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EXPERIMENTAL ARTICLES

The Structure of Phototrophic Communities of Soda Lakes of the Southeastern Transbaikal Region

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Abstract—The structure of benthic phototrophic communities of 24 soda lakes of the southeastern Transbaikal Region was studied. The physicochemical properties of the lakes were determined. The results of enumeration of anoxygenic phototrophic bacteria (APB) belonging to various groups are presented. The influence of salinity on the structure of APB communities was investigated. The APB reaction to environmental conditions was determined. Massive development of phototrophic microorganisms in the form of mats and films was observed in the majority of the investigated lakes. The APB communities were characterized by a wide diversity and evenness of species composition. Purple sulfur bacteria of the families *Ectothiorhodospiraceae* and *Chromatiaceae* were predominant. Purple nonsulfur bacteria of the family *Rhodobacteraceae*, green filamentous bacteria *Oscillochloris* sp., and heliobacteria were also detected. According to preliminary data, no less than 15 species of APB occur in the studied lakes. Among them, three novel genera and four species have already been described. Identification of other isolates is still in progress. The lakes make an almost continuous series of fresh, brackish, and saline water bodies, varying in their degree of mineralization. It was demonstrated that the structure of APB communities was unaffected by changes in salinity from 5 to 40 g/l. At salt concentrations of lower than 5 g/l, the level of water mineralization became a limiting factor. Experiments with the isolated cultures showed that the APB were obligately dependent on the presence of carbonate ions in the medium. They were haloalkalitolerant or haloalkaliphilic. Thus, they are well adapted to the conditions of soda lakes with a low of moderate mineralization. It was demonstrated that soda lakes of the southeastern Transbaikal Region represent a special type of habitat which harbors a peculiar autochthonous microflora and differs from both highly mineralized soda lakes and shallow saline water bodies of the sea origin.

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Key words: soda lakes, microbial mat, anoxygenic phototrophic bacteria, alkalitolerant and alkaliphilic bacteria, water mineralization.

Soda lakes with high water mineralization occur widely in arid regions with spacious drainless zones. Since these lakes represent an extreme habitat, they have been the subject of investigation for a long time, and scientists' interest in them is still strong because of the specificity of haloalkaliphilic microorganisms, among which many new taxa belonging to almost all known physiological groups have been detected and described. This interest is also due to the hypothesis that the microbial communities which inhabit soda lakes may be considered as the relics of early Proterozoic biota [1, 2]. African alkaline hypersaline lakes have been studied in the most detail. Investigations of a narrower scope have been conducted at a number of soda lakes of the Western United States, Hungary, Mongolia, etc. [1, 3]. In Russia, a series of investigations have been carried out at the soda lakes of the Kulunda Steppe and in Tuva [1]. Over the last decade, the attention of Russian researchers has been attracted by the epicontinental soda lakes of the southeastern Transbaikal Region, to which the present study is also devoted [4, 5]. A peculiarity of these lakes is their relatively low water mineralization. Unlike the previously studied saline and hypersaline alkaline lakes of other regions, most lakes of the southeastern Transbaikal Region are brackish. The microflora of such lakes has been poorly studied. Of particular interest is the specificity of brackish lakes (as compared to saline alkaline lakes and marine water bodies) as habitats of phototrophic microorganisms.

The physiographic and geological features of the soda lakes of the southeastern Transbaikal Region, as well as the chemical composition of lake water, the mineralogical composition of bottom sediments, and

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Table 1. Physicochemical parameters of the studied lakes of the southeastern Transbaikal Region

Location	Lake	Stations	pH	Mineralization, g/l	Total alkalinity (CO_3^{2-} + HCO_3^-), g/l	Eh, mV	O_2, mg/l	Water transparency and color	Water taste
Chita Oblast, Onon District	Barun-Torei	A-1–A-6	9.1	1.8	0.7	103	9.0	turbid, white	fresh
	Ostozhe	A-7, A-8	9.2	2.2	1.1	108	4.3	very turbid; beige	fresh
	Ilim-Torom	A-9–A-11	9.5	2.5	1.8	75	6.3	transparent	fresh
	Malyi Kasytui	A-12	9.5	1.9	1.6	127	4.8	transparent	fresh
	Dabasa-Nur	A-13, A-14	9.4	10.0	1.0	122	7.4	transparent	brackish
	Nizhnii Mukei	A-51	9.5	8.3	4.7	–	–	transparent	brackish
	Ulan-Nur	A-52	10.5	22.5	3.2	–	–	slightly turbid, grayish	saline
Agin–Buryat Autonomous Area	Gorbunka	A-15–A-18, A-41, A-42	10.0	6.1 3.5	1.1	109	5.3	transparent, yellowish	fresh
	Gonzogor	A-19	9.3	0.9	0.8	117	6.1	transparent	fresh
	Khilganta	A-20, A-40	9.5	40	1.5	70	6.2	transparent	saline
	Bezymyannoe	A-21	9.2	0.8	0.7	112	6.2	transparent	fresh
	Nozhei	A-22, A-23	8.9	0.5	0.4	97	5.3	transparent	fresh
	Bortogo-nuur	A-43	9.6	3.5	1.5	–	–	slightly turbid, yellowish	fresh
	Khoito-Kholvo-Torom	A-44	9.5	14.5	1.1	–	–	transparent, yellowish	brackish
	Kholvo-Torom	A-45	9.9	35.4	1.8	–	–	transparent	saline
	Khuzhirta	A-46	10.0	5.6	1.1	–	–	transparent	fresh
	Tokhoryuun-nuur	A-47	9.5	4.3	1.0	–	–	transparent	fresh
	Oshoroi-nuur	A-48	9.9	4.7	2.1	–	–	transparent	fresh
Buryat Republic, Dzhidin District	Verkhnee Beloe	A-24–A-26	10.1	7.5	4.1	143	3.9	transparent	brackish
	Nizhnee Beloe	A-27	9.8	3.7	2.0	129	4.5	transparent	fresh
	Tsaidam	A-29–A-32	10.1	15.8	5.2	156	4.5	turbid, white	brackish
Buryat Republic, Selenga District	Selendumskoe	A-33, A-34	8.5	0.7	0.3	–	–	transparent	fresh
	Sul'fatnoe	A-35, A-36	9.2	7.7	1.1	111	4.8	transparent	brackish
Buryat Republic, Kurumkan District	Nukhe-Nuur	BG-35	9.9	16.8	7.8	–	–	transparent	brackish

the processes of organic matter decomposition, have been previously investigated [4, 5]. However, the structure of the phototrophic community has been described in detail only for Lake Khilganta [6, 7].

This work presents the results of a comparative study of the phototrophic communities of 24 soda lakes of the southeastern Transbaikal Region. The main emphasis has been placed on anoxygenic phototrophic bacteria (APB) and their adaptation to the environment, as well as on the dependence of the APB community structure on the level of water mineralization.

MATERIALS AND METHODS

A total of 24 soda lakes of the southeastern Transbaikal Region (Table 1), located in the Onon District of

Chita oblast (7 lakes), Agin–Buryat Autonomous Area (11 lakes), as well as Dzhidin, Selenga, and Kurumkan Districts of Buryatia (6 lakes), have been investigated. A series of field investigations were carried out in 1995–1997 by joint expeditions of the Winogradsky Institute of Microbiology, Russian Academy of Sciences (Moscow) and the Institute of General and Experimental Biology, Siberian Branch, Russian Academy of Sciences (Ulan-Ude, Buryatia).

During field work, we determined the following physicochemical parameters of the environment: water temperature (with a mercury thermometer), pH and Eh (with a Checkmate field meter, Mettler, Toledo), alkalinity (by titration) [8], and the total mineralization of the water (with a densitometer and a conductometer). The sulfide concentration was determined by iodometric titration [8] and the oxygen content by the Winkler method with the addition of mercuric nitrate to sulfide-containing water samples [8].

APB-containing samples taken from sites of massive APB accumulation were smeared over microscope slides and dried. In the laboratory, the smears were stained with crystal violet [9] and examined under a phase contrast microscope. We also took samples of microbial mats and films for subsequent microscopic examination and fixed them with a 30% glycerol solution.

Phototrophic bacteria were enumerated by inoculating aliquots of serial tenfold dilutions of homogenized mat or film samples into agarized medium (agar shake method). For more complete enumerations of various APB groups, two variants of nutrient medium were used. The basal medium common to both variants contained (g/l) KH_2PO_4, 0.5; NH_4Cl, 0.5; $MgCl_2 \cdot 6H_2O$, 0.2; $CaCl_2$, 0.05; sodium acetate, 0.5; trace element solution, 1 ml; and vitamin B_{12}, 20 µg, as well as, depending on the water composition of the particular lake, 1–40 g/l NaCl, 2.5–10 g/l $NaHCO_3$, and 2.5–10 g/l Na_2CO_3. One variant additionally contained 0.5 g/l $Na_2S_2O_3 \cdot 5H_2O$ and 0.5 g/l $Na_2S \cdot 9H_2O$; another was supplemented with 0.5 g/l sodium malate and 0.5 g/l yeast extract. The bacterial numbers were determined on the variants of the medium that provided for the best growth. Colonies exhibiting characteristic pigmentation were counted and inspected microscopically. The APB were enumerated and isolated at pH 9.5. In other experiments, the acidity of the medium was varied by varying the ratio of carbonate and bicarbonate in the medium without changing their total concentration. Inoculated media were incubated in a luminostat at 25°C at an illumination intensity of about 2000 lx.

The APB reaction to environmental conditions (pH, salinity, and alkalinity) was studied using 20 pure cultures isolated from the sampled microbial mats and films. The optical density of the cell suspensions was measured with a KFK-3 spectrophotometer at 650 nm.

Ultrathin sections of bacteria, obtained by the standard method described in [10], were examined under a JEM 100C electron microscope (Jeol, Japan).

RESULTS AND DISCUSSION

Physicochemical Conditions

The physiographic features of the southeastern Transbaikal Region [4], such as its geology, hilly terrain, poorly developed river network, arid harsh continental climate, as well as permafrost and seasonally freezing ground, promote the formation of numerous small shallow soda lakes. The water mineralization and salt reserves of these lakes are low.

The limited drainage capacity and the climatic conditions of the region are responsible for the extreme instability of the hydrochemical regime, which is the most characteristic property of all the lakes of the southeastern Transbaikal Region. The water level, mineralization, alkalinity, and the pH level undergo considerable variations, both seasonal and long-term. It should be noted that, during our experiments, the water mineralization was low due to a significant amount of precipitation. Furthermore, over the last decades, the general tendency has been toward an increase in precipitation in the region [4].

Out of 24 investigated lakes (Table 1), 17 lakes were brackish (1.8–16 g/l). In Lakes Nozhei, Selendumskoe, Bezymyannoe, and Gonzogor, the total salt concentration did not exceed 1 g/l. Three lakes, Ulan-Nur, Kholvo-Torom, and Khilganta, are saline and have a mineralization of 22.5–40 g/l.

In all the studied lakes, the water has an alkaline reaction (pH 8.5–10.5). Alkalinity ranged from 0.3 to 7.8 g/l (5–130 mM) but was mostly within 1.0–2.0 g/l (16–33 mM).

The water temperature in the daytime ranged from 25 to 35°C and went down to 18°C at night.

In some lakes, the water was muddy because of suspended clay particles (Table 1). The densest grayish milky suspension was observed in Lake Ostozhe. No visible growth of phototrophic microorganisms occurred, evidently due to the deficiency of light.

In the daytime, the conditions in the lakes were oxidative. The Eh varied from +70 to +156 mV, and the oxygen concentration ranged from 3.9 to 9 mg/l (Table 1). At the same time, reductive conditions predominated in the bottom sediments in most cases. As a consequence of intense sulfate reduction [4], sulfide production was observed; a certain amount of sulfide was also recorded in the near-bottom water. Hence, at the water/sediment interface, in the zone of development of benthic microbial communities, a gradient of physicochemical conditions was observed, which promoted the development of diverse physiological groups of microorganisms.

In the lakes, considerable daily fluctuations of redox conditions were recorded. At night, in the absence of photosynthetic activity, the oxygen concentration in the water decreased, whereas the sulfide concentration in the sediments, and sometimes in the water, increased. The dynamics of these processes occurring in Lake Khilganta were earlier described in detail in [7].

Characteristics of the Phototrophic Microbial Communities

In warm seasons, the conditions for the development of phototrophic microbial communities in the soda lakes of the southeastern Transbaikal Region are favorable. In the majority of the studied lakes, we observed massive development of phototrophic microorganisms in the form of thin (1–3 mm) layered mats on the sediment surface or friable or slimy films on the surface of sediments, algae, and decaying remains of higher plants. APB formed lilac-pink, crimson, or light green layers in cyanobacterial mats and often predominated in amorphous microbial films, giving them various tints of purple. The development of microbial mats and films was more frequent in the shallow zones of lakes and in lagoons. Only in the saline lakes Kholvo-Torom and Khilganta did layered microbial mats (1–2 cm thick) cover the entire bottom. The structural basis of the microbial mats in these lakes was formed by the filamentous cyanobacterium *Mastigocladus chtonoplastes*. In addition, *Phormidium molle*, the unicellular cyanobacterium *Aphanothece salina*, and other cyanobacteria were detected [6, 7]. Purple bacteria grew under the upper layer of cyanobacteria, forming pink or crimson layers 1.5–2.5 mm thick. The structure of the haloalkaliphilic mat of Lake Khilganta and its daily dynamics depending on the physicochemical conditions of the environment is described in detail in [7].

In the saline lakes, prokaryotic organisms—cyanobacteria and APB—were the main producers of organic matter; the abundance of eukaryotic photosynthesizers was insignificant. In brackish and freshwater lakes, the proportion of algae in the phototrophic community increased. These lakes are also characterized by a great diversity of cyanobacteria; among them, members of the family *Oscillatoriaceae* were the most abundant.

The Structure of APB Communities

To study the APB species composition, a number of fixed samples and dry preparations of microbial mats and films sampled from the studied lakes were examined under a microscope; the APB enumeration by the agar shake dilution series method was performed.

The studied lakes were characterized by a great diversity of the APB species (Table 2). Purple sulfur bacteria of the families *Ectothiorhodospiraceae* and *Chromatiaceae* prevailed. In almost all samples, we detected spheroidene-containing purple nonsulfur bacteria of the family *Rhodobacteraceae*. In many lakes, green filamentous bacteria of the genus *Oscillochloris* were present. Microscopic analysis often revealed massive development of *Oscillochloris* sp. When counted using the inoculation technique, their numbers were most likely underestimated, since these bacteria showed poor growth under laboratory conditions and could not be maintained in culture. The same is true for heliobacteria, which were detected in only three lakes.

Table 2 shows the results of enumeration of APB of various groups. Some columns of this table contain the names of several genera simultaneously. This is due to the fact that, after the reorganization of most APB species, which was based, for the most part, on the results of 16S rDNA sequencing, it became impossible to distinguish the newly created taxa not only by their morphology and pigment composition, but even by their phenotype as a whole. In many cases, molecular biology techniques must be used for identification at the species and genus levels.

According to preliminary data, no less than 15 species of APB were present in the studied lakes. Investigation and identification of the isolates is still in progress.

A total of three new genera and four species of APB possessing unique complexes of phenotypic properties have been described to the present moment (Fig. 1). Members of the family *Ectothiorhodospiraceae* that accumulate sulfur granules inside cells and have a previously unknown membranous photosynthetic apparatus were discovered (Fig. 1b). They were described as a novel genus and species *Thiorhodospira sibirica* gen. nov., sp. nov. [11]. Obligately alkaliphilic members of the family *Chromatiaceae* possessing a tubular membranous photosynthetic apparatus (Fig. 1d) and bacteriochlorophyll *b* were discovered. They were described as *Thioalkalicoccus limnaeus* gen. nov., sp. nov. [12]. We also discovered alkaliphilic heliobacteria, which were described as belonging to a novel genus, *Heliorestis* gen. nov. (*Hrs. daurensis* sp. nov. and *Hrs. baculata* sp. nov.) [13, 14]. Bacteria of the species *Hrs. daurensis* have a morphology unusual for APB: their cells form tight spirals (Figs. 1e–1h). From Lake Gorbunka, a strain of aerobic APB was isolated and described as *Roseinatronobacter thiooxidans* gen. nov., sp. nov. [15].

Members of the genus *Ectothiorhodospira* were represented by two forms: large rods without gas vacuoles, phenotypically close to the species *Ect. mobilis*, and small rods with gas vacuoles, close to the species *Ect. schaposhnikovii.* Among the strains of *Allochromatium–Marichromatium–Thiocystis,* *Amoebobacter–Thiocapsa*, and *Rhodobacter–Rhodovulum–Rhodobaca*, we also discovered phenotypically different forms, some of which, according to our preliminary data, represent novel taxa. The study of these organisms is currently in progress.

Table 2. Cell numbers (log cells/ml) of various groups of APB determined by inoculation of selective media (pH 9.5) with natural samples of microbial mats and films

Lake*	Mineralization, g/l	*Ectothiorhodospiraceae*		*Chromatiaceae*			Purple nonsulfur bacteria	Green filamentous bacteria	*Heliobacteriaceae*
		Ectothiorhodospira	*Thiorhodospira*	*Allochromatium, Marichromatium, Thiocystis*	*Amoebobacter, Thiocapsa*	*Thioalkalicoccus*	*Rhodobacter, Rhodovulum, Rhodobaca*	*Oscillochloris*	
Nozhei	less than 1	–	–	***7*****	6	–	2	4	–
Selendumskoe		–	–	***6***	5	–	4	2	
Bezymyannoe		2	–	6	***7***	–	2	5	–
Gonzogor		3	–	5	***6***	–	5	***6***	–
Barun-Torei	1–5	6	–	***8***	–	–	6	4	3
Malyi Kasytui		5	***7***	5	***7***	–	4	***7***	–
Ostozhe		–	–	–	2	–	3	–	1
Ilim-Torom		7	7	***9***	6	–	5	4	–
Bortogo-nuur		5	–	4	***6***	–	3	–	–
Nizhnee Beloe		6	5	***8***	3	–	6	4	–
Tokhoryuun-nuur		6	–	***7***	–	–	–	–	–
Oshoroi-nuur		7	–	***8***	6	–	6	–	–
Khuzhirta	5–10	***6***	–	–	5	–	3	3	–
Gorbunka		***8***	–	***8***	5	7	7	5	–
Verkhnee Beloe		8	***9***	8	7	7	6	6	–
Sul'fatnoe		***7***	–	5	–	–	6	–	–
Nizhnii Mukei		***8***	–	6	5	–	3	3	3
Dabasa-Nur		***9***	–	7	8	8	6	4	–
Khoito-Kholvo-Torom	10–20	***6***	–	–	5	–	4	–	–
Tsaidam		***5***	–	–	4	4	3	3	–
Nukhe-Nuur		***8***	6	5	–	–	5	–	–
Ulan-Nur	20–40	***7***	–	5	6	–	4	–	–
Kholvo-Torom		***6***	–	–	5	–	–	2	–
Khilganta		***7***	–	6	6	–	6	–	–

* The list is sorted in accordance with the increase in lake water mineralization.
** The abundance indexes of dominant APB groups are shown in bold italics.

Influence of Water Mineralization on the Community Structure of APB

The influence of a certain environmental factor on the structure of microbial communities can be studied by comparing a number of ecosystems in which the variation of this factor takes place against a background of relative stability of (or at least of nonextreme values) of other important environmental parameters.

The lakes of the southeastern Transbaikal Region are a convenient model for studies of the influence of water mineralization on the development of benthic phototrophic communities. According to this parameter, the studied lakes constitute an almost continuous series of fresh, brackish, and saline water bodies. It is in this order that they are arranged in Table 2.

The composition of APB communities changed regularly with the increase in the water mineralization. Three groups of lakes could be distinguished in which the structure of APB communities differed significantly: (1) freshwater lakes (mineralization of less than 1 g/l),

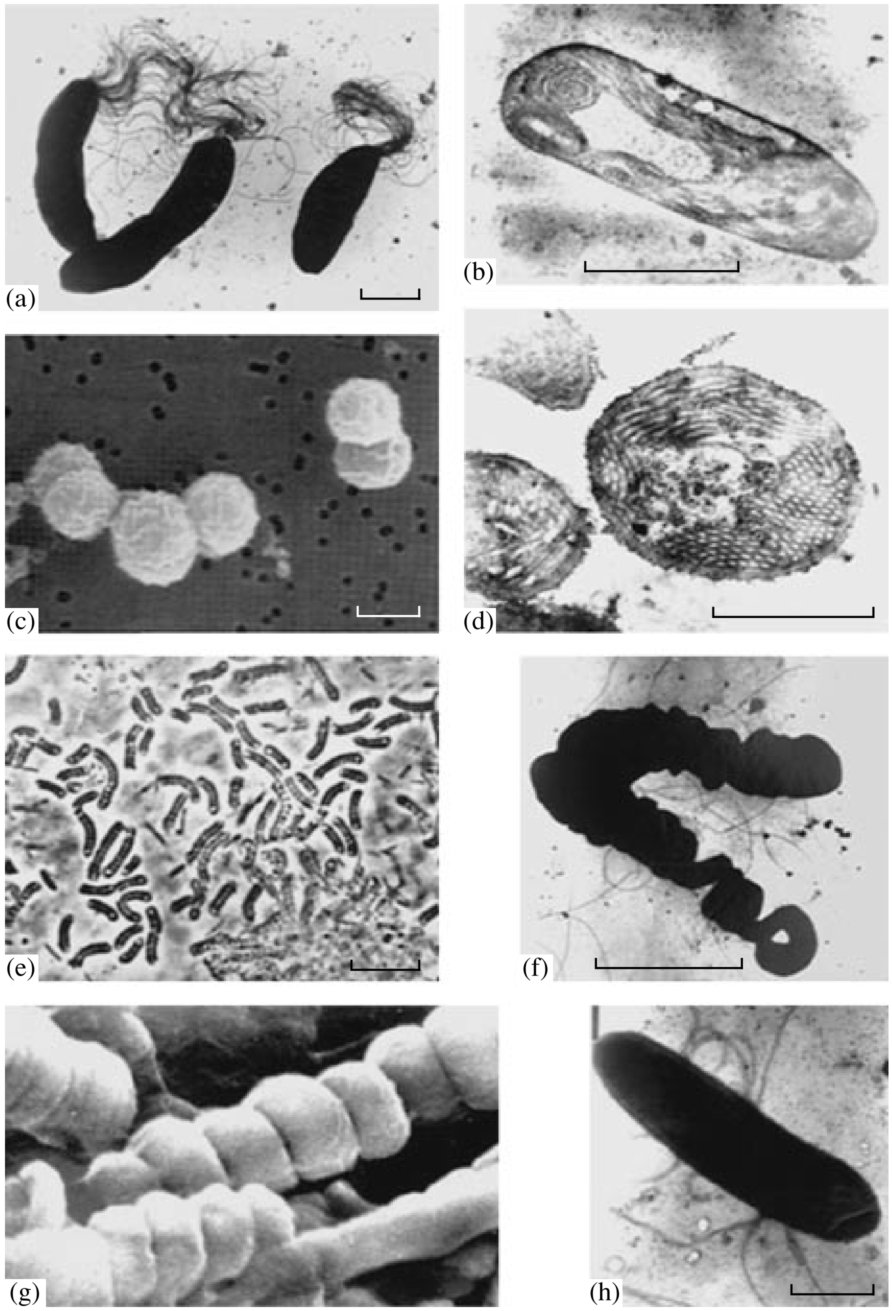

Fig. 1. New forms of APB from soda lakes of the southeastern Transbaikal Region: (a, b) *Thiorhodospira sibirica*; (c, d) *Thioalkalicoccus limnaeus*; (e, f, g) *Heliorestis daurensis*; (h) *Heliorestis baculata.* Transmission electron microscopy of (a, f, h) whole-cell preparations contrasted with phosphotungstic acid and (b, d) ultrathin sections, (c, g) scanning electron microscopy, and (e) phase contrast microscopy. Bars correspond to (c, d, g, h) 1 μm, (a, b, f) 5 μm, and (e) 20 μm.

(2) lakes with water mineralization from 1 to 5 g/l, and (3) brackish and saline lakes (5–40 g/l).

In freshwater lakes with a water mineralization of less than 1 g/l, members of the family *Chromatiaceae* prevailed. Bacteria of the family *Ectothiorhodospiraceae* were not detected or were detected as minor component of the community. In the lakes which contained salts in concentrations from 1 to 5 g/l, members of the family *Chromatiaceae* were also dominant; however, bacteria of the family *Ectothiorhodospiraceae* were abundant, except for in Lake Ostozhe, where the numbers of APB were low, probably due to the abundance of suspended clay particles, which prevented light penetration. In other brackish and saline lakes with water mineralization ranging from 5 to 40 g/l, members of the family *Ectothiorhodospiraceae* prevailed. The cell numbers of other APB groups were also rather high. Such lakes are characterized by a considerable diversity and evenness of the APB species composition. We did not observe any notable differences between the structures of the APB communities developing in waters with salinity ranging from 5 to 40 g/l.

Purple nonsulfur bacteria and green filamentous bacteria of the genus *Oscillochloris* were detected in all types of the lakes. The obligately alkaliphilic purple sulfur bacteria *Thiorhodospira sibirica, Thioalkalicoccus limnaeus*, as well as heliobacteria, were not detected in the lakes with water mineralization less than 1 g/l.

Hence, changes in salinity from 5 to 40 g/l exerted no significant effect on the APB community structure, whose variability was governed by other environmental parameters. At salt concentrations of lower than 5 g/l, water mineralization became a limiting factor for the development of haloalkalitolerant and haloalkaliphilic forms of APB. In lakes where mineralization was no higher than 1 g/l, the composition of APB communities approached that observed in freshwater neutral water bodies.

It should be noted that the influence of salinity is illustrated most dramatically by changes in the position that members of the family *Ectothiorhodospiraceae* (which may be considered indicators of water mineralization level) occupy in the community. The predominance of *Ectothiorhodospira* in the APB community of the studied lakes corresponded to salinity levels of higher than 5 g/l. Their presence as a constant, but not dominant, constituent of the community was observed at salt concentration ranging from 1 to 5 g/l, whereas at water mineralization lower than 1 g/l, they occurred in small numbers or were not detected.

While the study of the lakes of the southeastern Transbaikal Region allowed us to investigate the influence of low mineralization values on the structure of APB communities, the shallow lakes of sea origin with a broad salinity range (the steppe Crimea) previously studied by us, presented a convenient model for the study of the influence of high levels of water mineralization on the phototrophic communities [16]. It was demonstrated that high mineralization determines the species composition of bacterial communities, which, unlike communities of freshwater lakes, are composed of halophiles. An increase in the salinity level of these lakes from 1 to 20% had little effect on the APB species diversity, which depended on other environmental factors. However, further increase in salinity reduced the number of species, caused a decrease in the evenness of the species composition, and resulted in dominance and even in a monopolistic position of the most adapted forms, which were represented by members of the family *Ectothiorhodospiraceae.* A salinity greater than 20–25% acted as a limiting factor.

The soda lakes of the southeastern Transbaikal Region and Crimean saline lakes encompass the whole salinity range from fresh water bodies to hypersaline ones. Their investigation allowed us to determine both the top and bottom limiting boundaries of water mineralization (for Crimean saline lakes and soda lakes of the southeastern Transbaikal Region, respectively). However, it should be borne in mind that, in soda lakes, other factors, such as alkalinity and high pH, may have a limiting effect on the APB communities, apart from water mineralization. The available data do not allow us to assess either the influence exerted by any of these factors on the structure of APB communities or the combined influence of these factors together with water mineralization. However, when two or more limiting factors operate simultaneously, their limiting effects usually increase, and the range of favorable and neutral conditions narrows. Therefore, in soda lakes, the top boundary of water mineralization at which it becomes a limiting factor may be much lower than in saline water bodies. For instance, the predominance of *Ectothiorhodospira* in the studied soda lakes was observed at a water mineralization as low as 5–40 g/l.

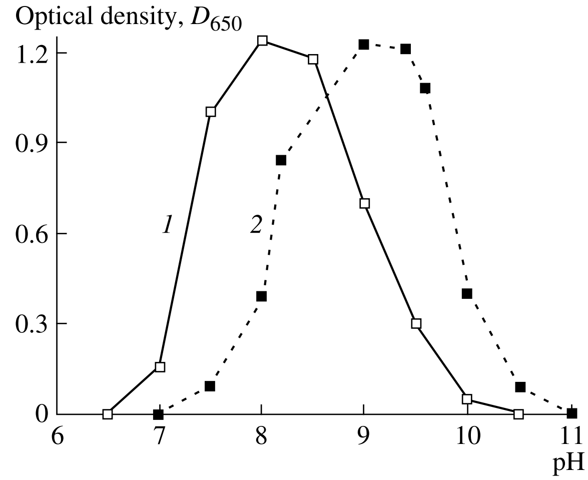

Fig. 2. Effect of pH on the growth of (*1*) the alkalitolerant bacterium *Rhodovulum* sp. A-18 and (*2*) the alkaliphilic bacterium *Thiorhodospira sibirica* BG-35, isolated from the soda lakes of the southeastern Transbaikal Region.

APB Reaction to Physicochemical Conditions of the Environment

More than 20 strains of APB were isolated from the microbial mats and films collected in the soda lakes. To determine the extent of APB adaptation to the environment, we studied the dependence of bacterial growth on pH level, as well as on the soda and salt concentrations (Figs. 2, 3).

With respect to pH, the studied bacteria could be divided into two groups: alkalitolerant bacteria, growing at pH 7–9.5 with an optimum at 8.5, and alkaliphiles, growing at pH 8–10.5 with an optimum at 9–9.5. Purple sulfur bacteria of the *Allochromatium–Marichromatium–Thiocystis* and *Amoebobacter–Thiocapsa* morphotypes and purple nonsulfur bacteria of the family *Rhodobacteraceae* were found to be alkali-

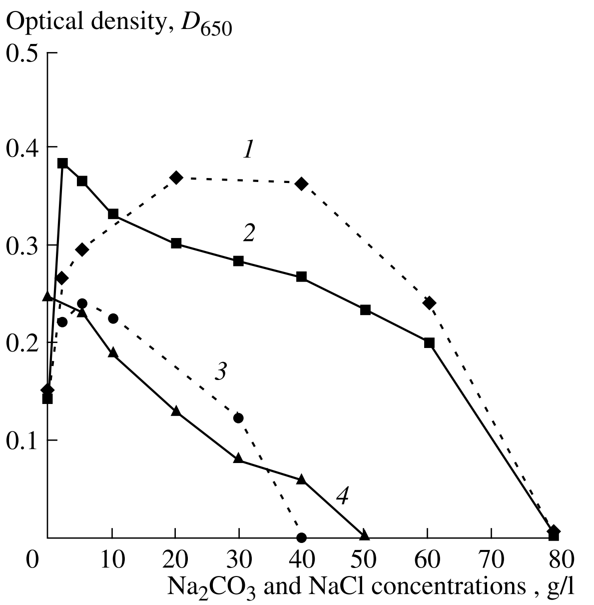

Fig. 3. Dependence of the growth rates of (*1, 2*) the purple bacterium *Thioalkalicoccus limnaeus* A-26 and (*3, 4*) the heliobacterium *Heliorestis baculata* OsH-H1, isolated from the soda lakes of the southeastern Transbaikal Region, on the concentrations of (*1, 3*) soda and (*2, 4*) NaCl.

tolerant, whereas *Ectothiorhodospira*, *Thiorhodospira sibirica, Thioalkalicoccus limnaeus,* and heliobacteria proved to be alkaliphilic. Figure 2 shows two typical curves illustrating the pH dependence of alkalitolerant (*Rhodovulum* sp. A-18) and alkaliphilic (*Thiorhodospira sibirica* BG35) microorganisms.

Obligate dependence of all the studied APB strains on the presence of carbonate ions in the medium was demonstrated. As to the soda concentration in the medium, different results were obtained for purple bacteria and heliobacteria. All purple sulfur and nonsulfur bacteria grew at carbonate concentrations of up to 7–8%, with an optimum at 1–5%, whereas heliobacteria grew at soda concentrations of up to 3%, with an optimum at 0.5–1.5%.

The reaction of purple bacteria to salinity also differed from that of heliobacteria. Heliobacteria proved to be halotolerant; they were capable of growing at NaCl concentrations of up to 4%. The salt tolerance of purple bacteria (sulfur and nonsulfur) was higher, 7–8%. Optimal growth was observed at NaCl concentrations ranging from 0.5 to 3% for different strains. Some strains did not endure subculturing in the absence of NaCl in the medium, while other microorganisms grew in both freshwater and saline media. Thus, the studied purple bacteria were slightly halophilic or moderately halotolerant microorganisms. Figure 3 shows typical examples of the dependence of purple bacteria (*Thioalkalicoccus limnaeus* A-26) and heliobacteria (*Heliorestis baculata* OsH-H1) on the soda and salt concentrations in the medium.

Thus, the results of our laboratory experiments demonstrate that the APB inhabiting the soda lakes of the southeastern Transbaikal Region are obligately dependent on the presence of carbonate ions in the medium; they are alkalitolerant or alkaliphilic and moderately halotolerant or slightly halophilic. One can conclude that the studied APB are well adapted to the environmental conditions of soda lakes with low and medium water mineralization and obviously represent the autochthonous microflora of these lakes.

The results obtained demonstrate that the soda lakes of the southeastern Transbaikal Region are a peculiar type of habitat with a specific autochthonous microflora, different from that of highly mineralized soda lakes and shallow saline water bodies of the sea origin.

Highly mineralized soda lakes differ significantly from the slightly mineralized soda lakes studied by us both in terms of the physicochemical conditions of the environment and the composition of their phototrophic communities, which consist exclusively of prokaryotes [1]. In these extreme habitats, massive development of phototrophic bacteria occurs in the water column. Unicellular planktonic organisms predominate among cyanobacteria, and, among APB, extreme haloalkaliphilic purple sulfur bacteria of the genus *Halorhodospira* predominate.

In their physicochemical parameters, the soda lakes of the southeastern Transbaikal Region are similar to shallow saline water bodies of the sea origin [6, 16, 17], differing from the latter in their higher values of alkalinity and pH, as well as by their lower average mineralization. Both types are distinguished by sufficient illumination, high concentrations of biogenic elements, and, as a consequence, by natural eutrophication, high rates of sulfate reduction in the sediments, and a substantial vertical gradient of physicochemical conditions at the water/sediment interface. These circumstances create conditions favoring the development of phototrophic microorganisms, including APB. The microbial mats developing in shallow saline and soda lakes share many common features [6, 7]. As for APB, purple bacteria of the families *Ectothiorhodospiraceae* and *Chromatiaceae* prevail in the water bodies of both types. Nonsulfur bacteria of the family *Rhodobacteraceae* are widespread. APB on the whole are represented by halotolerant and halophilic organisms [16, 17]. Unlike in neutral saline water bodies, no neutrophilic green sulfur bacteria were found in the soda lakes of the southeastern Transbaikal Region; APB were represented by alkalitolerant and alkaliphilic microorganisms, and the predominance of members of the family *Ectothiorhodospiraceae* was more pronounced.

The uniqueness of the soda lakes of the southeastern Transbaikal Region as a habitat is also evidenced by the abundance of new, previously unknown, forms of APB, described as new taxa, including taxa of the generic level.

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REFERENCES

1. Zavarzin, G.A., Zhilina, T.N., and Kevbrin, V.V., The Alkaliphilic Microbial Community and Its Functional Diversity, *Mikrobiologiya*, 1999, vol. 68, no. 5, pp. 579-599 [Microbiology (Engl. Transl.), vol. 68, no. 5, pp. 503-521].
2. Zavarzin, G.A., Epicontinental Soda Lakes as Possible Relict Biotopes of Terrestrial Biota Formation, *Mikrobiologiya*, 1993, vol. 62, no. 6, pp. 789–800.
3. Sorokin, D.Yu., Gorlenko, V.M., Namsaraev, B.B., Namsaraev, Z.B., Lysenko, A.M., Eshinimaev, B.T., Khmelenina, V.N., Trotsenko, Yu.A., and Kuenen, J.G., Procaryotic Communities of the North-Eastern Mongolian Soda Lakes, *Hydrobiologia*, 2004, vol. 522, pp. 235–248.
4. Gorlenko, V.M., Namsaraev, B.B., Kulyrova, A.V., Zavarzina, D.G., and Zhilina, T.N., The Activity of Sulfate-reducing Bacteria in Bottom Sediments of Soda Lakes of the Southeastern Transbaikal Region, *Mikrobiologiya*, 1999, vol. 68, no. 5, pp. 664-670 [Microbiology (Engl. Transl.), vol. 68, no. 5, pp. 580-585].
5. Namsaraev, B.B., Zhilina, T.N., Kulyrova, A.V., and Gorlenko, V.M., Bacterial Methanogenesis in Soda Lakes of the Southeastern Transbaikal Region, *Mikrobiologiya*, 1999, vol. 68, no. 5, pp. 671-676 [Microbiology (Engl. Transl.), vol. 68, no. 5, pp. 586-591].
6. Gerasimenko, L.M., Mityushina, L.L., and Namsaraev, B.B., *Microcoleus* Mats from Alkaliphilic and Halophilic Communities, *Mikrobiologiya*, 2003, vol. 72, no. 1, pp. 84-92 [Microbiology (Engl. Transl.), vol. 72, no. 1, pp. 71-79].
7. Kompantseva, E.I., Sorokin, D.Yu., Gorlenko, V.M., and Namsaraev, B.B., The Phototrophic Community Found in Lake Khilganta (an Alkaline Saline Lake Located in the Southeastern Transbaikal Region), *Mikrobiologiya*, 2005, vol. 74, no. 3, pp. 410-419 [Microbiology (Engl. Transl.), vol. 74, no. 3, pp. 352-361].
8. Reznikov, A.A., Mulikovskaya, E.P. and Sokolov, I.Yu., *Metody analiza prirodnykh vod* (Analytical Methods for Natural Waters), Moscow: Nedra, 1970.
9. Kuznetsov, S.I. and Romanenko, V.I., *Mikrobiologicheskoe izuchenie vnutrennikh vodoemov. Laboratornoe rukovodstvo* (Microbiological Studies of Inner Water Bodies), Moscow, Akad. Nauk SSSR, 1963.
10. Ryter, A. and Kellenberger, E., Etude au microscope electronic des plasmas contenant de l'acide desoxyribonucleique. I. Les nucleoides des bacteries en croissance active, *Z. Naturforsch.*, 1958, vol. 13b, pp. 597–605.
11. Bryantseva, I.A., Gorlenko, V.M., Kompantseva, E.I., Imhoff, J.F., Sling, J., and Mityushina, L., *Thiorhodospira sibirica* gen. nov., sp. nov., a New Alkaliphilic Purple Sulfur Bacterium from a Siberian Soda Lake, *Int. J. Syst. Bacteriol.*, 1999, vol. 49, pp. 697–703.
12. Bryantseva, I.A., Gorlenko, V.M., Kompantseva, E.I., and Imhoff, J.F., *Thioalkalicoccus limnaeus* gen. nov., sp. nov., a New Alkaliphilic Purple Sulfur Bacterium with Bacteriochlorophyll *b*, *Int. J. Syst. Bacteriol.*, 2000, vol. 50, pp. 2157–2163.
13. Bryantseva, I.A., Gorlenko, V.M., Kompantseva, E.I., Achenbach, L.A., and Madigan, M.T., *Heliorestis daurensis*, gen. nov. sp. nov., an Alkaliphilic Rod-to-Coiled-Shaped Phototrophic Heliobacterium from a Siberian Soda Lake, *Arch. Microbiol.*, 1999, vol. 172, pp. 167–174.
14. Bryantseva, I.A., Gorlenko, V.M., Kompantseva, E.I., Kuznetsov, B.B., and Osipov, G.A., Alkaliphilic Heliobacterium *Heliorestis baculata* sp. nov. and Emended Description of the Genus *Heliorestis, Arch. Microbiol.*, 2000, vol. 174, pp. 283–291.
15. Sorokin, D.Yu., Tourova, T.P., Kuznetsov, B.B., Bryantseva, I.A., and Gorlenko, V.M., *Roseinatronobacter thiooxidans* gen. nov., sp. nov., a New Alkaliphilic Aerobic Bacteriochlorophyll *a*-containing Bacterium Isolated from a Soda Lake, *Mikrobiologiya*, 2000, vol. 69, no. 1, pp. 89-97 [Microbiology (Engl. Transl.), vol. 69, no. 1, pp. 75-82].
16. Kompantseva, E.I., Purple Nonsulfur Bacteria in Benthic Microbial Communities, *Cand. Sci. (Biol.) Dissertation*, Moscow: Inst. Microbiol., Russ. Acad. Sci., 1985.
17. Gorlenko, V.M., Kompantseva, E.I., Korotkov, S.A., Puchkova, N.N., and Savvichev, A.S., Phototrophic Bacteria of Shallow Saline Bodies of Water in the Crimea: Conditions in the Habitat and Species Composition, *Izv. Akad. Nauk SSSR, Ser. Biol.*, 1984, no. 3, pp. 362–374.