsequent salinity is at least two weeks, and when determining the salinity step at each stage, the value of the tolerant range at the previous stage of the experiment is taken into account. Studies of subsequent years have confirmed that this method is most suitable for studying the potential salinity tolerance of organisms (Filippov, 1995). The method is based on the data obtained using significant experimental material on various Metazoa and Protista taxa. This method provides reliable estimates of the potential tolerance of organisms and is currently one of the best tools for assessing the consequences of introducing organisms to new conditions. Its main disadvantage is the considerable time (sometimes up to 2–3 months) required to complete laboratory experiments.

The lethal limits of salinity tolerance for three species were estimated using the stepwise acclimation method: *Ecrobia grimmeri*, *Abra segmentum*, and *Cerastoderma glaucum*.

The upper limit of salinity tolerance of 100–110 g/L obtained by Filippov for *E. grimmeri* is controversial (Table 1). We conducted studies of the salinity tolerance of the White Sea *E. ventrosa* (unpublished data), a species close to *E. grimmeri*. According to a recently published study, these species diverged about 2.7 million years ago (Vandendorpe et al., 2019). According to our data, the potential tolerance range of *E. ventrosa* was 2–62‰, but when the salinity was above 62‰, the mollusks closed the operculum and in this state were able to survive up to three weeks. A tolerance range similar to *E. ventrosa* was also indicated by the much lower salinity of extinction of this species in the Greater Aral Sea (Table 1). Another interesting fact is the ability *E. ventrosa* to exist in greatly freshened water (2‰). Representatives of this species, in the course of competition with *Peringia ulvae*, were pushed back to more freshened habitats under the conditions of the White Sea (Berger and Gorbushin, 2001). If the salinity reactions of *E. grimmeri* and *E. ventrosa* are similar, it can be assumed that, with further freshening of the Small Aral Sea, this species will not disappear, since some salty places will remain along the edges of the sea due to water evaporation.

Estimation of the potential limits of salinity tolerance for *Abra segmentum* at 80–85‰ (Filippov, 1994) almost coincided with the salinity at which this species disappeared from the fauna of the Large Aral Sea.

Stepwise acclimation of *Cerastoderma glaucum* was conducted by both Andreev and Andreeva (1990) and Filippov (1995a). In the first case, it was shown that mollusks can survive at not less than 52.5‰ (survival at higher salinities was not tested). In the second case, the mollusks began to die in experiments at 80–90‰. In fact, this species disappeared from the Large Aral Sea at a salinity slightly exceeding 60‰. The discrepancy between the results of experiments and the sur-

vival of *C. glaucum* in the Aral Sea may be due to the fact that the mollusk has lost the ability to reproduce at a lower salinity of the environment, similarly to how it was shown for *Dreissena* spp. and *Adacna* spp.

The method for assessing the potential tolerance was based on **studies of salt tolerance of isolated tissues** applicable only to multicellular animals with the tissue level of organization. The researchers studied the salinity resistance of gill preparations according to the method developed by L.M. Yaroslavtseva (1976).

Estimation of lethal limits of salinity tolerance using gill preparations was performed for *Dreissena polymorpha aralensis*, *D. caspia*, *Cerastoderma glaucum*, and *Abra segmentum* (Table 1). In all cases, the limits obtained by this method were lower than those obtained by the physiological adaptation and stepwise acclimation methods. As can be seen from Table 1, the limits of salinity tolerance obtained using the isolated epithelium depend on the salinity at which the organisms lived. Subsequently, experiments on the White Sea mollusks and *A. segmentum* from the Aral Sea demonstrated that the limits of cellular resistance in all cases were linearly related to acclimation conditions (Filippov and Filippova, 2006). In addition, the nature of this dependence differed significantly from that found for intact organisms. Obviously, the indicators of cellular activity, at least in the form in which they were determined in the course of the experiments discussed here, cannot be used to assess correctly the possibilities of adaptation at the organism level (Filippov and Filippova, 2006).

Nine species of bivalve mollusks belonging to four families and two orders (Baymurodov, 2015) and 19 gastropods of three families (Andreeva et al., 2016) inhabit the Syr Darya River; however, these species were practically not found in the Aral Sea even at low salinity of the water. The reason for this is, on the one hand, the history of regressions and transgressions of the Aral Sea itself, and, on the other hand, the rhopic factor (i.e. ionic balance) of the action of salts. The concept of rhopic factor now mentioned in hydrobiology textbooks is the result of the efforts of the Romanian researcher E. Pora, who noticed that certain ratios of ions in brackish water could dramatically impoverish the fauna (Pora, 1969). In particular, he showed that the Black Sea, at the same salinities as the Baltic Sea, is poorer in terms of species composition due to the abnormality of certain ratios of ions.

All salts dissolved in the water of the modern Aral Sea are of river origin. They appeared as a result of the evaporation of river water, as evidenced by the chemical composition of salt deposits. This composition is significantly different from the chemical composition of the waters of the ocean and the Caspian. Previously, using the example of barnacles and branchiopods, it was shown that the critical salinity barrier (5–8‰) in continental waters is shifted to a higher side than that for the ocean (Aladin, 1983, 1988, 1989). Recently, a

Table 1. Salinity tolerance of mollusks of the Aral Sea

Species	Method	Author	Testing	Optimal salinity range, g/L	Lethal salinity limits, g/L	Salinity at which the species disappeared, g/L	Year of disappearance in the Aral Sea (Large Aral)
<i>Dreissena polymorpha aralensis</i>	Physiological adaptation	Karpevich, 1947	Adults	0–14		?	1978 (Andreeva and Andreev, 1989)
	Direct transfer from 4 g/L	Andreev and Andreeva, 1990	Gills	3.6–5.8	3.1–10.6		
	Direct transfer from 4 g/L	Andreev and Andreeva, 1990	Adults		0–9.3		
	Direct transfer from 11 g/L	Karpevich, 1953	Adults		12.5–15	~15.5 (Andreev, 1999)	1980 (Andreeva and Andreev, 1989)
	Direct transfer from 11 g/L	Khusainova, 1958	Adults		12.5–15		
	Direct transfer from 11 g/L	Khusainova, 1958	Spawning		5–12.3	13–16	
<i>Dreissena caspia</i>	Direct transfer from 11 g/L	Karpevich, 1947	Adults			17–20	1983–1989 (Andreeva and Andreev, 1989)
	Physiological adaptation	Karpevich, 1947	Adults		0–27		
	Direct transfer from 11 g/L	Karpevich, 1953a	Adults		5–20		
	Direct transfer from 11 g/L	Andreev and Andreeva, 1990	Gills		7.1–16.6		
	Direct transfer from 11 g/L	Karpevich, 1947; Karpevich, 1953a	Adults		2–20	22 (Aladin, 1991)	<i>A. vitrea bergi</i> (1980)
	Physiological adaptation	Karpevich, 1947	Adults		2–22		<i>A. minima minima</i> (1978)
<i>Cerastoderma glaucum</i>	Physiological adaptation	Khusainova, 1958	Adults		2.5–21.9		<i>A. sidorovi</i> (1978)
	Direct transfer from 11 g/L	Khusainova, 1958	Spawning, fertilization, metamorphosis		4.8–14		(Andreeva and Andreev, 1989)
	Direct transfer from 11 g/L	Karpevich, 1947	Adults		6–27	67	Late 1990s (Large Aral Sea)
	Physiological adaptation	Karpevich, 1947	Adults		5–40		(Aladin and Plotnikov, 2008)
	Direct transfer from 11 g/L	Khusainova, 1958	Spawning		8.1–27.3		

Table 1. (Contd.)

Species	Method	Author	Testing	Optimal salinity range, g/L	Lethal salinity limits, g/L	Salinity at which the species disappeared, g/L	Year of disappearance in the Aral Sea (Large Aral)
<i>Abra segmentum</i>	Direct transfer from 11 g/L	Khusainova, 1958	Metamorphosis		?–32.2		
	Direct transfer 11 g/L	Khusainova, 1958	Fertilization		?–44		
	Direct transfer from 20 g/L	Andreev and Andreeva, 1990			7–38		
	Direct transfer from 20 g/L	Andreev and Andreeva, 1990			7–39		
	Direct transfer from 35 g/L	Filippov, 1995			?–90		
	Stepwise acclimation	Filippov, 1995	Adults		?–80–90		
	Physiological adaptation	Bekmurzaev, 1971	Gills	7–32	8–30	>85 (Zavialov et al., 2004; Zavialov et al., 2012)	2003 Western Basin of the Large Aral Sea
	Direct transfer from 17 g/L	Andreev and Andreeva, 1990	Spawning	7–40	5–42		
	Direct transfer from 17 g/L	Andreev and Andreeva, 1990	Adults		5–35		
	Direct transfer from 17 g/L	Andreev and Andreeva, 1990	Adults		5–43		
<i>Ecrobia grimmeri</i>	Stepwise acclimation	Andreev and Andreeva, 1990	Adults		?–52.5>		
	Stepwise acclimation	Filippov, 1995	Adults		?–80–85		
	Direct transfer from 35 g/L	Filippov, 1994	Gills		20<–90>		
	Physiological adaptation	Karpevich, 1953a	Adults	8–30	?–30	>60 (Aladin and Plotnikov, 2008)	Late 1990s
	Physiological adaptation	Bekmurzaev, 1971	Adults		6–42		
	Direct transfer from 20 g/L	Andreev and Andreeva, 1990	Adults		?–110		
<i>Theodoxus pallasi</i>	Stepwise acclimation	Filippov, 1995	Adults	5–20	4–25	22 (Aladin, 1991)	1984
	Physiological adaptation	Bekmurzaev, 1970	Adults		4–30		
	Direct transfer	Andreev and Andreeva, 1990	Adults				

The salinity value 0 corresponds to the salinity of fresh water. Empty cells mean the corresponding experiments were not carried out by the authors of this study.

similar result was obtained for ciliates (Smurov et al., 2017). This phenomenon is associated with a change in the proportions of sodium and chlorine. However, even at low salinity values, which do not differ much from the salinity values of fresh water, the ion ratios are changed. First of all, this affects divalent ions, and these ratios are unfavorable for freshwater organisms.

At the same time, the mineralization of the waters of the Syr Darya River in the years 1981–1985 increased 3.4 times compared to the period of 1911–1960. The increase in mineralization of river waters was accompanied by a sharp change in their ionic composition. Thus, the relative content of carbonates in the water of the Syr Darya River decreased by four times. The relative decrease in carbonates in the river runoff was offset by an increase in the absolute and relative content of chlorides and a significant increase in the absolute and relative content of sulfates (Andreeva and Andreev, 2003). Accordingly, this led to a change in the ratio of ions in the estuarine areas of the sea.

To date, the negative effect of low-mineralized waters of the Aral Sea on various animals has been almost not studied. However, even in the greatly freshened waters of the Aral Sea, mollusks from Valvatidae, Unionidae, and Lymneidae, which inhabit the water bodies adjacent to the Aral Sea, occur rarely.

MODERN REGRESSION OF THE ARAL SEA

The main reason for the changes in the mollusk fauna of the Aral Sea that have occurred since the early 1960s is the modern anthropogenic regression (Figs. 1b, 1c), which resulted in a change in the hydrological regime of the reservoir and water salinity.

For several centuries, the state of the Aral Sea had remained conditionally stable. Since 1961, mainly due to the beginning of an increase in the irretrievable withdrawal of river flow, mainly for irrigation, as well as the onset of a period of natural low water, the river flow has begun to decrease, which caused a regression. The level of the Aral started to decrease, and salinity started to increase (Bortnik and Chistyeva, 1990). During the years 1961–1970, the desiccation of the Aral Sea and the accompanying increase in salinity proceeded slowly, and by 1971 the average salinity had increased insignificantly, by only 1.5‰, i.e., up to 11.5‰. The Aral Sea was still brackish.

During the period considered, there was a rapid decrease in the total abundance and biomass of all species and subspecies of brackish-water bivalve mollusks of the genus *Dreissena*. From 1963 to 1970, these indicators decreased by about ten times. The occurrence (Fig. 6) of *Dreissena* also decreased (Plotnikov, 2016). Unfortunately, due to the lack of data on their distinct forms, it remains unknown to what extent this affected each of them. An increase in salinity and a reduction in the area of freshened zones in front of river deltas should have primarily affected *D. polymorpha aralensis*,

which is less resistant to salinity, but it is unlikely that these factors had a significant effect on *D. p. obtusecarinata* and *D. caspia pallasii*, which are more resistant to salinity (Dengina, 1959; Andreeva, 1989).

A similar situation was observed with bivalves of the genus *Adacna*, which was represented in the Aral Sea in three forms. From 1963 to 1970 their total numbers and biomass also rapidly declined (Andreeva and Andreev, 1987; Andreeva, 1989) by an order of magnitude. Their occurrence also decreased (Fig. 7). As in the case with *Dreissena*, it remains unknown to what extent this affected each of the species and subspecies of these bivalves (Plotnikov, 2016).

The decrease in the abundance of *Dreissena* spp. and *Adacna* spp. in the zoobenthos of the Aral Sea was reflected in a decrease in the total number of larvae of bivalve mollusks in plankton, which was observed in 1967–1969 (Andreeva, 1989), i.e., before the alien *Abra segmentum* spread throughout the sea.

The bivalves *Cerastoderma* sp. A, formerly considered *C. rhomboides*, and *C. glaucum* in the Aral Sea were initially characterized by low abundance compared to *Dreissena* spp. and *Adacna* spp. These two species of the genus *Cerastoderma* had different salinity optima and were found in different areas of the sea. The main part of the Aral Sea was inhabited by *Cerastoderma* sp. A. The distribution of *C. glaucum* was limited to saline areas of the sea (kultuks of the Akpetki archipelago and bays of the eastern coast of the Large Sea). With the advance into these salinized areas and as salinity increased, the abundance of *Cerastoderma* decreased until the disappearance of these mollusks, but with a further increase in the salinity in this gradient, *Cerastoderma* reappeared. Its abundance increased, reaching its maximum at 24–28‰. Thus, the first species was replaced by the second species (Dengina, 1959; Starobogatov, 1974; Andreeva, 1989). In the years 1964–1970 the increase in sea salinity caused only a reduction in the range of *Cerastoderma* sp. A (Fig. 8), but did not lead to the extinction of this species (Andreeva, 1989).

After 1965, there was a sharp and rapid decrease and by 1967 the abundance and biomass of the gastropod mollusk *Theodoxus pallasii*, as well as its occurrence, decreased (Fig. 5) (Plotnikov, 2016).

In the 1970s, a sharp reduction in the flow of the Amu Darya and Syr Darya rivers started and the already existing deficit of the water balance of the Aral Sea increased, accelerating the process of its desiccation and salinization. The impact of the ongoing increase in the salinity of its waters on the fauna of the Aral Sea intensified. The Aral Sea ceased to be a brackish water body after achieving the upper limit of the first barrier salinity of 12–13‰ and the subsequent passage through it.

The first crisis period occurred in 1971–1976, and the reduction of species diversity started (Plotnikov et al., 1991). A further increase in salinity during this

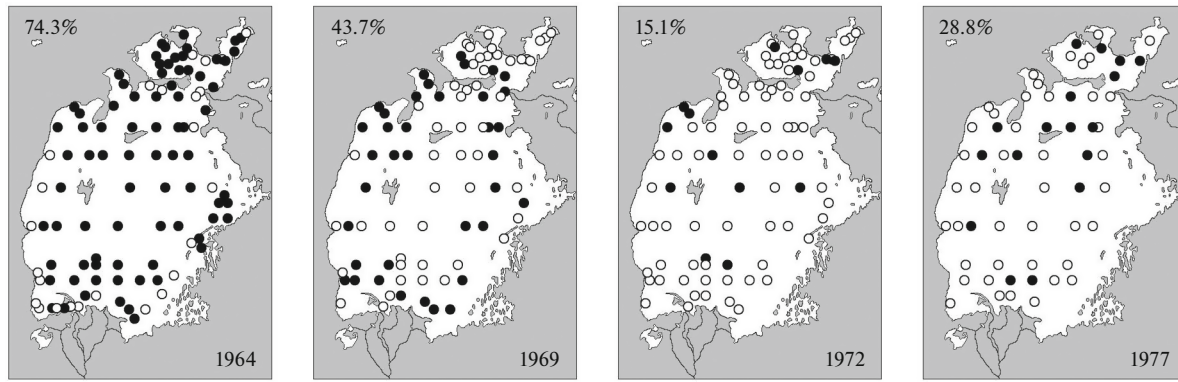


Fig. 6. Distribution of *Dreissena* spp. (Symbols as in Fig. 2.)

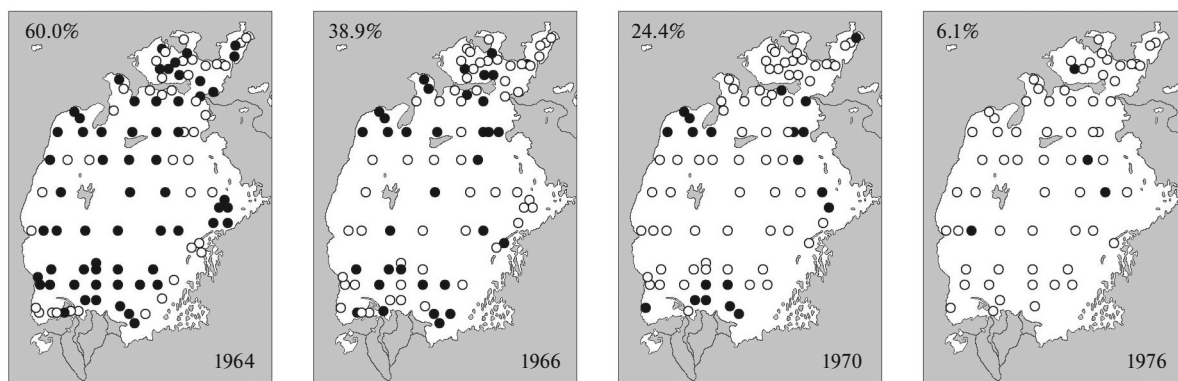


Fig. 7. Distribution of *Adacna* spp. (Symbols as in Fig. 2.)

crisis period had a different effect on the *Dreissena* species and subspecies of bivalve mollusks inhabiting the Aral Sea. On the one hand, this period was already unfavorable not only for *Dreissena polymorpha aralensis*, but also for *D. p. obtusecarinata*, and the abundance of this species also decreased. Both species became extinct in 1978–1979. On the other hand, due to the oppression and subsequent extinction of these two species, conditions for increased abundance of more halophilic *D. caspia pallasii*, which can withstand salinity up to 17–20‰, were created (Dengina, 1959; Andreeva, 1989). As a result of the above processes, as well as due to a decrease in the abundance of other bivalve mollusks, in the years 1974–1976 some stabilization of the general range and even an increase in the total abundance of *Dreissena* were observed (Plotnikov, 2016).

The abundance of bivalve mollusks of the genus *Adacna* inhabiting the sea, which had already decreased in the 1960s, continued its decline under the influence of increasing salinity (Andreeva and Andreev, 1987; Andreeva, 1989), and their range also decreased (Fig. 7). All three subspecies of these mollusks, *Adacna vitrea bergi*, *A. minima minima*, and

A. m. sidorovi, became completely extinct in 1978–1979 (Andreev and Andreeva, 1981; Andreeva, 1989).

The continued increase in the salinity of the Aral Sea contributed to a further reduction in the range and a decrease in the abundance of bivalves *Cerastoderma* sp. A, which began in the 1960s, and, conversely, was favorable for *C. glaucum*. Since 1971, due to the continued increase in salinity, more halotolerant *C. glaucum* started to spread actively from saline areas in the east of the Aral Sea throughout the sea, rapidly increasing its population (Fig. 8). After 1978, when salinity reached 15‰, *Cerastoderma* sp. A was no longer found in the Aral Sea, but *C. glaucum* not only occupied its place, but even became a more numerous species than its predecessor (Andreeva and Andreev, 1987; Andreeva, 1989).

An increase in salinity above 12–14‰ also favored the recently introduced euryhaline bivalve *Abra segmentum*, the distribution of which throughout the Aral Sea was mainly completed by 1976. The increase in salinity also favored the halophilic gastropod mollusk *Ecrobia grimmi*, and its abundance increased (Andreeva, 1989).

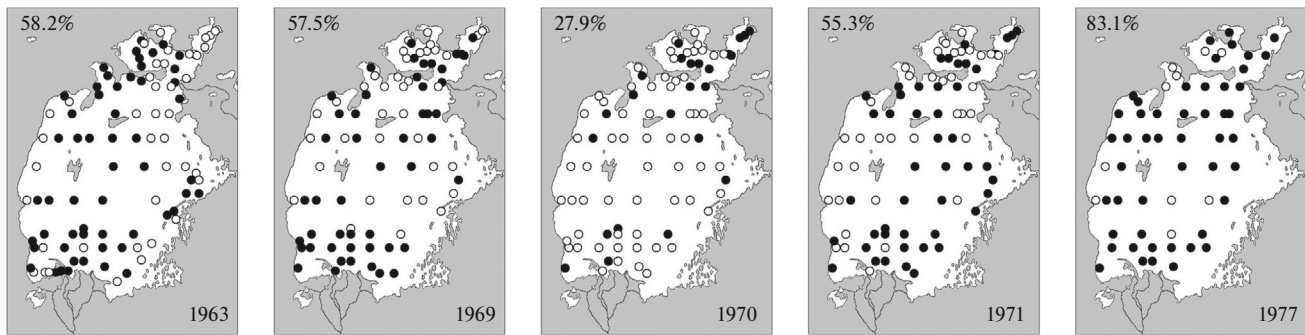


Fig. 8. Distribution of *Cerastoderma* spp. (Symbols as in Fig. 2.)

After the first crisis in the malacofauna of the Aral Sea, only *Dreissena caspia pallasii*, *Cerastoderma glaucum*, *Abra segmentum*, *Ecrobia grimmi*, and *Theodoxus pallasii* (Plotnikov, 2016) were preserved.

With the continued increase in salinity, the first crisis period was followed by a period of relative stabilization. It should be noted that this stabilization did not mean the absolute immutability of the mollusk fauna of the Aral Sea: in the 1980s the last surviving and the most halotolerant species of *Dreissena*, *D. caspia pallasii*, and the gastropod *Theodoxus pallasii* disappeared (Fig. 1b) (Andreeva, 1989; Andreeva and Andreev, 2003; Plotnikov, 2016).

By 1987, the salinity of the Aral Sea increased to 27‰, which corresponded to the lower limit of the second barrier salinity (27–32‰) (Plotnikov and Aladin, 2011). After this limit was passed, the mollusk fauna of this reservoir in the late 1980s entered the second crisis period (Plotnikov et al., 1991), during which there was again a rapid reduction in its species diversity.

By the end of the 1980s, as a result of the continued decline in the level of the Aral Sea and the drying up of the straits between the Small and Large Aral seas, they turned into two residual reservoirs with different hydrological regimes (Fig. 1b). Since the flow of the Syr Darya River into the Small Aral Sea exceeded evaporation from its surface, the decrease in the water level stopped and its condition stabilized, and the excess water started to flow into the Large Aral Sea. Evaporation from the surface of the Large Aral Sea exceeded the flow of the Amu Darya River and the inflow of water from the Small Aral Sea, and the reservoir continued to dry out and become saline (Aladin and Plotnikov, 1995). Since that time, all changes in the Small and Large Aral seas have proceeded in different directions.

In 1992, in order to keep the water flowing into the Large Aral Sea, as well as to raise the level of the Small Aral Sea and reduce its salinity, the former Berg Strait was blocked by a dam. In 2004–2005 it was replaced by the new capital Kok-Aral dam. This created all the conditions not only for the conservation of the Small Aral Sea, but also for the restoration of its biological

diversity (Plotnikov, 2016). Now, this part of the Aral Sea has again become brackish.

The level of the Small Aral Sea, after being regulated by the dam in the Berg Strait, increased and stabilized. The salinity of the waters of this residual reservoir, due to its positive water balance and seasonal flow (in winter-spring), gradually decreased, and by now the mean value has become even lower than before the start of the modern regression and the salinization caused by it. At the same time, if near the mouth of the Syr Darya River, due to freshening by river runoff, salinity is decreased, then in the Bolshoi Sarycheganak and Butakov bays it is still higher than in the main water area of the Small Aral Sea.

Now the most numerous species among mollusks is *Abra segmentum*, which also is the dominant species of the zoobenthos. Compared to the first half of the 1990s (Filippov, 1995a), the abundance of all mollusks has decreased significantly. For *Cerastoderma glaucum* and *Ecrobia grimmi*, this can be explained by a decrease in salinity unfavorable for these mollusks (Plotnikov et al., 2016). Another reason for the decreased abundance of mollusks, primarily *A. segmentum*, was the return of generative freshwater fish species to the Small Aral Sea, most of these species are benthophages, which originally formed the basis of its ichthyofauna and disappeared in the late 1970s due to salinization of the sea (Ermakhanov et al., 2012).

The decrease in the average salinity of the Small Aral Sea and the formation of a vast freshened zone in front of the Syr Darya River delta made possible the natural reintroduction of many invertebrate species, including mollusks that became extinct in the Aral Sea during its salinization, but inhabited refugia, like the Syr Darya River and floodplain lakes of its lower reaches (Grishaeva, 2010). Of the mollusks, such species are *Dreissena polymorpha aralensis* and *Theodoxus pallasii*. By the 2000s, *T. pallasii* had reappeared in the Small Aral Sea. Recently *D. polymorpha aralensis* also returned to the Small Aral Sea (Fig. 1c). However, the distribution of these mollusks is limited to the estuarine freshened zone, and they are rare in this zone

(Krupa et al., 2019; Toman et al., 2015; Plotnikov et al., 2016).

After the separation of the Great Aral Sea, the increase in its salinity continued and accelerated, and in the late 1990s, this isolated part of the Aral turned into a hyperhaline reservoir, which caused a sharp reduction in biodiversity. The last surviving three species of mollusks completely disappeared (Fig. 1c). By 2001, the bivalve mollusk *Cerastoderma glaucum* had become extinct, and since 2004 *Abra segmentum* no longer occurs. In the 2000s the gastropod *Ecrobia grimmi* was not found in the Large Aral Sea (Aladin and Plotnikov, 2008; Zavialov et al., 2012; Plotnikov, 2013); it disappeared in the second half of the 1990s, but when exactly this happened remains unknown.

THE FUTURE OF MOLLUSK FAUNA OF THE ARAL SEA

Mollusks currently inhabit only the Small Aral Sea out of all the residual water bodies of the Aral Sea. The future of its malacofauna will be determined primarily by how the salinity of the water will change in the future.

Under the current hydrological regime of the Small Aral Sea, its salinity, due to seasonal flow, can continue to decrease until a balance between the inflow of salts with river runoff and their removal with water through the Kok-Aral dam is established. The salinity value will depend on the volume of the Syr Darya River water reaching the sea.

A further decrease in the salinity of the Small Aral Sea could cause new changes in the composition of the mollusk fauna; those species that will be unable to survive under the new conditions will disappear. Strong freshening of the sea will have a negative impact on marine species and native species of saline water bodies of the arid zone, which were favored by the salinization of the Aral Sea, as well as on brackish water species, up to the point that it will lead to their loss from the fauna. Freshening of the main water area of the Small Aral Sea below 7‰ will lead to the disappearance of the native marine bivalve mollusk *Cerastoderma glaucum* from it; at salinity below 6‰ (Andreev and Andreeva, 1990), gastropods *Ecrobia grimmi*, which are native species of saline water bodies of the arid zone, may disappear from the main water area of the sea. These species have already become rare and close to extinction. If the salinity becomes less than 5‰, then the invader, the marine bivalve mollusk, *Abra segmentum*, which is still among the dominant species (Plotnikov et al., 2016) of the benthic fauna of the Small Aral Sea may disappear. However, it should not affect the isolated Butakov and Bolshoy Sarycheganak bays, where salinity is increased due to limited water exchange with the main part of the Small Aral Sea. Mollusks preserved in these bays will not become extinct.

There is the possibility of further increase in the volume and area of the Small Aral Sea due to the water that is now discharged through the Kok-Aral dam in the former Berg Strait.

If the project that involves the creation of a dam in the mouth of Bolshoy Sarycheganak Bay with a spillway into the main water area of the Small Aral Sea and the laying of a canal from the Aklak hydroscheme on the Syr Darya River to redirect part of the flow to this bay will be implemented then the Small Aral Sea will become a cascade of two reservoirs, which will differ in the hydrological and salinity regimes. In place of the flooded bay, a low-mineralized flowing reservoir will form and the main part of the Small Aral Sea will remain brackish. In Bolshoy Sarycheganak Bay, the water of which in the possible future is characterized by very low salinity, due to hydrobionts from the Syr Darya River, freshwater fauna will form, which will replace the existing one. *Cerastoderma glaucum*, *Abra segmentum*, and *Ecrobia grimmi* inhabiting there at present will not be preserved, but *Dreissena polymorpha aralensis* and *Theodoxus pallasii* will penetrate into the bay. The main part of the Small Aral Sea will remain brackish.

If the alternative project will be implemented, which involves only the reconstruction of the dam in the Berg Strait with an increase in its height, then the level will rise and the area of the entire Small Aral will increase. In this case, the entire Small Aral Sea will be brackish with a salinity not lower than the modern one and with a freshened zone in front of the Syr Darya River delta.

The implementation of either of these two options will prevent further freshening of the Small Aral Sea (and even slightly increase its salinity compared to the current one) and new changes in its fauna.

It seems appropriate to introduce into the Small Aral Sea from the Caspian the brackish-water mollusks *Adacna minima* and *A. vitrea*, which have become extinct during the salinization of the sea and can serve as good food for the benthivorous fish that currently inhabit the reservoir.

PREVIOUS ARAL REGRESSIONS

The history of the Aral Sea is the history of its repeated regressions and transgressions that have taken place throughout the entire period of its existence. The level and, accordingly, the salinity of the Aral Sea was influenced only by natural factors that determined the volume of flow of the Amu Darya and Syr Darya rivers, which reached this drainless lake. First, the volume of runoff depended on the climate, whether it was drier or wetter in the area where these rivers formed (Pamir and Tien Shan). Secondly, if the waters of the Syr Darya River always flowed into the Aral Sea, then the Amu Darya River could turn into Sarykamysh and further along its ancient channel

Uzboy into the Caspian Sea (as it was in the Pliocene) and could even flow simultaneously into both reservoirs. In ancient times alone, anthropogenic factors were added to these two natural factors, the emergence and development of irrigated agriculture in the Aral Sea basin. In ancient Khwarazm, people could direct the river not to the Aral Sea, but to the Caspian, or vice versa. Control over the Amu Darya River could only be maintained during periods of relative social stability. Social upheavals and wars in the region could lead to the loss of control over the river when protective dams and irrigation systems were destroyed, and then, by chance, it turned in one direction or another (Aladin and Plotnikov, 1995). The lack of flow volumes of the rivers flowing into the Aral Sea led to the regression of the sea. As the level dropped, the single body of the reservoir broke up into separate lakes filled with highly mineralized water, and, at the confluence of rivers, into freshened shallow waters, which are reed beds (Svitoch, 2009).

Since the regressions of the Aral Sea were accompanied by an increase in salinity, and the transgressions that replaced them were accompanied by its decrease, this was reflected in the fauna. The changes in the fauna can be traced from the remains of aquatic organisms such as mollusks, which have well-preserved shells in the bottom sediments. If the range of salinities in which a particular species can exist is known, then it is possible to determine approximately what the salinity was at the time when this specimen lived. If at the same time it is possible to establish the age of these remains, then it is possible to link salinity changes to the time scale.

At the beginning of its history, the last Aral Sea, probably, was initially filled with glacial melt water and, accordingly, was characterized by low salinity. This is evidenced by both the nature of sedimentation and the composition of the ostracod fauna (Burr et al., 2019). In the period 13800–15300 years ago, the character of sedimentation in the Aral changed and the halophilic ostracods *Cyprideis torosa* and foraminifera *Retroelphidium littorale* and *Ammonia beccarii* started to dominate in the lacustrine benthos. This period can be attributed to the marine stage of the development of the Aral Sea (Burr et al., 2019).

By the beginning of the Holocene, the lake passed into the lacustrine–saline stage, which was characterized the presence of lakes of varying degrees of salinity in the relief depressions, which, when dried, turned into solonchaks. The sediments of this time are characterized by the presence of gypsum and shells of highly euryhaline and freshwater mollusks (Svitoch, 2009). This stage ended at the moment of invasion of *C. glaucum* in the Aral Sea about 5000 years ago. The next stage in the development of the Aral Sea was proposed to be called marine (Svitoch, 2009). This stage began with the transgression of the Aral Sea. In the period of 3600–4900 years ago, the sea level reached

56–57 m above the Ocean level. The freshwater mollusks *Limnaea auricularia* and *Planorbis sieversi*, the brackish water mollusks *Dreissena polymorpha obtuscarinata* and *D. caspia pallasii*, and the marine species *Cerastoderma glaucum* were found in the sediments.

The next transgression of the Aral Sea took place 3000–1600 years ago (Khrustalev et al., 1977; Maev et al., 1983). At that time, the sea level reached 54.5 m, and the salinity was 8–9‰. The mollusk fauna of this time was characterized by an abundance of Caspian species *Adana minima* and *Theodoxus pallasii* (Svitoch, 2009).

The last 2000 years of the history of the lake have been studied much better than the previous periods of its existence. Even before the modern anthropogenic regression, the Aral Sea experienced two regressions that can be compared in scale with the anthropogenic one (the sea level dropped to +29 m abs.) and which were replaced by transgressions. The dating of regressions is based on geological, geomorphological, and archaeological data and on the results of the study of fossilized remains of aquatic organisms in bottom sediments. The first dates back to around the 1st century BC to the 4th century BC. The second, medieval, regression, which occurred in the 12th–15th centuries, is dated more precisely, and there is documentary evidence of it by its contemporaries (Krivonogov et al., 2010, 2014).

Filippov and F. Riedel (Filippov and Riedel, 2009) analyzed changes in the mollusk fauna in terms of their distribution and occurrence in sediment cores covering the last thousand years taken from the bottom of the Aral Sea.

The most constant element in these deposits was the widely euryhaline *Ecrobia grimmeri*. In the lower parts of the sediment cores, there were shells of the brackish-water gastropod mollusk *Turricaspia spica*, on the basis of which the authors suggested that this species inhabited the Aral Sea until the middle of the 14th century. According to Filippov and Riedel (Filippov and Riedel, 2009), these shells were not redeposited from outcrops of ancient rocks, but belong to mollusks that actually inhabited the Aral Sea at that time. These shells were present in cores from the most ancient layers to the layer corresponding, according to their dating, to ~1300–1350 BC. According to these authors, it can be concluded that the extinction of *T. spica* occurred due to a strong decrease in salinity to almost freshwater conditions in ~1250–1400 BC after the direction of the entire flow of the Amu Darya River to the Aral Sea and an increase in the water content of the Syr Darya River. At the same time, due to low salinity, as they believe, the bivalve mollusk *Adacna minima* also disappeared. These authors suggest that, in the future, around 1350–1400 according to their dating, salinity started to increase again as a result of a decrease in the inflow of fresh water, which continued until 1500–1550. This is evidenced by the

distribution of mollusks *E. grimmi* and *Cerastoderma glaucum*, which prefer higher salinity, with a decrease in the abundance of *Dreissena* spp., which prefers low salinity. According to these authors, around 1500 *A. minima* reappeared in the Aral Sea; possibly, it was introduced with human participation (Filippov and Riedel, 2009). It should be noted that there are strong doubts about the correctness of the dating data (Krivonogov et al., 2014).

REASONS FOR THE SCARCITY OF MOLLUSK FAUNA OF THE ARAL SEA

The question of the reasons for the scarcity of the Aral fauna was one of the first discussed by Berg (1908). He pointed out that the cause of scarcity is not in the physical conditions of the modern basin of the reservoir. He noted that out the total composition of the Aral-Caspian fauna in the lake, “only such elements were preserved that could endure complete freshening.” This quote refers not only to mollusks, but also to the entire fauna of the Aral Sea. Thus, the reason for the scarcity of the mollusk species diversity must be the overall scarcity of the Aral fauna.

The main reason, in our opinion, should be considered the young age of the sea, which barely exceeds 17000 years. This time was not enough for the formation of endemic fauna (Plotnikov, 2016). It is known that in the Caspian Sea, which lost its connection with the ocean several million years ago, the endemic fauna is rich by species (Bogutskaya et al., 2013). The regressions and transgressions of the Caspian, probably, have led to acceleration of the process of evolution of mollusks. Earlier based on the example of *Cerastoderma glaucum* and *Abra segmentum*, a significant increase in the morphological variability during the regression of the Aral Sea was shown, which in the future may lead to the appearance of new species (Andreeva and Andreev, 2003).

The newly formed lake was supposed to be, first of all, populated with mollusks from nearby reservoirs. First of all, *Dreissena* spp., *Theodoxus pallasi*, and *Ecreobia grimmi*. These species could either disappear in the sea during regressions or remain in residual water bodies with a salinity suitable for them. Recent reintroduction of *D. polymorpha aralensis* and *T. pallasi* into the sea after extinction shows that now there are no obstacles to the replenishment of the mollusk fauna from neighboring water bodies.

We assume that the transfer of juvenile mollusks by birds played an important role in the replenishment of the fauna with new species. This is probably true for mollusks of the Cardiidae family, *Ecreobia grimmi* and *Turricaspiya spica*. Only the most eurybiontic mollusk species were able to penetrate into the Aral Sea. It can be assumed that, if the salinity of the Aral had stabilized for a long time, the number of invasive species from the Caspian would have been much higher. How-

ever, long-term changes in the water salinity, exceeding those in the Caspian Sea in scope, are the reason for the poor representation of Caspian species in the mollusk fauna of the Aral Sea.

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CONFLICT OF INTEREST

Conflict of interest. The authors declare that they have no conflicts 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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