

Review

# Salinity-Dependent Species Richness of Bacillariophyta in Hypersaline Environments

Daria Balycheva , Elena Anufrieva \* , Raisa Lee, Alexander Prazukin and Nickolai Shadrin 

A.O. Kovalevsky Institute of Biology of the Southern Seas of RAS, 2 Nakhimov ave., 299011 Sevastopol, Russia; dashik8@gmail.com (D.B.); raisa-lee@yandex.ru (R.L.); prazukin@mail.ru (A.P.); snickolai@yandex.ru (N.S.)

\* Correspondence: lena\_anufrieva@mail.ru; Tel.: +7-(8692)-54-55-50

**Abstract:** Hypersaline habitats are among the most polyextreme habitats on Earth, but they contain a rather large diatom species diversity. A review of the diatom species' richness was made on three scales: 1. a separate lake in Crimea; 2. all hypersaline waters in Crimea; and 3. the world totality as a whole. In total, 51 species were found in Lake Chersonesskoye during sampling from 2004 to 2018. In ten Crimean hypersaline lakes, 91 species were noted in total. All diatom species found in the studied hypersaline water bodies of the world belong to 458 species, which is 2.7% of the total number of known species of Bacillariophyta. In all three scales, the similarity of the species' composition between water bodies as well as studied periods was not found. Most of all the identified species were found only in one of the studied water bodies, and only 59 species (13% of the total list) were found in more than three water bodies. An analysis showed that no more than 40% of the species that exist in hypersaline waters have been identified on a global scale. The diatom shell nanostructure from hypersaline waters has specific peculiarities that may be valuable for some technological applications. The knowledge of diatoms in hypersaline waters not only has pure scientific importance but also covers some needs of bio- and nanotechnologies.

**Keywords:** diatoms; hypersaline habitats; salinity; similarity; species' composition



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## 1. Introduction

Phylum Bacillariophyta Karsten, 1928, which is diverse and has a long evolutionary history, according to Algalbase [1], currently includes more than 17 thousand taxa of diatoms inhabiting a wide variety of habitats, including extreme ones [2–5]. Hypersaline environments that exist on all continents of our planet are among the most polyextreme habitats on the planet; however, they contain a rather large species diversity of organisms in different taxa [6,7]. Diatoms are no exception, many species of which can inhabit this inhospitable environment on different continents, which has been noted for a long time [7–11].

Life in a hypersaline environment requires specific adaptations; in unicellular organisms, including Bacillariophyta, this is primarily due to the accumulation of high concentrations of organic osmolytes, compatible, metabolic, and counteracting cytoprotectants in cells [12–15], and/or the creation of an exopolysaccharide matrix around cells [16–18]. For example, experiments with *Phaeodactylum tricornutum* Bohlin, 1898, showed that the species produced more exopolysaccharides in a hypersaline environment than in a less salty environment [16]. The adaptation of diatoms to high salinity occurs as a complex up-regulation of the metabolome, and specific secondary metabolites are produced [19,20]. Living in an extreme environment and being primary producers, diatoms also synthesize unique compounds that not only affect the metabolism of ecosystems as a whole but are also of undoubted interest to various industrial sectors [18,21,22]. The study of diatom diversity in hypersaline waters is therefore of undoubted value, not only for the development of various branches of biology but also for aquaculture, biotechnology, biodiesel production,

pharmacology, and the cosmetics industry [14,18,22]. To solve the problem of a lack of food and other resources for the growing human population, we need to develop aquaculture. However, the development of aquaculture, including diatoms, under the growing shortage of fresh water, makes the task of developing hypersaline aquaculture of current interest [23]. This can contribute to better general environmental management and reduce fresh water use. For the development of the industry of diatom cultivation in hypersaline waters, it is necessary to determine the list of species that are suitable for this.

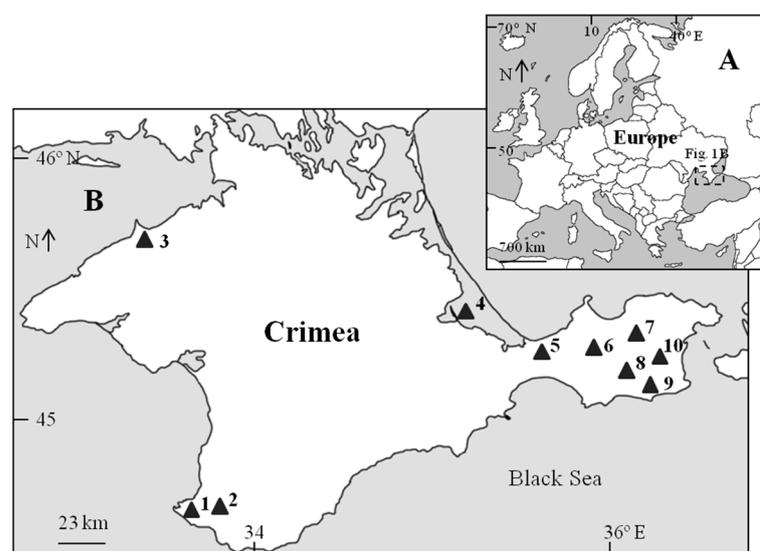
In addition, the study of diatoms in hypersaline water bodies is important for paleoreconstruction of the history of a particular water body, its origin, and hydrology [9,24,25].

The study of diatoms in hypersaline water bodies has received attention for more than 100 years [8,9,26–28], and by now, quite a lot of data on Bacillariophyta from various regions of our planet have been accumulated. However, despite this, there are still no answers to the next questions. How many of their species exist in hypersaline waters in total? What percentage of all the known diatoms are found and able to live in hypersaline water bodies? What factors and how do they influence the formation of the diatom flora in hypersaline habitats? Does their species' composition fundamentally differ from that of the seas and freshwater reservoirs? What marine and freshwater species can adapt to life in high salinity, or do these water bodies have their own unique flora?

The objectives of this work are as follows: 1. to compile a total list of Bacillariophyta species in hypersaline water bodies in the world based on modern nomenclature as full as possible; 2. to prove or disprove hypotheses that (a) there is a significant quantitative dependence of species richness on salinity but (b) salinity is not the only significant factor determining species richness and composition of diatoms; and 3. to show that the study of diatoms in hypersaline waters has both scientific importance and applications for bio- and nanotechnologies.

## 2. Materials and Methods

This work reviews the literature and our own data on diatoms from hypersaline water bodies of different regions in the planet including our new, previously unpublished data on the most studied hypersaline lake: Lake Chersonesskoye (Crimea) (Figure 1, Table 1).



**Figure 1.** The hypersaline water bodies in Crimea, data of which were used in this review (1—Lake Chersonesskoye; 2—small lake near Bay Cozachyia; 3—Lake Bakalskoye; 4—Lagoon Sivash (the Sea of Azov); 5—Lake Achi; 6—Lake Marfovskoye; 7—Lake Shimakhanskoye; 8—Lake Kirkoyashskoye; 9—Lake Koyashskoye; 10—Lake Tobechikskoye). (A)—Europe scale; (B)—local scale.

**Table 1.** The hypersaline water bodies in different regions, data of which were used in this review.

№	Water Body	Salinity, g·L <sup>-1</sup>	The Number of Found Diatom Species	References
1	Lake Chersonesskoye, Crimea	27–340	51	(New data, [10,29,30])
2	Lagoon Sivash, The Sea of Azov, Crimea	140–200	27	[31]
3	Lake Bakalskoye, Crimea	60–110	57	[10]
4	Small lake near Bay Cozachyia, Crimea	20–50	6	[10]
5	Lake Marfovskoye, Crimea	270–300	10	[10]
6	Lake Koyashskoye, Crimea	240–350	10	[10]
7	Lake Tobechikskoye, Crimea	160–290	20	[10]
8	Lake Shimakhanskoye, Crimea	30–360	3	[10]
9	Lake Kirkoyashskoye, Crimea	16–360	1	[10]
10	Lake Achi, Crimea	116–158	0	[10]
11	Lagoon Kuyalnitsky Liman, NW coast of the Black Sea	56–285	39	[32,33]
12	Kara-Bogaz-Gol Bay, Caspian Sea	40–272	67	[34]
13	Sal-Ilets Lake (Razval, Dunino, and Tuzluchnoye), Orenburg Oblast, Russia	110–290	12	[35,36]
14	The Aral Sea	82–130	83	[37–39]
15	Hypersaline lakes of Spain	40–174	19	[40,41]
16	La Poza Pond, Mexico	55–105	49	[42]
17	Hypersaline evaporation ponds and tidal channels of Guerrero Negro Baja, California Sur, Mexico	40–130	19	[12]
18	Experimental Solar Ponds, Dead Sea	58–128	11	[43]
19	Lakes and streams from south-west Western Australia	50–156	43	[25]
20	Vermelho lagoon, Brazil	50–63	23	[44]
21	Araruama Lagoon, Brazil	40–69	45	[45]
22	Great Salt Plains, USA	159–311	31	[46]
23	Great Salt Lake, USA	>200	56	[9]
24	Mono Lake, USA	95	25	[47]
25	Salt pans of the southern coasts of India	98–150	56	[48]
26	Salterns from Korea	65–324	41	[49]
27	Megalon Embolon solar saltworks, northern Greece	60–144	23	[50]
28	Lakes from the Kamloops and Cariboo/Chilcotin regions of British Columbia, Canada	58–369	14	[24,51]
29	Hypersaline lakes in the Rauer Islands, eastern Antarctica	50–66	17	[51]

The main results on diatoms in Lake Chersonessus were published previously [10,29,52]. Additionally, to the published data, here the authors have also used their own new data, which were obtained due to a more detailed analysis of microalgae in bottom sediments and the green algae *Cladophora* mats, which were taken in different seasons of 2017–2018 [29,53]. The methods of collection and processing of samples have been previously published [29,53]; due to this, they are not described here. New analyses of our old samples included the following: microphotography and determination of diatoms were carried out under an Olympus BX53F light microscope using a  $\times 100$  immersion lens (Olympus immersion oil  $n = 1.518$ ) with a Jenoptik ProgRes Gryphax Arktur camera with Gryphax Arktur software. In addition, to analyze the fine structures of diatom shells, they were photographed under a Hitachi SU3500 scanning electron microscope (magnification factor: 5–300,000; resolution: up to 3 nm; depth of field: 0.5 mm). To determine the species of diatoms, their shells were cleaned of organic matter by the “cold” and “hot” methods, and permanent preparations were made according to the method described [36]. The species identification was made using [32,54–61], as well as numerous articles.

A detailed description of Lake Chersonesskoye was also provided before [29,53,62]; due to this, information about it will be briefly given here. It is a hypersaline marine lake with an area of 0.05 km<sup>2</sup> and is located on the Black Sea coast (near Sevastopol, Crimea), separated from the sea by a narrow boulder–pebble embankment. Its average depth is about 0.4 m with a maximum of >1.5 m. There is high spatial and temporal salinity variability, ranging from 27 to 340 g L<sup>-1</sup>.

Published data were searched by various sets of keywords (hypersaline and algae; hyperhaline and algae; hypersaline and Bacillariophyta; hyperhaline and Bacillariophyta; hypersaline/hyperhaline lakes; hypersaline/hyperhaline lagoons) in various search engines such as Scholar Google, ResearchGate, eLibrary, Scopus, Web of Science, and ScienceDirect. This review covers 29 hypersaline water bodies or their groups from different regions (Table 1). The species indicated in the lists as sp. were not taken into account. For species designated in the literature as cf. or sp. aff, this status was saved. Taxonomy and nomenclatural names of microalgae are given following [1]. Ecological and phytogeographic characteristics of microalgae were determined using [1,60,63].

The parameters of the regression equations and the correlation coefficient were calculated in the program MS Excel 2010. The similarity of species' compositions of microalgal communities between lakes and regions was evaluated by the Jaccard and Czekanowski–Sørensen–Dice similarity indices [64]:

$$KJ = c/(a + b - c), \quad (1)$$

$$KCSD = 2c/(a + b), \quad (2)$$

where KJ and KCSD are the Jaccard and Czekanowski–Sørensen–Dice similarity coefficients, respectively; c is the number of species common to both plots or periods; a is the number of species found in the first case; b is the number of species found in the second case.

The threshold values used to conclude that the species' composition is similar/dissimilar are 0.42 (Jaccard) and 0.59 (Czekanowski–Sørensen–Dice) [64].

### 3. Results and Discussion

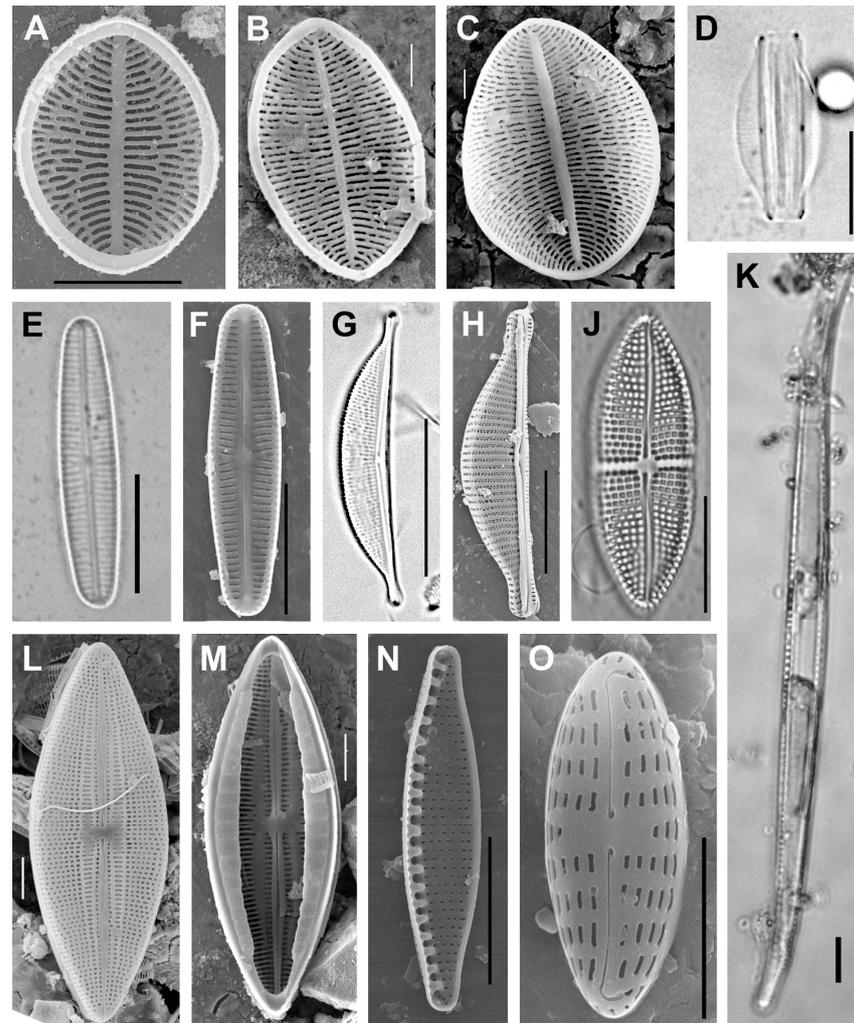
#### 3.1. The Diatom Species' Composition in the Single Lake Chersonesskoye

During 2004–2018, the diatom species' composition was studied in Lake Chersonesskoye, which is probably the most studied lake on this issue worldwide. According to our own data and the literature data for this lake, we summarized the species' composition of not only diatoms but also other microalgae. To date, a total of 99 species of microalgae have been found in it: 51 species belong to Bacillariophyta, 20 to Miozoa, 8 to Cyanobacteria, 9 to Chlorophyta, 6 to Haptophyta, 2 to Cryptophyta, and 2 to Euglenozoa. To calculate these values, previously published data [10,29,30,53] were supplemented by 22 new species not included in published studies after their additional identification in earlier collected samples [29,31]. In plankton, 61 species of microalgae were noted, and 62 species in mats of the green filamentous algae *Cladophora* spp. and bottom sediments were noted. Diatoms are an almost diverse group in the microphytobenthos of Lake Chersonesskoye, including 51 species. Among them, 11 species belong to the genus *Nitzschia*, 6 species belong to *Navicula*, and 5 species belong to *Cocconeis* (Table S1). In plankton, most of the species (19) were dinophytes. The calculated Jaccard and Czekanowski–Sørensen–Dice similarity coefficients between plankton and benthos values were 0.21 and 0.12, respectively. This confirms their difference, despite the shallow depth and strong mixing of the lake. In our studies, 28 species of microalgae were identified only at the genus level [10,29,30,53]. Consequently, not all species existing in the lake have already been identified. The number of species found increased with the number of examined samples. In the case of Lake Chersonesskoye, as shown earlier [31], this relation can be described by a power equation ( $R = 0.964$ ,  $p = 0.0005$ ):

$$K = 5.520 \times N^{0.612}, \quad (3)$$

where K is the number of species found; N is the number of analyzed samples.

The calculation by Equation (3) showed that when processing 500 samples, approximately 142 microalgae species, including 126 diatoms, in total can be found in the lake. 9 species of diatoms were noted in all periods of the study: *Achnanthes brevipes* C. Agardh, 1824; *Cocconeis kujalnitzkensis* Gusliakov et Gerasimiuk, 1992; *Dickieia subinflata* (Grunow) D. G. Mann 1994; *Halamphora coffeiformis* (C. Agardh) Mereschkowsky, 1903; *Halamphora hyalina* (Kützing) Rimet et R. Jahn in Rimet et al., 2018; *Mastogloia braunii* Grunow, 1863; *Navicula ramosissima* (Agardh) P. T. Cleve, 1895; *Nitzschia frustulum* (Kützing) Grunow in Cleve et Grunow, 1880; and *Nitzschia sigma* (Kützing) W. Smith, 1853 (Figure 2).



**Figure 2.** The most common diatom species in Lake Chersonnesskoye (SEM photos): (A–C)—*Cocconeis kujalnitzkensis*; (D)—*Halamphora hyalina*; (E,F)—*Dickieia subinflata*; (G,H)—*Halamphora coffeiformis*; (J)—*Achnanthes brevipes*; (K)—*Nitzschia sigma*; (L,M)—*Mastogloia braunii*; ((L)—external valve view; (M)—internal valve view); (N)—*Nitzschia frustulum*; (O)—*Navicula ramosissima*. Scale bar: (B,C,L)—2  $\mu\text{m}$ ; (O)—3  $\mu\text{m}$ ; (A,H,M,N)—5  $\mu\text{m}$ ; (D–F), K—10  $\mu\text{m}$ ; (G,J)—20  $\mu\text{m}$ .

Among them, only three species, *A. brevipes*, *C. kujalnitzkensis*, and *H. coffeiformis*, were found in all the samples. These species were also encountered by us in the microphytobenthos of Lagoon Sivash [53] and other saline lakes in the Crimea [10]. Even though the nine species mentioned above were found in all the periods, the total species' composition varied greatly in different periods of research; the calculated values of the coefficients of species' similarities (Equations (1) and (2)) were below the critical ones. Such high variability in the algae species' composition in the lake, as well as in other hypersaline water bodies, can probably be explained by the fact that the species' composition is determined by the

interaction of many environmental factors, among which the random factor also plays an important role [28,46,49,53].

In Lake Chersonesskoye, according to [1,60], marine microalgae species predominate (40%), and marine brackish water species account for 17%. The predominance of marine species can be easily explained by the fact that the lake is constantly fed by seawater due to its filtration through the boulder barrage and the splash of seawater into the lake during storms. In total, in the Black Sea, the salinity of which is 17–19 g L<sup>-1</sup>, more than 1000 species of benthic microalgae have been found to date [63], and 47 of them are common with Lake Chersonesskoye, i.e., accounting for almost half of the total species found in the lake. There are more than 200 species of microalgae in Bay Cozachyia (the Black Sea), which is closest to the lake [63], 33 of which are common with the lake. Only 15–16% of species that can enter lakes from adjacent marine waters can exist in the lake. The presence in the hypersaline lake of a sufficiently large number of species (27% of all the species found), which are considered freshwater [1,60], probably requires a revision of their status. The authors think that, at least, it is incorrect to attribute to freshwater species those that are massively found in hypersaline waters. In general, the ecological classification of species concerning salinity cannot be considered adequately due to this classification, which was practically made up without taking into account data on hypersaline waters.

### 3.2. The Diatom Species' Composition in the Crimean Hypersaline Lakes

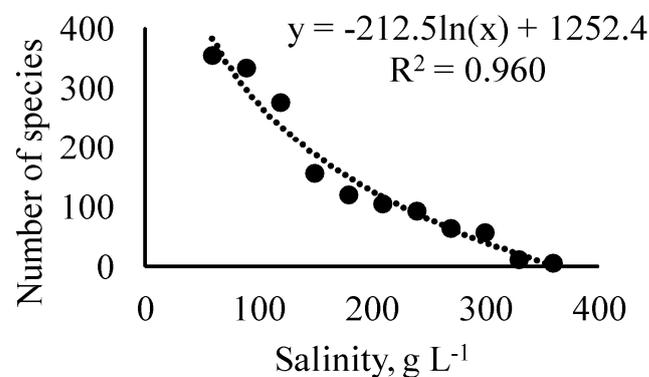
In the Crimean Peninsula (Figure 1), the largest in the Black Sea (area 27,000 km<sup>2</sup>), there are a large number of hypersaline lakes (more than 50) and the world's largest hypersaline lagoon, Sivash [31,65,66], but the diatom species' composition was studied in only 10 lakes and the lagoon (Table 1). In total, 91 species of diatoms were found (Table S1), while 33 species were not recorded in any other hypersaline water bodies in the world. The highest diatom species' richness among the Crimean water bodies was found in Lake Bakalskoye (57 species), Lake Chersonesskoye (51 species), and Lagoon Sivash (27 species). Only in Lake Achi, diatoms were not found in 3 taken samples. When comparing the diatom species' composition in the Crimean lakes using Jaccard and Czekanowski–Sørensen–Dice coefficients, no similarity was found, and the values of both coefficients were less than critical values. Despite the geographical proximity of the Crimean lakes, the diatom species' composition differs between them; it is unique for each lake. However, there is a complex of species that are found in half or more of the Crimean lakes (Table S1). The following species were recorded in six lakes: *A. brevipes*, *H. coffeiformis*, *Navicula pennata* var. *pontica* Mereschkowsky, 1902; in five lakes, *Rhopalodia musculus* (Kützing) O. Müller, 1900; in four lakes, *C. kujalnitzkensis*, *C. placentula* var. *euglypta* (Ehrenberg) Cleve, 1895; *C. scutellum* Ehrenberg, 1838; *Hantzschia petitiiana* (Grunow) Grunow in Cleve et Grunow, 1880; *M. braunii*, *M. pumila* (Cleve et Möller) P.T. Cleve, 1895; *Nitzschia sigma* (Kützing) W. Smith, 1853; and *Tabularia tabulata* (C. Agardh) Snoeijis, 1992.

### 3.3. Diatoms in the World's Hypersaline Waters

The complete list of diatom species noted in the studied hypersaline water bodies of the world (Table 1) includes 458 species (Table S1), which is 2.7% of the total number of known species of Bacillariophyta [1]. This list does not cover all the existing diatom species' richness, if only because it does not include species defined only to the genus level [67], as well as dubious taxon names [68]. It can be concluded that the diatom flora in the hypersaline water bodies is still insufficiently studied. Let us assume that Lake Chersonesskoye is one of the most studied hypersaline water bodies in the world in terms of diatom species' richness, and only about 40% of species have been identified in it, as shown above. It is logical to conclude that no more than 40% of the species that exist in hypersaline waters have been identified on a global scale. Consequently, we can assume that no more than 7% of the total Bacillariophyta species existing in nature can exist in hypersaline habitats.

The largest number of diatom species was found in the hypersaline water bodies of Russia (218 species), of which 91 species were in Crimea (Table S1). In the Aral Sea, 139 species were found; in the USA, 81 species were found, including in the lakes of the Great Salt Plains, where 31 species were found; in Mono Lake, where 25 species were found; and in the Great Salt Lake, where 56 species were found; in Brazil, 60 species were found, including in the Araruama Lagoon, where 45 species were found, and in Lagoon Vermelha, where 23 species were found. In general, the number of species found in the studied water bodies varies from 1 (Lake Kirkoyashskoye) to 139 (Aral Sea). The following genera prevailed in the general list by the number of species: *Nitzschia*, 52 species; *Navicula*, 37; *Halamphora*, 22; and *Amphora*, 21 (Table S1).

In general, for hypersaline water bodies, a trend toward a decrease in the number of species with an increase in salinity was noted [6,12,28,48,49,69]. The data from Table S1 made it possible to quantitatively analyze the total species' richness depending on salinity. The number of species monotonously decreases with an increase in salinity (Figure 3). The dependence is highly significant ( $R = -0.980$ ,  $p = 0.0001$ ).



**Figure 3.** Dependence of diatom species' richness on their tolerated upper salinity limit at the global scale.

In a global comparison of the diatom species' composition between water bodies in different regions, the similarity of the species' composition was also not found. Such results of comparative analysis are expected due to the fact that most of all the identified species were only found in one of the studied water bodies (Table S1). Only 59 species of diatoms (13% of the total list) were found in more than three water bodies. In seven water bodies, *C. placentula* var. *euglypta*, *Mastogloia lanceolata* Thwaites ex W. Smith, 1856; *N. ramosissima*, *Nitzschia scalpelliformis* Grunow in Cleve et Grunow, 1880; and *Pleurosigma elongatum* W. Smith, 1852, were found; in seven, *Cylindrotheca closterium* (Ehrenberg) Reimann et Lewin, 1964; *M. pumila* (Cleve et Möller) P. T. Cleve, 1895; and *Tryblionella punctata* W. Smith, 1853, were found; in nine, *A. brevipes*, *C. scutellum*, *Navicula salinarum* Grunow in Cleve et Grunow, 1880, were found; and in ten, *C. placentula* Ehrenberg 1838 var. *placentula*, *N. frustulum*, *N. sigma*, *Rhopalodia musculus* (Kützing) O. Müller, 1900, were found. Among the species found in more than three lakes, the most represented were the genera *Navicula*, *Nitzschia* (seven species), *Cocconeis* (five species), *Mastogloia*, *Rhopalodia*, and *Tryblionella* (three species). Thus, the species' composition of each water body can be considered unique. From this follows the obvious conclusion that salinity, up to a certain critical value, is not the main factor in the formation of the species structure of hypersaline water bodies. This has already been shown by the example of the spatiotemporal variability of the species' composition of diatoms for the individual water bodies, Sivash Bay [27] and Lake Chersonesskoye [49]. At the same time, salinity acts as an important ecological filter that limits the possibility of the existence of species in water bodies with different salinity levels. The realization of this possibility and the formation of the species structure of an individual water body depends on a whole variety of abiotic and biotic factors, including

the factor of chance, the position in the landscape, and the geological history of the water body [9,28,31,46,49,52,63].

There is currently growing interest in the use of diatoms for various applications [21]. One of the reasons for this is the value of secondary metabolites that are synthesized by diatoms for various goals. The different biologically active compounds are very valuable, among them are PUFA, antibiotics, enzyme inhibitors (to treat various diseases caused); other pharmacology active compounds, and toxins [70]. The nanostructured silica of diatom shells is also a very promising source of material for different technological applications [71,72]. The diatom cells are surrounded by a porous biosilica microshell of nanostructured morphology with pores sized in ten hundreds of nanometers and a large specific surface area of up to  $200 \text{ m}^2 \text{ g}^{-1}$  [71]. These characteristics are very similar to those of the technologically produced porous silica used in different nanotechnologies. Some other valuable properties of the diatom biosilica are also biocompatibility, tailored surface chemistry, chemical inertness, and thermal stability [71]. The worldwide diatoms' availability combined with their low cost make their nanostructured silica an attractive source for new materials in the fields of photonics, nanoengineering, biosensing, drug delivery, regenerative medicine, and others [71–74]. As shown above, in hypersaline waters, there is a rather high species diversity of diatoms, while individual species can reach very high biomass, up to more than  $200 \text{ g m}^{-2}$  of the bottom [10,29,31]. Existence in a harsh hypersaline environment requires a wide range of adaptations in diatoms, and not only biochemical ones, as mentioned above. Salinity is a very important factor influencing pore sizes and other silica shell properties, and, as an example, some diatom species have the double frustule in hypersaline media [26,27]. There are optimal shell pore sizes for different technological applications [75–78]. So, a diatom's shell nanostructure from hypersaline waters has specific peculiarities that may be valuable for some technological applications. Summarizing all the above, the authors concluded that knowledge of diatoms in hypersaline waters has not only pure scientific importance but also for diatom cultivation in hypersaline waters to cover some needs of bio- and nanotechnologies. Diatoms are a promising and valuable component of hypersaline aquaculture, the development of which can contribute to more sustainable water use [23]. Due to this, the ecology and biotechnological potential of high halotolerant diatoms must be studied deeper. For the transition to sustainable management of aquatic ecosystems, not only fundamental knowledge of biodiversity and ecosystem functioning is required, but also opportunities for the practical use of their bioresources to solve the problems of developing humanity.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/w15122252/s1>, Table S1: Diatoms of hypersaline water bodies of the world.

**Author Contributions:** Conceptualization, E.A. and D.B.; methodology, N.S.; formal analysis, E.A., N.S. and A.P.; investigation, D.B., E.A., R.L. and A.P.; writing—original draft preparation, N.S.; writing—review and editing, D.B., E.A., R.L., A.P. and N.S.; project administration, E.A.; funding acquisition, E.A. All authors have read and agreed to the published version of the manuscript.

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**Data Availability Statement:** All data used in this study are available upon request from the corresponding author.

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**Conflicts of Interest:** The authors declare no conflict of interest.

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