

# Salinity as a Factor Limiting the Potential Taxonomic Richness of Crustaceans in Ecosystems of Hypersaline Reservoirs around the World (Review)

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**Abstract**—Crustaceans (Crustacea) are one of the most diverse and successful groups in the biosphere, having also mastered different extreme habitats (in addition to freshwater and marine). Based on our own data and >200 literary sources, the way in which the degree of environmental extremeness can limit a potential taxonomic richness of crustaceans has been analyzed using the example of hypersaline waters. It is demonstrated that, with an increase in salinity, the number of classes and orders of the subtype Crustacea decreases linearly; the number of genera and species decreases exponentially. With an increase in environment salinity, the contribution of Arthropoda species to a total species richness of animals in hypersaline waters increases from 49 to 100%, the contribution of Crustacea species to the total species richness of Arthropoda increases from 66 to 78%, and the contribution of Branchiopoda to the species richness of Crustacea increases from 19 to 71%. In hypersaline reservoirs of Crimea in the range from 35 to 120 g/L, salinity is not the main factor determining the species richness and composition of the fauna. A combination of all other factors (first and foremost biotic) plays a more important role, and salinity becomes a tough environmental filter only at higher values (>100–120 g/L).

**Keywords:** Crustacea, taxonomic richness, salinity, hypersaline waters, environmental filters

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## INTRODUCTION

Crustaceans (Crustacea Brünnich, 1772) are one of the most diverse and successful groups in the biosphere. They are represented by a paraphyletic group, in which the taxa of “traditional crustaceans” are combined. At the same time, the Arthropoda and Crustacea taxa are not used at all in some modern systems, for example (Schram and Koenemann, 2021). These issues are currently under discussion; therefore, the authors adhere to the traditional system (Brusca and Brusca, 2003). Some have been able to master different extreme habitats (in addition to regular ones), including underground habitats (caves and ground and artesian waters) as well as terrestrial and marine ones (Pesce, 1981; Bayliss and Laybourn-Parry, 1995; Karanovic, 2005; Turbanov, 2015; Benvenuto et al., 2015; Marin, 2017; Sha et al., 2018). Crustaceans are one of the most species-rich groups existing in black smoker communities (Ramirez-Llodra et al., 2007; Pedersen et al., 2010; Ivanenko et al., 2011; Benvenuto et al., 2015). Life in groundwater and communities of black smokers developed a complex of adaptations in a

number of species, including the use biomass of chemolithotrophs (an alternative source of energy) not associated with photosynthesis (Dov, 2007; Benvenuto et al., 2015). Among inhabitants of these habitats, there are true extremophiles who are not able to exist in a “normal” environment.

Crustaceans exist in biotopes with a very high temperature. For example, higher crayfish *Thermosbaena mirabilis* Monod, 1924 (Malacostraca, Thermosbaenacea) live in hot springs at +46 to 48°C, and are found up to +70°C (Bruun, 1940; Dumont, 1978); *Thermosphaeroma smithi* Bowman, 1981 (Malacostraca, Isopoda) lives at a temperature up to 44°C (Bowman, 1981). The species of seed shrimp *Thermopsis thermothermophila* Kulköylüoğlu, Meisch and Rust, 2003 (Kulköylüoğlu et al., 2003), *Heterocypris balnearia* (Moniez, 1893), and *H. sabirae* Gülen, 1985 (Klie, 1939; Gülen, 1985) live at temperatures reaching 51–54°C. There are other crustacean species able to exist at temperatures >40°C (Laprida et al., 2006; Benvenuto et al., 2015). It should be noted that there are no truly thermophilic species. All species found at >35°C also live at lower temperatures, where the optimum of their development is observed. Crustaceans have developed in habitats with high concentrations of

**Abbreviations:** EF, environmental filter; CV – coefficient of variation; *p* – level of significance; *R* – correlation coefficient; *R*<sup>2</sup> – coefficient of determination.

different toxic substances; for example, anostracan brine shrimp *Artemia monica* Verrill, 1869 (Anostraca) was found in the Mono Lake (United States) at a concentration of arsenic thousands of times higher than is acceptable for the vast majority of animal species (Oremland et al., 2004). Some species of Copepoda (Harpacticoida, Cyclopoida, and Calanoida), Amphipoda (Gammaridae and Hyperiididae), Mysida, and Decapoda live in the pore hypersaline waters of sea ice in Arctic and Antarctic (Arndt and Swadling, 2006; Arrigo, 2014). This is possible, because the freezing point of water decreases with an increase in salinity, and the brine, decreasing in volume, can remain liquid down to  $-35^{\circ}\text{C}$  (Shadrin and Anufrieva, 2018).

With an increase in salinity, not only does the freezing point of water decrease, but so does the solubility of oxygen, and the solubility of a number of toxic substances increases (Shadrin and Anufrieva, 2018). With an increase in salinity, the heat capacity of brine decreases, which leads to the fact that its temperature can reach  $50\text{--}55^{\circ}\text{C}$  in hypersaline reservoirs (Shadrin and Anufrieva, 2018). These and other peculiarities make hypersaline waters polyextremal in nature. At present, the dependence of animal species richness on salinity is well studied in freshwater and marine reservoirs (Khlebovich, 1974, 2012; Khlebovich and Aladin, 2010; Alimov et al., 2013). Despite numerous studies (Moore, 1952; Hedgpeth, 1959; Hammer, 1986; Britton and Johnson, 1987; Zhao and He, 1999; Pinder et al., 2005; Timms, 2009), the question of a dependence of animal species richness on salinity is still insufficiently studied for hypersaline waters. The latest review (Sacco et al., 2021) demonstrated that the total number of all taxa in the hypersaline waters of the world decreases with an increase in salinity of  $>35\text{ g/L}$ . The effect of salinity on species richness is not the same in different taxa. For example, the portion of crustaceans in the total species abundance in the diverse reservoirs of the Mediterranean region increases with an increase in salinity, while that of insects, on the contrary, decreases (Boix et al., 2007).

The aim of this work is to detect how salinity in a hypersaline range can limit the taxonomic richness of crustaceans and test two previously formulated hypotheses: the first is that the contribution of crustaceans to the total species richness of invertebrates in water reservoirs increases with an increase in salinity; the second is that the dependence of the species richness on water salinity is quite reliably approximated by regression equations, but the equation parameters are not the same for different taxa of crustaceans.

## MATERIALS AND METHODS

In addition to the results of our own studies of the fauna of hypersaline water reservoirs, we used data from 203 sources found, for the most part, using a Google Scholar search system <https://scholar.goo->

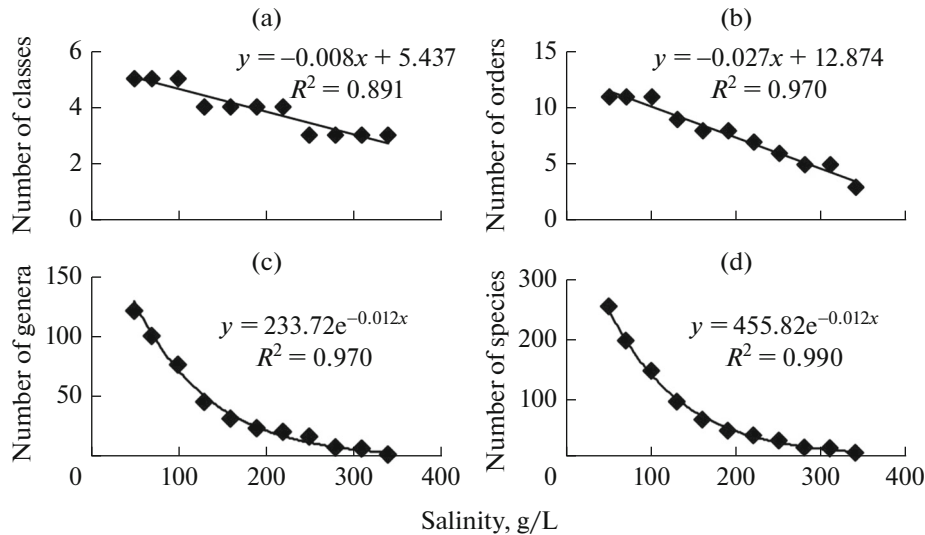
[gle.com](https://scholar.google.com) (Anufrieva, 2022). Different combinations of the key terms “hypersaline/hyperhaline” + “taxon name” (for example, “Crustaceans”, “Copepods”, etc.) were used in the search. As a result, data were obtained on crustacean species in heterogeneous hypersaline habitats (lakes, lagoons, ponds, estuaries, etc.) in all continents (except for Antarctica) in  $>300$  reservoirs around the world (Anufrieva, 2022). Previously, data of the authors on the number of species in all types of animals found for different salinity ranges were published with a map for the main regions of study on hypersaline waters (Sacco et al., 2021).

Common statistical approaches were used in data analysis. The calculation of means,  $CV$  coefficients of variation,  $R$  correlation,  $R^2$  determination,  $p$  levels of significance, and parameters of regression equations was carried out in MS Excel 2007. When calculating the parameters of the equations, data on 259 species of crustaceans were used.

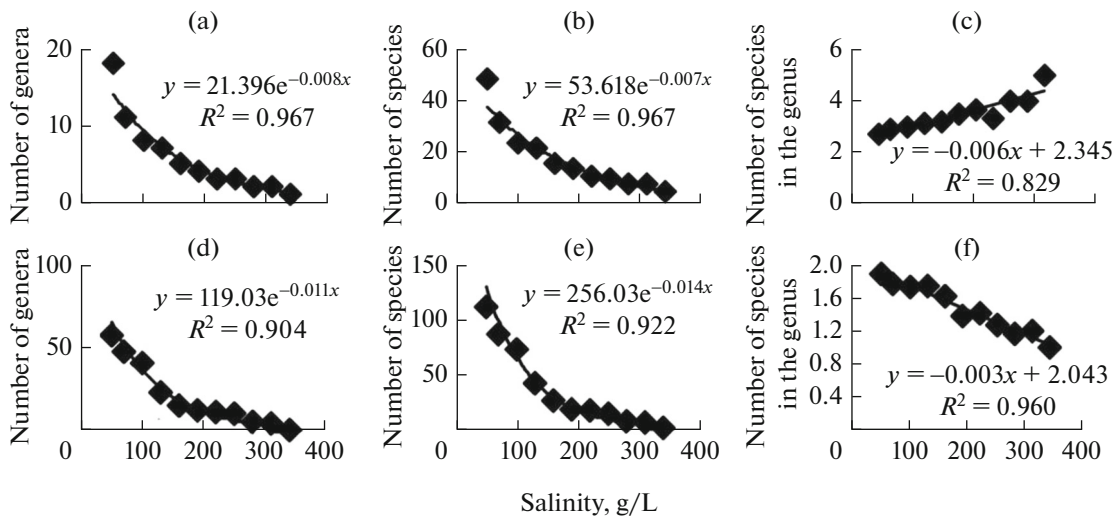
## RESULTS AND DISCUSSION

In total, animals belonging to 12 types, 25 classes, 83 orders, 455 genera, and 809 species were found around the world in the range of salinity from 35 to  $50\text{ g/L}$  (Sacco et al., 2021). Up to 49% of all these species belong to the type Arthropoda (Crustacea and Insecta). The analysis of the entire array of available data demonstrated that, with an increase in salinity, the number of classes and orders of the Crustacea subtype decreases linearly; the number of genera and species decreases exponentially (Fig. 1). With an increase in salinity by  $30\text{ g/L}$ , the number of classes of crustaceans decreases on average by 4% ( $CV = 0.100$ ), orders by 11% ( $CV = 0.142$ ), genera by 29% ( $CV = 0.239$ ), and species, by 29% ( $CV = 0.186$ ). The average number of species in the genus in the entire range of salinity was  $\sim 2$  ( $CV = 0.110$ ). No single trend of change in this index with an increase in salinity was detected.

**Class Branchiopoda.** In the range of salinity from 35 to  $250\text{ g/L}$ , two orders (Anostraca and Anomopoda (superorder Cladocera)) were noted; with salinity from 251 to  $>310\text{ g/L}$ , one order was found (Anostraca). The number of genera and species decreases exponentially with an increase in salinity (Fig. 2). The exponent for genera is  $-0.008$  and, for species,  $-0.007$  (Figs. 2a–2c); that is, a decrease in the number of genera and species is almost the same with an increase in salinity. With an increase in salinity by  $30\text{ g/L}$ , the number of genera decreases on average by 24% ( $CV = 0.210$ ); the number of species decreases by 20% ( $CV = 0.150$ ). The calculation demonstrated that the average number of species in the genus in the entire range of salinity reaches 3.5 ( $CV = 0.186$ ); at the same time, the value significantly increases with an increase in salinity from three to five (Figs. 2a–2c). Such an unusual type of dependence is associated with the fact that the number of genera decreases somewhat faster than the number of species. It should be noted that, if the num-



**Fig. 1.** Dependence of the number of classes (a), orders (b), genera (c), and species (d) of the Crustacea subtype on salinity (based on data for 259 species).



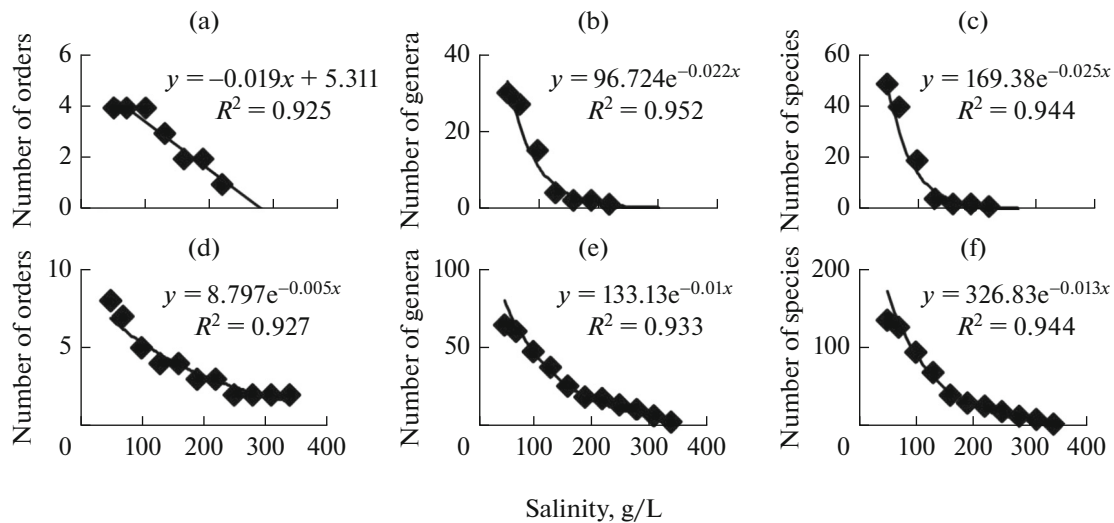
**Fig. 2.** Dependence of the number of genera (a, d), species (b, e), and average number of species in the genus (c, f) on salinity in Branchiopoda (a–c) (based on data for 49 species) and Copepoda (d–f) (according to data for 112 species).

ber of Anomopoda species strongly decreases with an increase in salinity and only one species *Moina salina* Daday, 1888 remains at salinity >220 g/L, then the number of species for Anosrtaca changes little, especially in the genera *Artemia* and *Parartemia*.

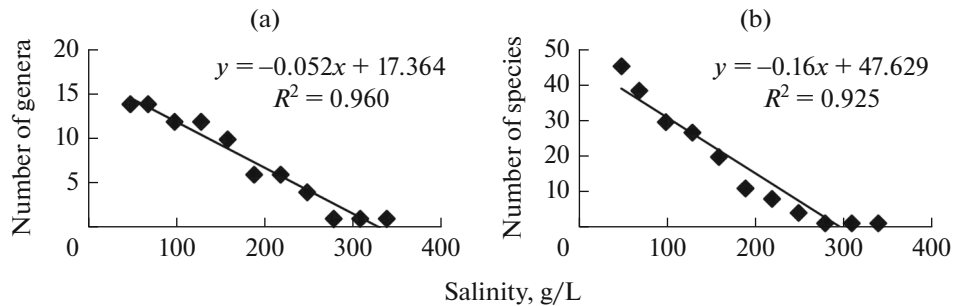
**Class Copepoda.** In the range of salinity 35–310 g/L, three orders (Calanoida, Cyclopoida, and Harpacticoida) were noted; at salinity >310 g/L, there was one order (Harpacticoida). The number of genera and species decreases exponentially with an increase in salinity (Figs. 2d–2f). With an increase in salinity by 30 g/L, the number of genera decreases on average by 28% ( $CV = 0.315$ ); the number of species decreases by 32%

( $CV = 0.335$ ). The calculation demonstrated that the average number of species in the genus in the entire range of salinity is 1.5 ( $CV = 0.202$ ) and gradually decreases significantly with an increase in salinity from two species to one (Figs. 2d–2f). At salinity from 310 to 360 g/L, only one species (*Cletocamptus retrogressus* Shmankevitch, 1875) was noted (reservoirs of Europe and Asia).

**Class Malacostraca.** With an increase in salinity, the number of orders decreases linearly; the number of genera and species, decreases exponentially (Figs. 3a–3c). With an increase in salinity by 30 g/L, the number of genera decreases on average by 38% ( $CV = 0.445$ )



**Fig. 3.** Dependence of the number of orders (a, d), genera (b, e), and species (c, f) on salinity of the class Malacostraca (a–c) (based on data for 49 species) and the subtype Hexapoda (d–f) (based on data for 135 species).



**Fig. 4.** Dependence of the number of genera (a) and species (b) of the class Ostracoda on salinity (based on data for 46 species).

and the number of species by 42% ( $CV = 0.480$ ). In the range of salinity from 35 to 130 g/L, the average number of species in the genus decreases with an increase in salinity from two species to one ( $R = 0.991$ ;  $p = 0.0005$ ); at a higher salinity of up to 200 g/L, only one species remains (*Gammarus aequicauda* (Martynov, 1931)).

**Class Thecostraca.** In the range of salinity 35–80 g/L, only three species were found that belong to two genera of the Balanomorphia order (*Amphibalanus amphitrite* (Darwin, 1854), *A. eburneus* (Gould, 1841), and *Fistulobalanus pallidus* (Darwin, 1854)).

**Class Ostracoda.** In the entire range of salinity, a single order (Podocopida) was noted. With an increase in salinity, the number of genera decreases linearly; the number of species decreases exponentially (Fig. 4). With an increase in salinity by 30 g/L, the number of genera decreases on average by 18% ( $CV = 0.304$ ) and the number of species by 27% ( $CV = 0.325$ ). In the range of salinity 35–250 g/L, the average number of species in the genus decreases with an increase in salinity from three to one species ( $R = 0.99$ ;  $p =$

0.0005); at a higher salinity 221–325 g/L, one species remains (*Eucypris mareotica* (Fischer, 1855)).

**Subtype Hexapoda.** In the entire range of salinity, only one class (Insecta) was noted. The number of orders, genera, and species decreases exponentially with an increase in salinity (Figs. 3d–3f). The total number of orders, genera, and species of Crustacea in all ranges of salinity exceeds those of Hexapoda: the number of orders on average by 2.2 times ( $CV = 0.237$ ), genera 1.4 times ( $CV = 0.174$ ), and species 1.8 times ( $CV = 0.343$ ).

The given data convincingly confirm the hypothesis that a dependence of the number of species on water salinity can be quite reliably described by regression equations, but their parameters are not the same for different taxa of crustaceans. With an increase in salinity, the contribution of different taxa to the total species richness of the fauna changes (Table 1).

With an increase in salinity, the contribution of Arthropoda species to the total species richness of animals of hypersaline waters, as expected (hypothesis 1), increases from 49 to 100%; the contribution of Crus-

**Table 1.** Contribution of representatives of different taxa to the species richness of animals from hypersaline waters

Taxon	Salinity, g/L										
	35–50	51–70	71–100	101–130	131–160	161–190	191–220	221–250	251–280	281–310	>310
Contribution of Arthropoda to the total number of all animal species, %											
Arthropoda	49	54	57	76	82	87	90	90	90	92	100
Contribution of individual subtypes of Arthropoda to the total number of Arthropoda species, %											
Chelicerata	<1	<1	0	0	0	0	0	0	0	0	0
Crustacea	66	61	61	58	62	61	60	61	57	65	78
Hexapoda	34	39	39	42	38	39	40	39	43	35	22
Contribution of individual Crustacea classes to the total number of all Crustacea species, %											
Branchiopoda	19	16	16	23	25	31	30	36	50	53	71
Copepoda	43	44	49	44	41	40	46	50	44	40	14
Malacostraca	19	20	13	4	3	4	3	0	0	0	0
Thecostraca	1	1	1	0	0	0	0	0	0	0	0
Ostracada	18	20	20	28	31	24	22	14	6	7	14

tacea species to the total species richness of Arthropoda increases from 66 to 78%; and the contribution of Branchiopoda to the species richness of Crustacea increases from 19 to 71%. From this, it can be concluded that there are certain patterns of change not only in the overall species richness of animals (particularly, crustaceans) with an increase in salinity, but also in the structure of the fauna. The presence of dormant stages that can maintain viability in the periods incompatible with active life is one of the factors that provide a success of crustaceans in hypersaline reservoirs (Shadrin et al., 2015).

Salinity should be considered an EF. EFs are non-random factors that narrow the range of possible variants of species sets (Chessman and Royal, 2004; Díaz et al., 2007; Shadrin et al., 2019). The composition of local communities is determined by two main things: the possibility of species entering the reservoir due to a settlement and filtering selection by a complex of abiotic and biotic factors of the ecosystem (Menéndez-Serra et al., 2023). The processes of passive and active settlement are random, often depending on rare climatic events (Anufrieva and Shadrin, 2018). The presence of EFs limits the possibility of the existence of a particular species in a particular reservoir and leads to the formation of a more predictable species composition (Kraft et al., 2015). The realization of such a possibility in a particular reservoir is determined by the totality of abiotic and biotic factors. Biotic relationships play a major role in a relatively comfortable marine and freshwater environment (Ivlev, 1955; Dgebuadze et al., 2008). In relatively extreme conditions, the factor providing the extreme nature of the environment begins to play a role of a hard EF, significantly limiting possible variants of the species composition (Shadrin et al., 2019; Chen et al., 2022). Thus, salinity is not the main factor determining the species richness and composition of the fauna in hypersaline reservoirs of Crimea in the range 35–120 g/L; the totality of all other factors (temperature mode, oxygen concentration, etc.), first and foremost

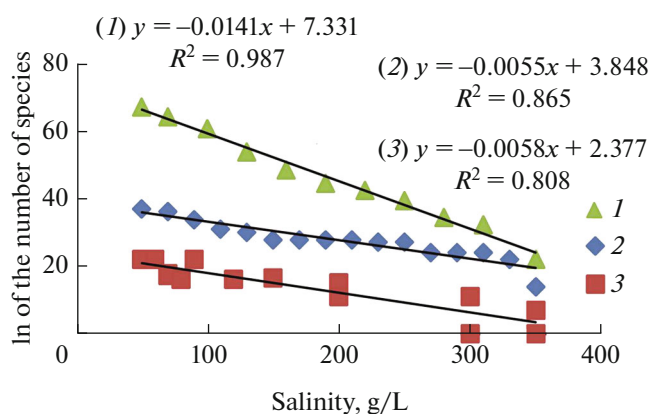
biotic (reservoir productivity, predation, competition, etc.), plays a more important role, and salinity itself begins to play the role of a hard EF only at higher values (Shadrin and Anufrieva, 2018; Shadrin et al., 2019; Anufrieva et al., 2022).

The quantitative analysis of a dependence of the species richness on salinity in hypersaline reservoirs for three spatial scales (a specific reservoir, reservoirs of Crimea, and global) demonstrated that the highest coefficient of determination was for a global scale and the lowest was for a specific reservoir (Fig. 5). Consequently, the association between the number of species with salinity and its role as an EF decreases with a decrease in the spatial scale. This is a general pattern: the larger the spatial scale of a species pool of organisms, the greater the role played by EF during its formation (Chessman and Royal, 2004; Chalmandrier et al., 2013). For example, we consider the ratio of regional and local scales. It can be said that there is a kind of filtration of species from a regional pool into separate communities of reservoirs (Sukhikh and Lazareva, 2022).

In this case, along with EF, established biotic relationships in a given particular reservoir begin to play a significant role (Leibold et al., 2010; Bello et al., 2013; Bruno et al., 2016).

## CONCLUSIONS

An increase in salinity above 35 g/L decreases the comfort of the environment, acting as a filter limiting the composition of the species that can exist in the reservoir. With an increase in salinity, a potential taxonomic richness decreases. Both hypotheses stated in the aim of the work were confirmed. In each individual reservoir at salinity <120 g/L, the selection of the species from this potentially possible set depends, first and foremost, on biotic relationships, as well as on a number of abiotic factors (temperature, oxygen concentration, etc.).



**Fig. 5.** Dependence of the number of species on salinity at different spatial scales ((1) global scale, (2) all hypersaline reservoirs of Crimea, and (3) in an individual Crimean hypersaline lake).

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### COMPLIANCE WITH ETHICAL STANDARDS

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

**Statement on the welfare of animals.** This article does not contain any studies involving animals performed by any of the authors.

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