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Salinity is a crucial abiotic factor. How does it affect animal life? What theoretical and practical conclusions follow from this? In the article below, the impact of the salinity factor on animal life is assessed proceeding from modern views on evolution. To demonstrate the practical significance of the subject under consideration, the consequences of the Aral Sea environmental disaster and possible ways to combat it are discussed.

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The Salinity Factor in Animal Life

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Life on the earth exists at different levels of environmental salinity, from weakly mineralized water in lakes with granite floors filled with snowmelt (the salt concentration being several milligrams per liter) to arid zone water bodies, where salt saturation reaches nearly 300‰ (g/l). The main phyla of aquatic fauna in fresh, brackish, marine, and oversalted water reservoirs do not change gradually but have distinct transfer zones within gradients of natural water salinity (Fig. 1).

The conditions of the existence of freshwater and marine fauna have been most important both for the current distribution of animals and for their evolution over hundreds of millions of years. The difference between them is formed by a relatively narrow salinity span, the absolute value of which is about 5–8‰. Below this range is the domain of freshwater organisms; if the salinity exceeds this level, the waters are inhabited by representatives of marine fauna. It is believed that marine organisms are primary in origin, which is confirmed by the presence of a great number of large taxa, such as phyla and classes, in seas. The simplest forms of embryogenesis (total fission), more primitive feeding (the opportunity to consume monomers extraintestinally, through integuments), and the absence of mechanisms of osmotic regulation of the internal environment (poikilosmotic nature) also testify to the antecedence of marine organisms.

Freshwater and seawater differ considerably, not only in salt concentrations but also in salt compositions. Freshwater bodies are characterized by a colossal diversity in the mineral composition of their waters. On the contrary, the constancy of the ratios of dissolved ions in seas is so strict (Knudsen rule) that the total salinity and individual ion contents may be calculated by the concentration of only one of them (as a rule, chlorine is used for such calculations because its content in seawater is high and its titer is easy to establish). Interestingly, as oceanic waters desalt (their salinity, as is known, is about 34.5‰), the Knudsen rule remains effective to a limit of about 5–8‰. In other words, the biological faunal and hydrochemical boundaries of transitional processes between seawater and freshwater practically coincide [1].

A graphic geological consequence of complex processes associated with the critical salinity zone, which occur in places of natural interaction of seawaters and river waters, is rapid rather than gradual local sedimentation due to the washout of organic and inorganic materials by the river; this phenomenon was later called the "marginal filter of the ocean" [2].

Critical salinity. As was noticed long ago, with regard to the ratio of basic ions, seawater is close to the liquids that are present in the internal environment of organisms, including the blood plasma, lymph, and hemolymph. As a result, the idea of *internal salinity*, or the *salinity of the internal environment* was formed. Respectively, attempts were made to express its concentration not by physical indices (osmols, freezing temperature, and osmotic pressure in atmospheres) but by the indices evaluated in parts per million (‰), i.e., in the units in which hydrobiologists and oceanologists evaluate the salinity of the external environment. It turned out that the salinity of the internal environment in the majority of freshwater and land animals does not usually drop below 5‰ [1]. Only in unionidae does it not exceed 2‰ [3]. The normal salinity indices of human internal environments are about 9‰; the following noteworthy fact shows the similarity between the composition of human blood plasma and seawater: during World War II, hospitals in besieged Leningrad and those of the Royal Navy used seawater dissolved to the necessary level of salinity as a blood substitute.

Thus, the narrow salinity range (5–8‰) turns out to be the upper limit beyond which the larger part of freshwater hydrobionts cannot spread and, at the same time, the lower limit beyond which representatives of marine fauna cannot penetrate into freshwater. In addition, this range is the lower boundary where the Knudsen rule can be applied and the hydrochemical

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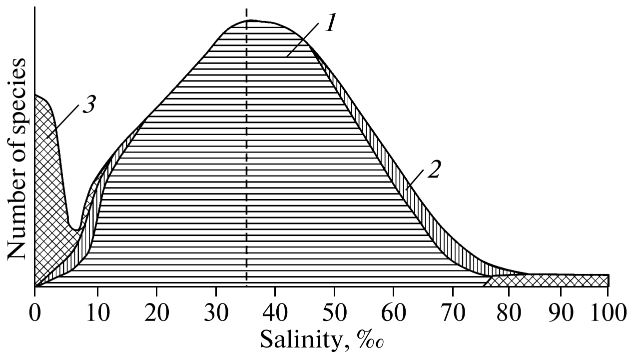

Fig. 1. Salinity and the number of species inhabiting a body of water.

(*1*) Marine species, (*2*) brackish water and estuarine euryhaline species of marine origin, and (*3*) freshwater species and their descendents.

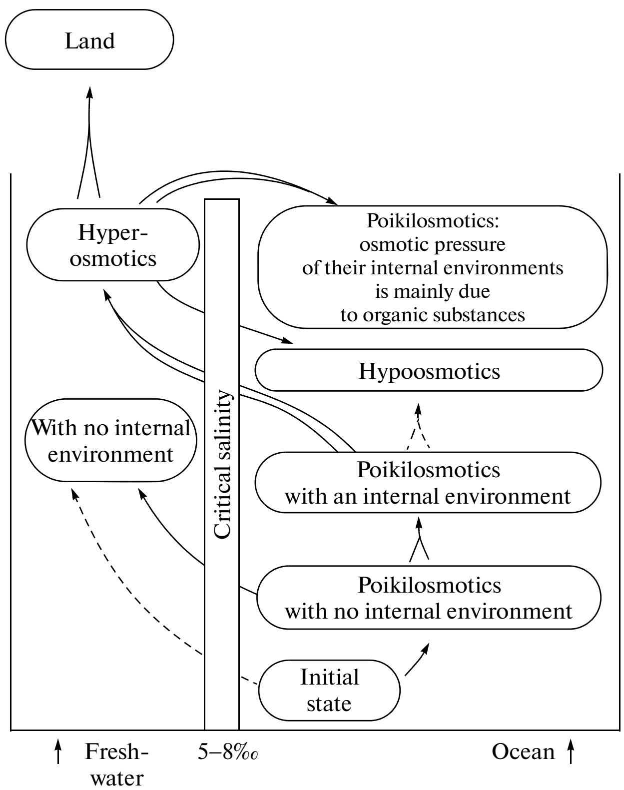

Fig. 2. Evolution of osmotic relations.

boundary between seawater and freshwater, as well as the lower limit of the salinity of the internal environment in physiology. All the above information has made it possible to identify this large-scale environmental and evolutionary phenomenon as *critical salinity* [1].

Osmoregulation. The overwhelming majority of originally marine species are unable to regulate the osmotic pressure of their internal environment. These are mainly the species that cannot overcome the range of critical salinity under the desalination of their environment. Only organisms with *hypertonic regulation*, which means trapping ions that are scarce in freshwater and transferring them into their internal environments, can penetrate into freshwater and live in it. *Hypotonic regulation,* which implies desalting the internal environment through releasing ions out, opposite to the salinity gradient, is obviously characteristic of some secondarily marine animals of freshwater origin (Fig. 2). In our opinion, the very fact that hypotonic regulation does exist testifies to the freshwater origin of this group. It includes crustaceans *Palaemonidae*, the seawater branchiopod *Cladocera*, and ray-finned fishes (*Teleostei*). Practically all the known forms of osmoregulation can be found in the ostracod and fairy shrimp groups, which made it possible to classify them according to this physiological mechanism and to establish within-group genetic relations [4].

Depending on the type of osmotic relations with the water environment, hydrobionts are divided into the following main groups [4, 5] (Fig. 3).

(1) *Osmoconformers* (the majority of present-day originally marine hydrobionts, including coelenterates, worms, mollusks, arthropods, echinoderms, and others):

osmoconformers I (A1), stenohaline marine hydrobionts (30–36‰);

osmoconformers II (A2), marine hydrobionts (20–40‰); and

osmoconformers III (A3), euryhaline marine hydrobionts (8–40‰).

(2) *Confohyperosmotics*, or organisms that combine osmoconformity at high salinities with hyperosmotic regulation at low salinities (the majority of present-day originally marine euryhaline hydrobionts, including polychaetes, gastropods, crustaceans, and so on):

confohyperosmotics I (B1), broadly euryhaline hydrobionts (3–50‰); and

confohyperosmotics II (B2), brackish-water hydrobionts of marine origin (0–30‰).

(3) *Hyperosmotics* (the majority of present-day freshwater hydrobionts, including oligochaetes, rotifers, mollusks, crustaceans, insects, freshwater fishes, and so on):

hyperosmotics I (C1), freshwater hydrobionts (0–8‰); and

hyperosmotics II, or secondary confohyperosmotic organisms (C2), brackish-water hydrobionts of freshwater origin (0–20‰).

(4) *Amphiosmotics,* or organisms that combine hypoosmotic regulation at high salinities with hyperosmotic regulation at low ones:

amphiosmotics I (D1), some Caspian brackish-water hydrobionts (0–20‰);

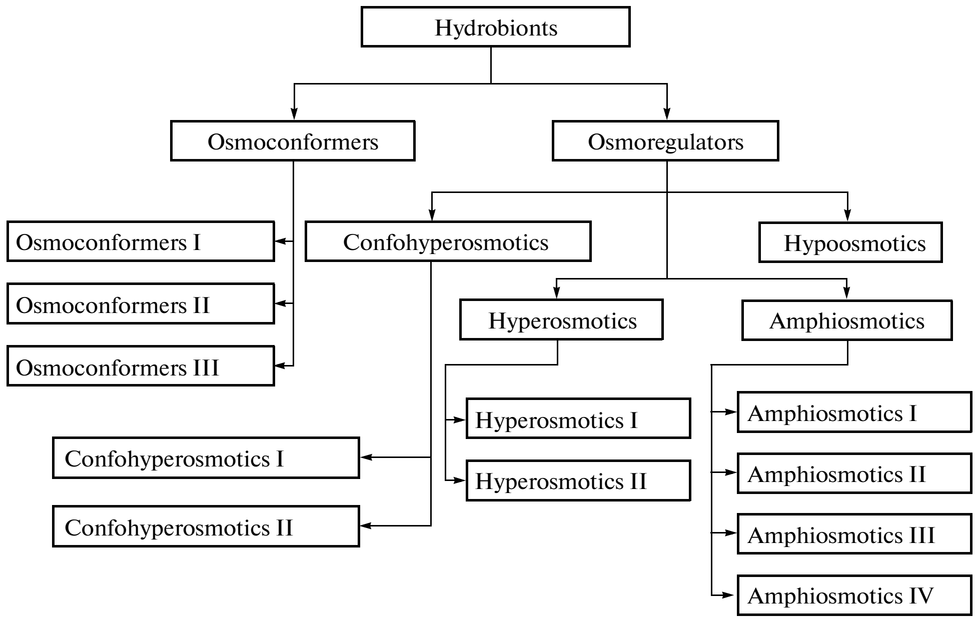

Fig. 3. Classification of osmoconformers and osmoregulators.

amphiosmotics II (D2), some euryhaline Australian hydrobionts of the freshwater origin (0–50‰);

amphiosmotics III (D3), euryhaline hydrobionts of the freshwater origin (0–50‰) some crustaceans, a number of insects, and anadromous fishes; and

amphiosmotics IV (D4), broadly euryhaline hydrobionts of the freshwater origin (0–300‰).

(5) *Hypoosmotics* (some secondarily marine crustaceans and the majority of present-day secondarily marine fishes):

hypoosmotics (E), euryhaline marine hydrobionts of freshwater origin (8–50‰).

Note that the commonly recognized ideas of environmental physiology about the osmotic factor and osmoregulation are not quite correct. Osmotic pressure is a function of the amount of dissolved particles irrespective of their nature. For the biological activity of the external and internal environments, however, the quality of the dissolved particles is also important. Experiments with White Sea organisms in mannitol-added seawater showed that biologically inertial mannitol acts as a neutral osmotic factor only if the environment already contains seawater with at least critical salinity [6]. Obviously, the biological sense of the phenomenon that is called hypertonic regulation and that allowed animals to penetrate into freshwaters and onto land consists of ionoregulation, which gives rise to an internal environment analogous to seawater with regard to the ion ratio.

Under certain conditions, primarily in monsoon-climate water bodies of Southeastern Asia, hypertonic regulation, which makes it possible to live in freshwater, may be developed by grown-up organisms of a clearly marine origin despite the absolute defenselessness of their larval stages. Although such animals, called physiologically freshwater [3], may live in freshwater for an infinitely long time, they need seawater during a short reproductive period. For reproduction, they either migrate seaward (for example, the Chinese mitten crab *Eriocheir sinensis*) or wait for an increase in water salinity (some estuarine polychaetes, mollusks, and Far Eastern lagoon crustaceans).

The key to another fundamental hydrobiological question is also associated with the salinity gradient; I mean the extraintestinal (through integuments) consumption of organic materials dissolved in water. There are proofs [7] that this process, with respect to some amino acids at any rate, turns out to be dependent on salinity. It occurs at salinities that exceed the critical salinity and is impossible in freshwater. Evidently, it is due to this that marine hydrobiologists (for example, A. Pütter) heatedly advocated the existence of this phenomenon, while Nobel Prizewinner A. Krogh, who experimented only with freshwater animals, denied it.

It is of interest that the level of internal salinity (slightly higher than the critical one) developed in freshwater turns out to be close to the level characteristic of organisms that have returned from freshwater to seawater. When in the sea, they engage mechanisms of hypotonic regulation, which desalt the internal environment. This was why the French traveler A. Bombar, who crossed the Atlantic Ocean in an inflatable boat, used fish juice, the salinity of which is about three times lower than that of seawater, to compensate for the lack of drinking water.

Sodiocentrism. The main ions of true seawater and internal environment liquids are sodium and chlorine ions, which total 80% of the ion content. Respectively, ionic regulation in the internal environment takes place primarily through their active transport [8–10]. Note that sodium chloride, essential for all animals, penetrates into the organism and is evacuated from it (with regard to equivalent relations of these ions) in an unchanged form as opposed to the huge diversity of substances that are used for nutrition and transformed in the course of metabolism. Why do animals need sodium chloride except that it produces the basically osmotic background of internal salinity?

As is known, an indicative feature of the living state of an organism is maintaining ionic asymmetry on both sides of the cell membrane between the internal environment and the internal content of the cell. As long as the cell is alive, the enzyme K^+–Na^+–ATPhase continually “pumps” Na^+ ions from it and maintains its high potassium content. The same mechanism helps catch sodium ions, deficient in number, from freshwater and transport them to the internal environment and thus forms the internal salinity of freshwater and land animals. The same enzyme participates in the hypotonic regulation of marine animals: it evacuates excess sodium. Sodium transport is linked with the movement of a great number of substances—products of catabolism and anabolism—through cell membranes. It is also connected with biogenic electricity production and nervous system activity. It will not be an exaggeration to say that the movement of sodium ions underlies the most important physiological functions of animal organisms. We can compare the role of sodium ions in this case with the role of money in the economy: just like money, they come and go unchanged, organizing the movement of many elements and the development of a great number of processes [9, 10].

It is noteworthy that there are water bodies with high salinities, but different from marine salinities. These are various salty lakes that are remote from seas, including the Caspian and Aral Seas with their “metamorphized” water, the ionic composition of which is different from that in the ocean. In the Caspian Sea, critical salinity is about 7–11‰; in the Aral Sea, 8–13‰. However, the NaCl concentration in them is similar to that in true seas with a salinity of 5–8‰.

The universal character of critical salinity and the environmental and physiological function of sodium as an element of transporting and electricity-producing systems in the organisms of animals makes it possible to speak about the central role of sodium in almost all vital processes in animals. Note that plants, as opposed to animals, have no such demand for sodium obviously because their main mechanism of transmembrane transport is H^+–K^+–ATPhase rather then Na^+–K^+–ATPhase. This is why herbivorous mammals, as opposed to predators, need sodium chloride in the form of cooking salt.

Potassiocentrism. The well-knit theory of sodiocentrism, which was developed over decades by different sciences, was completed in the works of Academician Yu.V. Natochin [9, 10]. He is also the founder of *potassiocentrism*. He paid attention to the fact that the main molecules of life, DNA and RNA, can live and be native only in a potassium environment. The subsequent suggestion that life, most likely, emerged in an environment where potassium ions predominated gained certain geological confirmation: the content of this element in fossil clays is high. The first primitive protomembranes, which separated primary living matter from nonliving, were also probably formed in that environment. Later, as sodium concentration in the external environment increased, there emerged the threat that it would dissolve the environment essential for the “molecules of life,” and it became critically necessary to develop mechanisms of pumping it out. In the ancestors of animals, most likely, this mechanism was ensured by Na^+–K^+–ATPhase. Then the function of harmful sodium evacuation was supplemented by the functions of transmembrane transport and electrogenesis. As a result, sodium turned from a harmful substance into an obligatory element of the external and internal environments of living organisms. The situation is quite similar to that with oxygen. It had emerged as a product of photosynthesis in green-blue algae, which was poisonous for the surrounding living, and then became an element necessary for anaerobic organisms.

The provisions of potassiocentrism are quite new and are only being formed today, but it is already clear that they are the base for sodiocentrism, developed in many sciences.

Practical aspects of the problem. The above ideas are applied in different fields. We will deal with only one application here.

The salinity factor in continental and oceanic waters often becomes the leading abiotic parameter of the external environment. Let us consider its role by the outstanding example of the environmental disaster of the Aral Sea. The sharp and rapid growth of salinity in it has led to substantial changes in its ecosystem. Before the second half of the 20th century, the Aral Sea was an integral terminal water body situated in the arid zone of Central Asia, a gigantic blind drainage lake with only two rivers running into it: the Syr Dar’ya in the northeast and the Amu Dar’ya in the south. The average salinity of the Aral Sea was 10‰. The larger part of the Aral aquatic area fell on the brackish water zone with specific aboriginal brackish water communities. In addition, the Aral Sea partly consisted of strongly desalinated zones in aquatic areas near river estuaries, where freshwater communities dominated. Originally, the Aral Sea was inhabited by about 20 species of fishes and, with no account for protozoa, more than 150 species of free-living invertebrates [11]. In the 1950s and the 1960s, 12 species of fishes and 8 species of free-living invertebrates were either intentionally or incidentally introduced during planned introduction; these species naturalized there [12, 13].

The widening of irrigated agricultural lands in the Aral basin, which began after 1960, led to a many-times increase in the volume of irreversible withdrawal of the river runoff, and the water balance of the basin became negative. By 1988–1989, the level of the Aral Sea had dropped by 13 m, and Berg Strait, which connected north and south Aral, dried up. The Aral Sea began turning into a group of vestigial water bodies. At first, the lake split into two terminal water bodies, the Lesser Sea (Small Aral Sea) for the Syr Dar'ya River, and the Greater Sea (Large Aral Sea) for the Amu Dar'ya River. By this time, its average salinity had reached 30‰. Thus, the brackish Aral Sea was replaced by two polyhaline water bodies with different hydrologic regimes and communities close to the marine type.

As a result of salinization and the introduction of new species of hydrobionts, the Aral fauna changed significantly. Numerous species of freshwater origin were the first to disappear as salinity grew; they were followed by brackish water Caspian species. Only broadly euryhaline species remained in the Aral Sea. In the ichthyofauna, invaders of marine origin dominated. Zooplankton was represented by a few species of aboriginal euryhaline rotifers and harpacticoid organisms, as well as invaders, such as halophilic copepods and marine copepods.

By that time, the Amu Dar'ya runoff had practically disappeared, and only Syr Dar'ya waters ran into the Aral Sea. As long as the water body was integral, excess water freely went to the Large Aral Sea through Berg Strait, but then the latter dried.

After the collapse of the Soviet Union, arable areas decreased, and the withdrawal of water from the Syr Dar'ya decreased as well. Owing to this, in the early 1990s, the runoff to the Small Aral Sea increased, and excess water started running to the Large Aral Sea. The flow from the Lesser Sea formed a channel on the bottom of the dry strait. In accordance with our proposal [14, 15] to confine water in the Small Aral Sea, decrease its salinity, and raise its level, a dam was built in the former Berg Strait. Salinity in the Lesser Sea stopped growing and began decreasing.

Owing to the decrease in salinity, previously extinct crustaceans of the *Polonidae* family appeared again in the plankton from dormant spawns. Chironomid larvae were found in the benthos. Freshwater fishes began returning from the Syr Dar'ya River to the Lesser Sea. Today, there are conditions that correspond to a transitional brackish water–marine saline zone, and it is expected that the Lesser Sea as a brackish-water body will be recovered.

As for the Greater Sea, after the splitting, the decrease in its level and the growth rates of salinity sharply accelerated. This has led to the isolation of its western and eastern basins and the separation of Tshchebas Bay. Since 2000, the growth of salinity in the eastern basin has been faster than in the deep western part. The increasing salinity of the Greater Sea leads to sharp changes in its fauna. By the late 1990s, the Large Aral Sea was a hyperhaline water body with a fauna characteristic of the new conditions. Today, copepods, various rotifers, bivalve mollusks, harpacticoids, prawns, crabs, and other species of plankton bottom macroinvertebrates, as well as all fishes, have disappeared. A number of species from Cisaral and Ciscaspian salty water bodies are naturally invading the hyperhaline Greater Sea (owing to the ash-residue transfer of the dormant stages of protozoa and invertebrates). For example, this was the case with the *Artemia* crustacean, an inhabitant of hyperhaline bodies of water. Halophilic infusorians, rotifers, cladocerans, copepod crustaceans, and chironomid larvae are invading the western part of the Large Aral Sea. The eastern part of the Large Aral Sea is invaded only by *Artemia*.

The implemented project of rehabilitating the Lesser (northern) Sea fully agrees with the above ideas about the significance of the role of the salinity factor in animal life. Owing solely to the dam in Berg Strait, we managed to decrease salinity below the critical level for the Aral Sea (8–13‰) and to restore to life this fragment of the pristine Aral Sea.

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