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EXPERIMENTAL ARTICLES

Structure and Formation Properties of the Haloalkaliphilic Community of Lake Khilganta

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Abstract—The structural features of a cyanobacterial mat from Lake Khilganta (Southeastern Transbaikal Region) developing at different values of salinity and pH were determined based on our long-term investigation of the natural community, as well as results obtained during experimentation with its laboratory analogue. At water mineralization of 40–50 g/l, *Microcoleus chthonoplastes* and *Phormidium molle* play a key role in the formation of the cyanobacterial mat. As water mineralization increases, the diversity of cyanobacteria in the natural mat increases as well, reaches its maximum at 80 g/l NaCl, and decreases at 100 g/l. In the laboratory community, *Nodularia* sp. prevailed. It was able to form matlike structures within a broad pH range and at a salinity of up to 50 g/l NaCl. As the water mineralization level increased up to 100 g/l or higher, a replacement of the dominant complexes occurred both in the laboratory and natural communities: cyanobacterial species were substituted with green algae.

Keywords: Lake Khilganta, cyanobacterial mat, community structure, laboratory gradient.

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Numerous soda and saline lakes with different hydrochemical and biological characteristics are located in the Transbaikal Region [1, 2]. In the nearshore shallow basins and lagoons of some lakes, local development of benthic microbial biofilms (mats) was observed. In most cases, these microbial mats develop during a short time period and consist of thin ephemeral layers. An ordered structured mat was detected only in the shallow-water soda/saline Lake Khilganta. Lake Khilganta differs from the other lakes of the Transbaikal Region in the high mineralization level of its water. According to the physicochemical properties of the lake, as well as M.G. Valyashko's classification (1995), it belongs to saline lakes of the sodium–sulfate type. The results of investigations carried out over the last decade show that the climatic conditions in this region (significant daily and seasonal temperature fluctuations, little precipitation) affect the hydrologic and hydrochemical regimes of the lake, as well as result in structural and functional changes in the natural microbial community [3].

During recent years, both general and specific aspects of the structure and functioning of the microbial community of Lake Khilganta have received intense scientific attention [4–6].

The goal of the present work was to determine the effects of the main ecological factors (pH and mineralization) on the structure of the cyanobacterial community of Lake Khilganta under natural conditions and during a controlled experiment.

MATERIALS AND METHODS

Characterization of Lake Khilganta. Lake Khilganta is situated in the Transbaikal Region. It is nearly round in shape. The maximum area of the lake is 0.5 km^2; its maximal depth is 0.6 m. The water level in the lake depends on climatic conditions and is subject to significant fluctuations. Cyclic changes in the annual total precipitation were detected. The last complete cycle including the "dry" and "wet" phases took 34 years, from 1965 to 1998. Since 1999, a tendency toward a decrease in annual total precipitation has been detected, accompanied by a further increase in atmospheric temperature during summer as compared to the previous cycle [7]. During the "dry" phase, an increased level of water mineralization of shallow lakes (including Lake Khilganta) due to water evaporation was observed, as well as fluctuations in pH and alkalinity [5, 8]. The water level of the lake is susceptible to considerable fluctuations. However, the results obtained in the course of our 2006 expedition

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demonstrated that, even during dry seasons, water can be found at a depth of 40–60 cm.

Water and mat samples were collected in the spring and autumn seasons of 2001, 2004, 2006, and 2007. Mat samples for microbiological analyses were collected into sterile containers and stored at 4°C. The pH value of the water was measured with a portable pHep2 pH meter (Portugal). Total mineralization (TM) was determined with a portable TDS-4 refractometer/conductometer (Singapore).

To determine the species composition of phototrophic microorganisms, mat samples were fixed with 4% formalin. For microscopic examination of dried mat specimens, portions of the mat sample were ground to powder on microscopic slides. Then a 5% solution of hydrochloric acid was applied to the slides to remove carbonates. The slides were then examined under an Axiostar plus microscope (Carl Zeiss, Germany) at 1000× magnification.

For laboratory determination of the effect of pH and salinity (as NaCl) on the community of oxygenic phototrophs, dry mat samples collected in August 2006 during the lake drying-up phase were used. In the pH–mineralization gradient used, pH ranged from 7 to 11. The following NaCl concentrations were used (g/l): 0, 1, 5, 10, 20, 50, 100, 150, 200, 250, and 300. The pH values were adjusted with the relevant volumes of 10% solutions of sodium carbonate and bicarbonate (the solutions were sterilized separately in vials sealed with rubber stoppers); pH was measured with a Hanna Instrument pH 211 pH meter (Russia).

To obtain the cultures of phototrophic microorganisms, a dry mat sample was wetted and incubated for 5 days. The wet mat sample was ground in a porcelain mortar until homogeneous. Portions (1 cm^3) of the obtained specimen were placed in tubes with 9 cm^3 of sterile distilled water; the mixture was then thoroughly agitated. Portions (1.5 cm^3) of the resulting suspension were placed in 20-cm^3 serum vials with 15 cm^3 of nutrient medium with predetermined pH and salinity levels. In this experiment, we used a modified medium for *Microcoleus chthonoplastes* containing the following (g/l): K_2PO_4, 0.5; KCl, 0.5; Na_2SO_4, 2.0; $MgCl_2$, 0.5, $NaNO_3$, 1.5; and A5 trace element solution, 1 ml [9]. Phototrophic cultures were grown under laboratory conditions in a luminostat (2000 lx). All the preliminary work for the preparation of the experiment was carried out under sterile conditions. The duration of the experiment was 8 weeks. The number of phototrophic microorganisms was determined using appropriate geometric shape-to-volume relationships and expressed as a percentage.

The chlorophyll *a* content in the cells serving as an indicator of biomass yield, as well as the pigment composition, were determined on a Shimadzu UV-Mini spectrophotometer (Japan).

The representatives of *Bacillariophyta* were identified according to the manual by Zabelina et al. [10]; for identification of *Chlorophyta* species, the manuals by Dedusenko-Shchegoleva et al. [11], Moshkova and Hollerbach [12], and Palamar'-Mordvintseva [13] were used. Identification and classification of *Cyanoprocaryota* were carried out and verified according to Komárek and Anagnostidis [14, 15].

RESULTS AND DISCUSSION

Structure of the natural community. The cyanobacterial mat of Lake Khilganta discovered in 1995 during the high water period (mineralization 46 g/l) consisted of one species of eukaryotic algae (*Chlorella minutissima*) and four species of cyanobacteria (*Microcoleus chthonoplastes, Aphanothece salina*, and two *Phormidium* species) [4].

The further description of the structure of the natural mat is arranged in order of increasing water salinity during the sampling period (table).

At a water mineralization of 30 g/l (April 2004), a green mat formed on the surface of bottom sediments. *M. chthonoplastes* was predominant in the upper layer of the mat followed by a layer consisting of *Ph. molle* and *M. chthonoplastes* filaments.

In the thin mat formed at a mineralization of 82 g/l (August 2001), colonies of green algae were detected in a biofilm consisting of cyanobacteria *Nodularia* sp. and *Oscillatoria tenuis*, as well as of residues of *Phormidium* filaments. At the same time, *M. chthonoplastes* and *Leptolyngbya woronichinii*, along with the unicellular green algae and diatoms *Navicula longirostris, Rhoicosphenia* sp., and *Nitzschia denticula*, were detected in the water samples.

A thin mat consisting of *L. woronichinii* and *Oscillatoria* sp. was formed under conditions characterized by sharp salinity fluctuations (43–170 g/l; August 2007). In addition, *Gloeocapsa* sp., fragments of *L. tenuis* filaments, and *Dunaliella salina* cysts, as well as empty wide sheaths, were detected in this mat.

During the drying-up phase (August 2006), the microbial mat of Lake Khilganta was transformed into a four-layer crust. On the surface of the mat, patches consisting of white minerals were observed. Considerable diversity of cyanobacterial (*M. chthonoplastes, Ph. molle, L. tenuis, Chroococcus minutes*) and algal (*Oocystis* sp., *D. salina*) morphotypes was observed. *Ph. molle* and eukaryotic algae prevailed in a 1-mm dry grayish layer underneath the mineral sediments. In the following layer, the mat basis, a new increase in microbial diversity was observed and *L. woronichinii* appeared. This brownish-green layer (3–4 mm) was softer and had a horizontally laminated structure. In the lower grayish-brown layer, in the zone of destruction, algal and cyanobacterial cells were scarce and their morphological diversity was insignificant.

Hence, during the sampling period (1995–2007), a total of eight cyanobacterial species, three species of eukaryotic algae, and three species of diatoms were

Oxygenic phototrophic microorganisms of Lake Khilganta

Microorganism	Isolation source and time of discovery	Reference	pH	TM, g/l
Nodularia sp.	Mat, August 2001; In cultures	Our data	9.0 9.0	82 5
Aphanothece salina Elenkina et Danilina	Mat, 1995	[4, 5]	9.5–9.8	45–46
Chroococcus minutus (Kützing) Nägeli	Crust, 2006	Our data	8.4	D.s.
Gloeocapsa sp.	Mat, 2007	Our data	9.0–9.5	43–128
Microcoleus chthonoplastes Thuret ex Gomont	Mats, 1995, 1996, 2001,2002, 2004, 2006	Our data	8.9–9.8	45–253
Oscillatoria tenuis Agardh ex Gomont	Mat, 2001	Our data	9.0	82
Oscillatoria sp.	Mat, 1996; Mat, 2007	[5]; our data	9.5	45
Phormidium molle Gomont	Mats, 1995, 1996; Crust, 2006; In cultures	[4, 5]; our data	9.5–9.8 9.0	45–46 5
Leptolyngbya tenuis (Gomont) Anagnostidis et Komárek	In cultures	Our data	9.0	5
Leptolyngbya woroniñhinii (Anissimova) Anagnostidis et Komárek	Mats, 2001, 2007; In cultures	Our data	9.0 9.0	82 5
Spirulina sp.	Mat, 1996	[5]	9.5	45
Chlorella minutissima Fott et Novak	Mats, 1995, 1996	[4, 5]	9.5–9.8	45–46
Dunaliella salina Teod.	Mats, 2001, 2006; In cultures	Our data	9.0 9.0	82 5
Oocystis sp.	Mat, 2006; In cultures	Our data	8.4 9.0	D.s. 5
Navicula longirostris Hust.	Mat, 2001	Our data	9.0	82
Rhoicosphenia sp.	Mat, 2001	Our data	9.0	82
Nitzschia denticula Grun.	Mat, 2001	Our data	9.0	82

Note: D.s., dry season (2006).

isolated from the natural mat samples and enrichment cultures obtained from Lake Khilganta.

Growth and development of the laboratory community. Using the laboratory pH–mineralization gradient made it possible to assess the reaction of cyanobacteria and eukaryotic algae to changes in the growth-limiting factors.

After 2.5 weeks from the beginning of the experiment, moderate growth of cyanobacteria was observed at low NaCl concentrations (1–20 g/l) and pH 8–9. Algae were not detected. After 3.5 weeks, intense growth of cyanobacteria was observed at all pH values (7–11) and at NaCl concentrations ranging from 1 to 50 g/l. After 5 weeks of the experiment, green algae developed at NaCl concentrations of 150–200 g/l; intense growth of cyanobacteria was observed within pH 7–11 and salinity from 1 to 50 g/l. Subsequently, an increase in the biomass yield of cyanobacteria and algae was detected. Algae colonized, albeit slowly, the highly mineralized (250–300 g/l NaCl) environments. At the final stage of the experiment, intense growth of cyanobacteria, up to formation of matlike structures, was observed across the pH (7–11)–salinity (1–50 g/l) gradient. Within the pH–salinity range of 7–11 and 100–300 g/l, respectively, weaker but pronounced growth of *D. salina* was observed.

The mature laboratory community consisted of one algal species (*D. salina*) and two cyanobacterial species (*Nodularia* sp. and *Leptolyngbya* sp.). Replacement of the dominant species in the community occurred as follows: at salinity of 1 g/l (pH 7.5–9.5), *Nodularia* sp. constituted 80% of the biomass, whereas 20% of the biomass was produced by *Leptolyngbya* sp. *D. salina* was often detected. As the NaCl content increased up to 10 g/l, the number of *Leptolyngbya* sp. cells decreased to 10%. An increase in NaCl concentration up to 50 g/l resulted in a 99% decrease in the number of *Leptolyngbya* cells, and *Nodularia* sp.

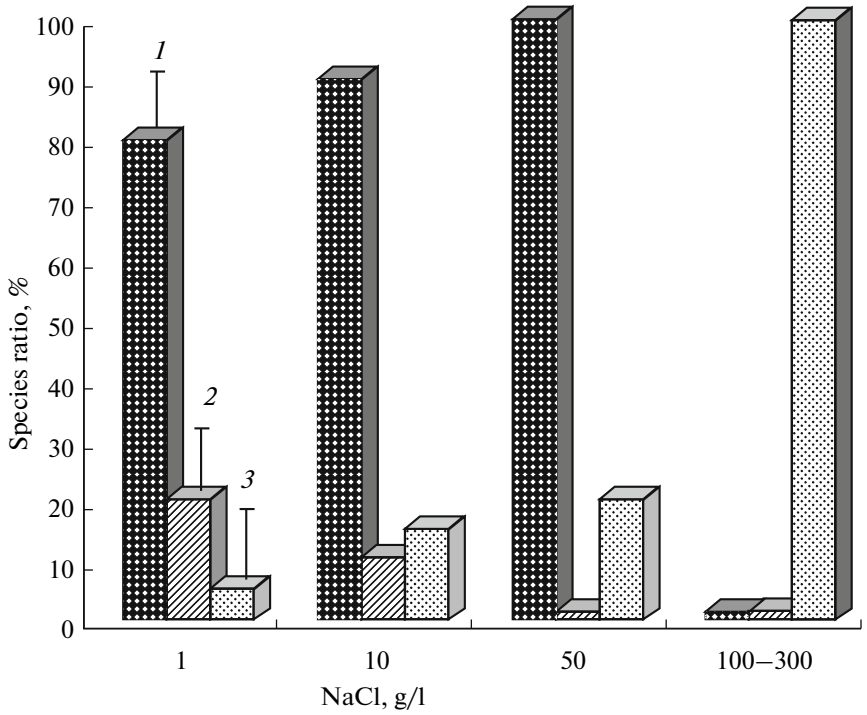

Fig. 1. Ratios of the cyanobacterial and algal species in the laboratory community across the pH-mineralization gradient (%): *Nodularia* sp. (*1*), *Leptolyngbya* sp. (*2*), and *Dunaliella salina* (*3*).

became the dominant species (Fig. 1). At NaCl concentrations of 100–300 g/l, the *D. salina* percentage in the community increased to 100% (Figs. 1, 2). The greatest number of green algae was observed at the NaCl concentration of 50 g/l.

The biomass yield assessed from the chlorophyll *a* content indicates that the best growth of cyanobacteria in the laboratory community occurred within the pH range of 7–10. At pH values above 10, growth was partially limited and was completely inhibited at this pH level in combination with high salinity. Optimal growth of cyanobacteria was observed within a salinity range of 1–50 g/l NaCl. Within the salinity range of 50–100 g/l NaCl, a qualitative and quantitative shift in the species composition of the community occurred: cyanobacteria were replaced by eukaryotic algae, which was confirmed by the changed spectrum of photosynthetic pigments. At the NaCl concentration of 100 g/l, the chlorophyll content decreased due to a decrease in the numbers of cyanobacteria, despite the fact that the number of *D. salina* cells increased, because the biomass yield of this unicellular algae was lower than that of cyanobacteria (Fig. 3).

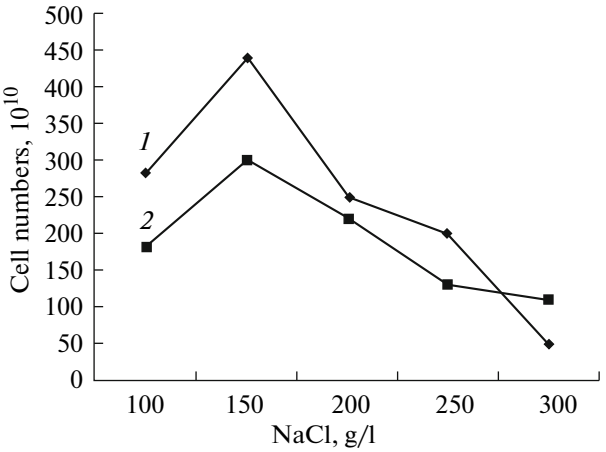

Fig. 2. Numbers of *D. salina* determined across the pH-mineralization gradient: pH 8.5 (*1*) and pH 9.5 (*2*).

The following properties of the microbial community developing across the laboratory gradient are of most interest.

(1) At the NaCl concentration of 150–200 g/l, the colonizing activity of algae was higher than at 100 or 250–300 g/l NaCl.

(2) The distribution areas of cyanobacteria and eukaryotic algae were well defined. Despite the fact that algae grew at low NaCl concentrations (0–50 g/l) as well, their role in the community (consisting mostly of cyanobacteria) was limited.

(3) At pH values below 10, more intense growth of both algae and cyanobacteria was observed.

The benthic alkaliphilic cyanobacterial mat covering the bottom of Lake Khilganta is a unique property of this lake. Cyanobacterial mats were formed during the whole warm season, from ice thawing until winter.

The results of observation of the natural community, as well as the data obtained from the study of its laboratory analogue, allowed us to describe the structure of the microbial mat of Lake Khilganta and study the ecological and physiological properties of the microorganisms forming this microbial community.

The revealed development patterns of the constituents of this community showed that each organism has its own range of favorable conditions. For example, the carbonate and calcium concentrations during the "dry" phase were several times lower than those required for growth of *M. chthonoplastes* [15]. This is most likely the reason that this microorganism was able to grow in Lake Khilganta at lower values of mineralization, but at more balanced water composition. Under laboratory conditions, this species acted as an extremely haloalkaliphilic microorganism with a growth optimum at 120–150 g/l [16]. At the same time, according to our data, this microorganism was replaced with *Nodularia* sp. in the laboratory gradient; therefore, we can gain insights into its physiology only during in situ experiments.

Across the "natural" and laboratory gradients, the salinity growth ranges of *Ph. molle* and *L. tenuis* were identical, 0–100 g/l NaCl; however, *L. tenuis* was found to be more adapted to high NaCl concentrations. *L. woronichinii* did not grow across the gradient and was not detected at NaCl concentrations higher than 50 g/l. The observation of *Nodularia* sp. revealed that this microorganism was able to grow under laboratory conditions in a pH range of 7.5–9.5 and a salinity range of 0–50 g/l; the best growth was observed at higher NaCl concentrations. In the natural mat, *Nodularia* sp. was detected at a water mineralization of 82 g/l. The colonial cyanobacterium *Aphanothece salina*, a pronounced alkaliphile [16], and *Chroococcus minutes* were not able to grow in cultures across the gradient. However, they were detected in the mats at a mineralization of more than 40 g/l (*A. salina*), in the dry mat samples collected in 2006, and in the mat samples collected in 2007 (mineralization 40 g/l) (*C. minutus*). The green alga *D. salina* was able to grow within the widest salinity range, 0–300 g/l NaC (Fig. 4).

The results of our experiments allowed us to describe the distributional patterns of the studied microorganisms across the mineralization gradient, as well as to get a complete picture of all stages of the community development.

The mats formed during the high-water period at the NaCl concentration of 46 g/l and pH of 9.5–9.8 were typical layered structures consisting mostly of cyanobacteria. During the low-water season, when the water level rose as a result of snow thawing or infrequent rains, development of cyanobacterial films (mats) was observed. During the dry season, when the water level was lowest and the water mineralization was highest, green algae incapable of producing layered mats were predominant in the pools.

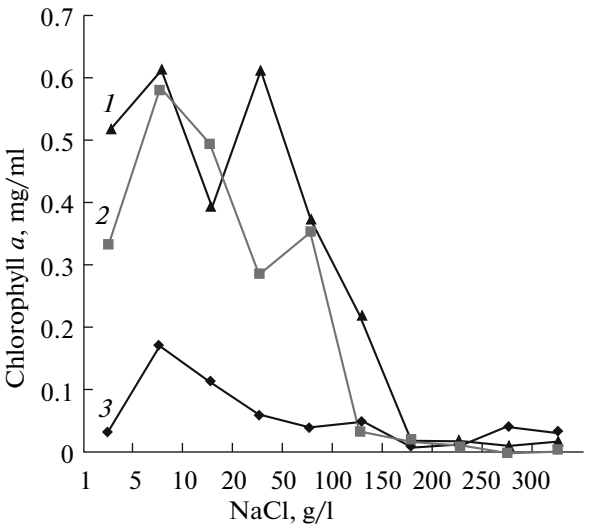

Fig. 3. Chlorophyll *a* content depending on the NaCl concentration and pH level: pH 7.5 (*1*), pH 8.5 (*2*), and pH 9.5 (*3*).

At high salinity levels (more than 150 g/l), mat formation was not observed; only eukaryotic algae (in particular, *D. salina*) incapable of producing matlike structures were detected in brine. Moreover, on the basis of the data obtained, we assume that this phenomenon should be observed at water mineralization of 100–110 g/l. However, at 100 g/l, the community will consist of three species—namely, *D. salina, Ph. molle*, and *L. tenuis*. The two latter species are able to form a mat. The results of our study of the development of microbial communities suggest that *Phormidium* and *Leptolyngbya*, which have higher growth rates and more rapid substrate colonization than do other microorganisms, penetrate through the layers of minerals and form the primary biofilm. Later, algae and other cyanobacterial species colonize this biofilm and the formation of a microbial mat begins. Then, during the dry season, the mat dries up; however, its structure remains intact and the whole process repeats upon hydration. This finding was supported by the fact that the highest species diversity was observed in dry mats, since these mats rapidly become "mummified" and their structure and constituents remain intact. In this mat, dry layers with high and low species diversity alternate, which presumably reflects the regular alternation of dry and wet phases in the lake.

As the water mineralization decreases to 80 g/l, the amount of species in the community increases to six due to the appearance of *M. chthonoplastes, Nodularia* sp., and *Oscillatoria* sp. Thin biofilms consisting of *Nodularia* sp., *Phormidium* sp., and *O. sp.* appear; other species remain in the form of unicellular planktonic organisms. We suggest that this species composition will remain unchanged at a water mineralization of up to 50 g/l. It seems likely that, in this locus (80–50 g/l), a typical layered mat is formed, like the one

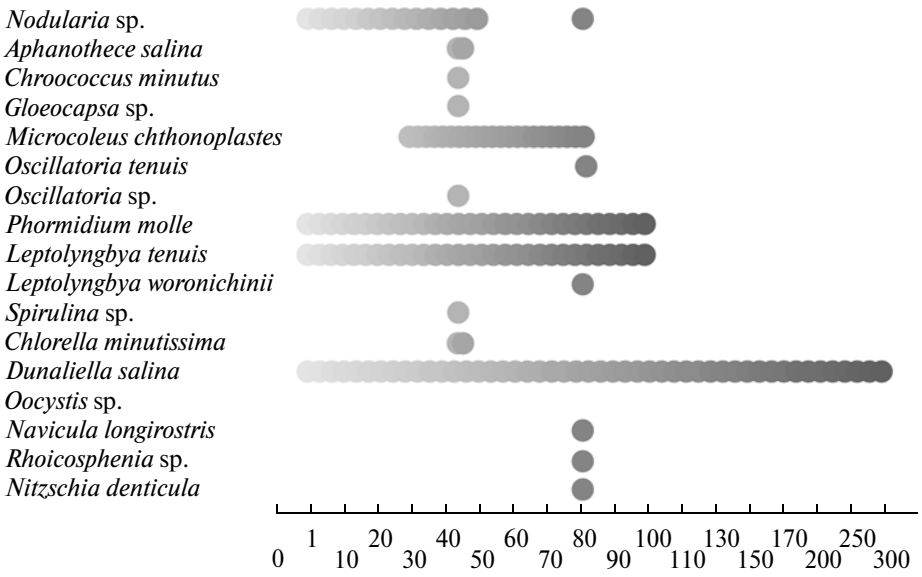

Fig. 4. Distribution of oxygenic phototrophic microorganisms as dependent on ambient conditions. Bottom scale, NaCl concentrations, g/l.

that developed during the long-term high-water period at a salinity of 46 g/l. In this mat, five species were detected, including four species of cyanobacteria (*M. chthonoplastes, Ph. molle, L. woronichinii* (presumably), and *A. salina*). However, according to the results of our observations, *Nodularia* sp., *D. salina, L. tenuis*, and *Oscillatoria* sp. may be present as well. As the mineralization level decreases further (to 30 g/l), the mat structure will remain unchanged, since the mat will consist of the same species. At salinity below 30 g/l, the typical haloalkaliphile *M. chthonoplastes* disappears and *Phormidium* and *Nodularia* become responsible for the mat structure, since *Oscillatoria* cannot be an active edificator in this community. At mineralization lower than 20 g/l, the number of species in the community decreases and remains at the same level until complete desalination. In this case, cyanobacteria will be responsible for the biofilm formation, whereas *D. salina* will remain in the form of unicellular planktonic organisms.

The results obtained indicate that the formation of microbial mats in Lake Khilganta occurs under the influence of sharply fluctuating physicochemical factors (water level, pH, mineralization, etc.). Depending on which and what combination of factors affect the biosystem within the period of interest, a microbial community with a structure corresponding to the morphological, physiological, and ecological properties of the mat constituents develops.

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