Salinity-Dependent Species Richness of Bacillariophyta in Hypersaline Environments

Subjects: Biodiversity Conservation

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Hypersaline habitats are among the most polyextreme habitats on Earth, but they contain a rather large diatom species diversity. The diatom species' richness was described 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.

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

1. Introduction

Phylum Bacillariophyta Karsten, 1928, which is diverse and has a long evolutionary history, according to Algabase [1], currently includes more than 17 thousand taxa of diatoms inhabiting a wide variety of habitats, including extreme ones [2][3][4][5]. Hypersaline environments that exist on all continents of 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][8][9][10][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][13][14][15], and/or the creation of an exopolysaccharide matrix around cells [16][17][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].

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][23][24].

2. 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. 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][25][26][27] were supplemented by 22 new species not included in published studies after their additional identification in earlier collected samples [25][28]. 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.

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.

Among them, only three species, *A. brevipes*, *C. kujalnitzkensis*, and *H. coffeiformis*, were found in all the samples. These species were also encountered by people in the microphytobenthos of Lagoon Sivash [27] 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 [27][29][30][31].

In Lake Chersonesskoye, according to [1][32], 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^{-1}, more than 1000 species of benthic microalgae have been found to date [33], 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 [33], 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][32], 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. The Diatom Species' Composition in the Crimean Hypersaline Lakes

In the Crimean Peninsula, the largest in the Black Sea (area 27,000 km^2), there are a large number of hypersaline lakes (more than 50) and the world's largest hypersaline lagoon, Sivash [28][34][35], but the diatom species' composition was studied in only 10 lakes and the lagoon. 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 petitiana* (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) Snoeijs, 1992.

4. Diatoms in the World's Hypersaline Waters

The complete list of diatom species noted in the studied hypersaline water bodies of the world 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 [36], as well as dubious taxon names [37]. It can be concluded that the diatom flora in the hypersaline water bodies is still insufficiently studied. Let people 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.

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][29][31][38][39]. 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. The dependence is highly significant ($R = -0.980$, $p = 0.0001$).

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 [40] and Lake Chersonesskoye [31]. 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][29][30][31][33][41].

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