=== EXPERIMENTAL ARTICLES =

The Effect of the pH Level on the Communities of Anoxygenic Phototrophic Bacteria of Soda Lakes of the Southeastern Transbaikal Region

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Abstract—The effect of pH on the structure of the communities of anoxygenic phototrophic bacteria (APB) was studied under laboratory conditions. Samples of natural APB communities were inoculated into media that differed in pH values, which were 7, 9.5, or 10.5. The structure of the APB communities in the obtained enrichment cultures at all pH values depended also on the mineralization levels of the media, which were the same as in the lakes from which samples were taken. The same dependence of the community structure on salinity was observed as in the case of the natural communities that had been described previously. APB were most diverse in the enrichment cultures grown at pH 9.5. The shift of the pH to either neutral or extremely alkaline values restricted the species diversity within the APB community, resulting in marked predominance of the most adapted forms. It was shown that the status of *Ectothiorhodospira* species within the community could serve not only as an indicator of salinity but also as an indicator of pH in soda lakes with a water mineralization of higher than 5 g/l. The statuses of various APB groups in the community as dependent on pH and salinity are discussed, as well as possible changes in these statuses due to changes in the water level and other environmental parameters in the studied lakes.

Key words: soda lakes, anoxygenic phototrophic bacteria, effect of pH, alkalitolerant and alkaliphilic bacteria, water mineralization.

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Due to the physico-geographical conditions of the region, small shallow-water lakes widely occur in the cryoarid zone of the southeastern Transbaikal Region. The characteristic trait of these lakes, which distinguishes them from the majority of saline and hypersaline alkaline water bodies of other regions [1], is their relatively low water mineralization and salt reserve. Most lakes of the southeastern Transbaikal Region are brackish and vary in their degree of mineralization from fresh water bodies to weakly saline ones.

In recent years, the soda lakes of the southeastern Transbaikal Region, as well as the microbial communities inhabiting them, have attracted the attention of Russian microbiologists. There are two publications on the physical, geographical, and geological properties of the region, the chemical composition of the lake water, the mineral composition of bottom sediments, and the processes of organic matter destruction inthese lakes [2, 3].

The saline Lake Khilganta (the Agin–Buryat Autonomous Area) and the layered cyanobacterial mats developing on the surface of its bottom sediments have been studied in detail. The structure of these microbial mats, the composition of the main producers, cyanobacteria and anoxygenic phototrophic bacteria (APB), as well as the daily dynamics of the vertical stratification of phototrophic microorganisms as dependent on the physicochemical environmental parameters, were studied. The leading roles of anoxygenic photosynthesis in the organic matter production and of phototrophic bacteria in sulfide detoxification were demonstrated [4, 5].

The results of our long-term investigations of the phototrophic communities of 24 soda lakes of the southeastern Transbaikal Region are presented in a recently published work [6]. The main emphasis was placed on the structure of the APB communities as a function of the physicochemical parameters of the environment and on the adaptation of these microorganisms to their habitat. We have demonstrated that the soda lakes of the southeastern Transbaikal Region represent a unique type of habitat with a unique autochthonous microflora, different from both highly mineralized soda lakes and shallow saline water bodies of the sea origin.

The lakes of the southeastern Transbaikal Region were found to be a convenient model for studies of the

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effect that water mineralization exerts on the structure of the APB community. According to this parameter, the studied lakes encompass the whole salinity range from fresh water bodies to brackish and saline ones. Three groups of lakes with pronounced differences in the structure of the APB communities have been discerned, namely: (1) freshwater lakes (with a mineralization of less than 1 g/l; (2) lakes with water mineralization ranging from 1 to 5 g/l; and (3) brackish and saline lakes (5-40 g/l). Changes in the salinity level within a range from 5.0 to 40.0 g/l has virtually no influence on the structure of the APB communities, the variations in which were determined by other environmental parameters. A water mineralization lower than 5 g/l was a limiting factor that restricted the development of the haloalkalitolerant and haloalkaliphilic bacteria APB. The structure of the APB communities inhabiting lakes with a water mineralization lower than 1 g/l approached that of fresh neutral water bodies.

In addition to salinity, other environmental parameters (first of all, alkalinity and pH) may be the limiting factors in soda lakes. On the whole, instability of the water and chemical regimes is a characteristic trait of the soda lakes of the Transbaikal Region. The water level, mineralization, pH, and alkalinity are subject to significant seasonal and perennial fluctuations [2]. The structure of phototrophic communities cannot remain unaffected by these changes. However, based on the data obtained during the comparative study of natural phototrophic communities of the lakes of the southeastern Transbaikal Region, we managed to determine only the effect of salinity.

We were not able to determine the effect of pH on the community structure in the compared lakes because the main condition of such a study, a significant variability of the environmental parameter under consideration against the background of relative stability of other important parameters, was not met. The pH values in the studied lakes varied within ranges close to optimal for most APB, and only in a few lakes did they exceed pH 10 (Table 1). Earlier, we showed [6] that the APB isolated from the lakes grew well at pH 8–9 (alkalitolerants) or 9.0–9.5 (alkaliphiles). Moreover, it was difficult to determine the effect of pH due to the instability of this parameter, as well as due to the fact that the more pronounced effect of salinity masks its influence.

The goal of this work was to study the influence of various pH values on the structure of the APB communities under laboratory conditions. For this purpose, samples of natural APB communities were placed under artificial conditions with fixed parameters.

MATERIALS AND METHODS

The subjects of this study were the benthic APB communities from 15 soda lakes of the southeastern Transbaikal Region, located in the Onon District of Chita oblast (Lakes Barun-Torei, Ostozhe, Ilim-Torom,

Malyi Kasytui, and Dabasa-Nur) and the Agin–Buryat Autonomous Area (Lakes Gorbunka, Gonzogor, Khilganta, Bezymyannoe, and Nozhei), as well as in the Dzhidin (Lakes Verkhnee Beloe, Nizhnee Beloe, and Tsaidam) and Selenga (Lakes Selendumskoe and Sul'fatnoe) Districts of Buryatia.

Samples of microbial mats and films were collected during field investigations carried out in 1995 by joint expeditions of the Winogradsky Institute of Microbiology, Russian Academy of Sciences (Moscow) and the Institute of General and Experimental Biology, Siberian Division, Russian Academy of Sciences (Ulan-Ude).

To study the effect of pH on the structure of APB communities, the samples were inoculated under anaerobic conditions in duplicates into selective liquid media (pH 7, 9.5, and 10.5) in 60-ml vials with screw caps. The composition of the media is described in our previous work [6]. The concentrations of NaCl and soda in the media corresponded to the salinity and alkalinity values in the particular studied lake. The acidity of the medium was varied by varying the sodium carbonate/bicarbonate ratio in the medium without changing their total concentration. Inoculated media were incubated in a luminostat at an illumination intensity of about 2000 lx and 25–30°C.

APB of various groups in the obtained enrichment cultures were enumerated by agar-shake dilution series method on medium of the same composition. The pigmented colonies obtained were counted under a microscope. The APB were preliminary identified on the basis of colony pigmentation, cell morphology, formation of cell aggregates, mode of reproduction, motility, presence or absence of gas vesicles and intra- or extracellular particles of sulfur, etc.

RESULTS AND DISCUSSION

Since in the studied lakes the acidity and other parameters are subject to significant fluctuations, of particular interest is the manner in which the phototrophic community responds to these changes, as well as which organisms are well adapted to unstable acidity, and which of them are adapted to lower or extremely high pH values.

To clarify these issues, samples of microbial mats and films from each lake were placed under conditions that were identical in all parameters (composition of the medium, temperature, illumination intensity) but differed in the pH values of the media (7, 9.5, and 10.5). In the obtained microbial communities, APB enumeration was performed (Table 1).

The Effect of pH on the Structure of the APB Communities

First of all, it should be noted that the structure of APB communities in the enrichment cultures

THE EFFECT OF THE pH LEVEL

					APB cell numbers in the enrichment cultures, log (cell/ml)									
Lake**	Lal	ke pro	operties***	ent	Ectothiorhodospi- raceae					Purple nonsul- fur bacteria		Green fila- mentous bacteria		
	Hq	Mineralization, g/l		pH	Ectothio- rhodospira	Thiorhodospira	Allochromatium Marichromatium Thiocystis	Amoebobacter Thiocapsa	Thioalkalicoccus	Rhodobacter Rhodovulum Rhodobaca	Rhodopseudo- monas	Oscillochloris	Heliobacteriaceae	
Nozhei	8.9	0.5	0.4	7	-	_	6	6	-	7****	6	4	_	
Selendumskoe	8.0	0.7	0.3	9.5 10.5 7 9.5 10.5	- - - -	- - -	6 - 6 5 -	3 - - 6 -	_ _ _ _	3 - 6 -	- 5 -	3 3 -	_ _ _ _	
Bezymyannoe	9.2	0.8	0.7	7 9.5	$-\frac{-}{4}$	-	7 4	$\frac{-}{5}$		6 -	4	2 4	_ _	
Gonzogor	9.3	0.9	0.8	10.5 7 9.5	$-\frac{-}{3}$	_ _ _	4 5 3	- 2 6	_ _ _	- 8 -	_ 7 _	$\frac{-2}{3}$	_ _ _	
Barun-Torei	9.1	1.8	0.7	10.5 7 9.5	- - 7	- - -	5 5 5	$\frac{-}{2}$	_ _ _	5 8 -	- 6 -	$\begin{array}{c} -\\ 2\\ 2\end{array}$	_ _ _	
Malyi Kasytui	9.5	2.0	1.6	10.5 7 9.5	6 - 4	- - 5	2 6 5	- - 6	_ _ _	- 7 3	_ _ _	- - 5	7 _ _	
Ostozhe	9.2	2.2	1.1	10.5 7 9.5	6 - -	_ _ _		- - 7	_ _ _	- 7 -		_ _ _	_ _ _	
Ilim-Torom	9.5	2.5	1.8	10.5 7 9.5	4 - 5	- - 4	- - 6	- - 3	_ _ _	- 6 - 7	- - -	_ _ _	6 - -	
Nizhnee Beloe	9.8	3.7	2.0	10.5 7 9.5	- - 7	- - 3	- - 4	- - 5	$-\frac{-}{3}$	7 8 4	_ _ _	4	-	
Gorbunka*	9.8	6.5	1.1	10.5 7 9.5 10.5	- 8 5	_ _ _	- 7 7	_ _ _	- - 5	- 5 6 4	-	_ _ _	-	
Verkhnee Beloe	10.1	7.5	4.1	10.3 7 9.5 10.5	- 8 7	_ _ 4	- 6 -	-	_ _ 4	8 4	-	- 2	-	
Sul'fatnoe	9.2	7.7	1.1	7 9.5	- 8	-	7	-	_ _ _		-	_ _ _	-	
Dabasa-Nur	9.4	10.0	1.0	10.5 7 9.5	5 - 5	_ _ _	- 5 -	-		4 5	_ _ _	_ _ _	_ _ _	
Tsaidam	10.2	15.8	5.2	10.5 7 9.5	6 - 6	- - -	- 4 -	- - -	— — —	6 8 -	- - -	– – –	_ _ _	
Khilganta	9.5	40.0	1.5	10.5 7 9.5 10.5	8 - 7 8	— — —	- 6 6	- - 5	— — —	5 4	_ _ _	– – –	_ _ _	
* Some colu	nne re		n coveral A D					-	Ļ —		-	_		

Table 1. Cell numbers of various groups* of APB in enrichment cultures grown at various pH values

 * Some columns report on several APB genera which cannot be distinguished without special studies.

** The lake list is sorted in order of increasing lake water mineralization.

*** Data from [6].

**** The cell numbers of the dominant APB groups are shown in bold italic.

depended, at all pH values, on water mineralization, which was the same as in the relevant lakes. We observed the same dependency of the community structure on salinity as that detected in the studied natural communities [6]. For instance, the enrichment cultures grown at the water mineralization levels lower than 1 g/l, 1-5 g/l, and higher than 5 g/l were different with respect to the structure of the APB communities. Thus, the effect of pH must be considered separately for each salinity range.

In the enrichment cultures from freshwater lakes (with salinity lower than 1 g/l), representatives of the family *Chromatiaceae* were dominant at pH 9.5. Bacteria of the genus *Oscillochloris* were present constantly, whereas members of Ectothiorhodospiraceae and Rhodobacteraceae were found only in a few lakes and in low numbers. At pH 10.5, the growth of the APB in the freshwater enrichments was weak or absent. At pH 7, purple bacteria belonging to Allochromatium-Thiocystis and Rhodobacteraceae were predominant. Purple nonsulfur bacteria of the genus Rhodopseudomonas were also abundant. These microorganisms were found only at pH 7 and only in these lakes and in Lake Barun-Torei. Members of the genus Oscillochloris were less abundant.

In the enrichment cultures from the lakes with water mineralization from 1 to 5 g/l at pH 9.5 representatives of the families *Ectothiorhodospiraceae* and *Chromati*aceae were alternately predominant. Rhodobacteraceae and Oscillochloris spp. were found occasionally. Heliobacteria or representatives of Ectothiorhodospiraceae or Rhodobacteraceae were predominant in different lakes at pH 10.5. At pH 7, members of the family Rhodobacteraceae prevailed or were the only APB. In Lake Barun-Torei, Rhodopseudomonas sp. and Oscillochloris sp. were also detected. Lake Barun-Torei is intermediate in the water mineralization (1.8 g/l) between freshwater and brackish lakes. In the enrichment cultures obtained from this lake, members of the genus Ectothiorhodospira were predominant at pH 9.5; at pH 7, neutrophilic freshwater bacteria of the genus Rhodopseudomonas were present.

In the enrichment cultures from all the studied lakes with a water mineralization of 5–40 g/l, members of the family *Ectothiorhodospiraceae* prevailed at pH 9.5. Bacteria of the families *Chromatiaceae*, *Rhodobacteraceae*, and, in one case, *Oscillochloris* sp. were also present. Either *Ectothiorhodospira* sp. or *Ectothiorhodospira* sp. and *Rhodobacteraceae* developed at pH 10.5, whereas, at pH 7, only *Allochromatium–Thiocystis* and *Rhodobacteraceae* were detected.

Thus, the APB were most diverse in the enrichment cultures developing at pH 9.5. The structure of the APB communities and its variations depending on the salinity levels were similar to those of natural communities (Tables 1 and 2). However, the species diversity and evenness were somewhat lower as compared to natural samples. The occurrence frequency of various APB groups in the enrichment cultures (Table 2) at pH 9.5 was often lower than that in natural samples of microbial mats and films, for which APB enumeration was also performed at pH 9.5. It is obvious that this phenomenon was caused by the higher homogeneity of the culture conditions as compared with the natural habitats, where microzonality and gradients of physicochemical parameters are observed.

The shift of the pH to either neutral or extreme alkaline values usually limited the APB diversity and caused changes in the composition of APB communities (Table 2). Hence, the pH values of 7 and 10.5 were the limiting factors for the phototrophic communities and affected the APB species diversity, restricting it to alkalitolerant and neutrophilic or to alkaliphilic species.

Although this work studied the effect of pH on the structure of APB communities, the results in fact reflect the simultaneous effect of pH and salinity. The conditions in which the obtained enrichment cultures were grown formed a continuous series from freshwater (pH 7) to saline (pH 10.5) ones. In this series, regular gradual succession of communities was observed, from freshwater to haloalkaliphilic ones. In the former case, the presence of neutrophilic bacteria of the species *Rhodopseudomonas* was the most indicative; in the latter case, the monopoly of *Ectothiorhodospira*.

The effect of high salinity on the structure of APB communities had been previously studied in shallow saline water bodies of sea origin (the Crimean steppe). In these water bodies, the growth of APB communities at pH 7.5–8.5 is limited only by extremely high mineralization (higher than 200–250 g/l). The species diversity of APB was low; representatives of the family Ectothiorhodospiraceae, being the most adapted to the conditions mentioned above, prevailed and, at higher salinity levels, even monopolized the community [7, 8]. The present study has demonstrated that, in the soda lakes of the southeastern Transbaikal Region with water mineralization ranging from 5 to 40 g/l, similar changes in the structure of APB communities are caused by an increase in the pH level to extreme values. At pH 9.5, members of Ectothiorhodospiraceae were predominant; at pH 10.5 they monopolized the community (sometimes together with *Rhodobacteraceae*).

All the water bodies studied in the present work were soda lakes, although, at the moment of sampling, the water was diluted by rainfall. Even at a water mineralization lower than 1 g/l, the alkalinity level was 0.3–0.8 g/l, and alkalitolerant bacteria prevailed in the APB communities.

The Response of Various APB Groups to pH

The maximum diversity of the APB at pH 9.5 and the mineralization level higher than 1 g/l (Table 2) indicates that most APB inhabiting the soda lakes of the

		pH of the medium	Ectothiorho- dospiraceae		Chi	romatiac	eae	Purple fur ba	nonsul- cteria	Green fila- mentous bacteria		
Lake type	Isolation source		Ectothiorhodospira	Thiorhodospira	Allochromatium Marichromatium Thiocystis	Amoebobacter Thiocapsa	Thioalkalicoccus	Rhodobacter Rhodovulum Rhodobaca	Rhodopseudomonas	Oscillochloris	Heliobacteriaceae	Numbers of detected APB groups
r wer	Sample***	pH 9.5	50	0	100	100	0	100	0	75	0	5
Lakes with water mineralization lower than 1 g/l	Enrichment cultures	pH 7	0	0	75	50	0	100	100	75	0	5
		pH 9.5	50	0	100	100	0	25	0	100	0	5
		pH 10.5	0	0	50	0	0	25	0	0	0	2
ter	Sample	pH 9.5	80	60	80	80	0	100	0	80	40	7
Lakes with water mineralization from 1 to 5 g/l	nt	pH 7	0	0	40	20	0	100	20	20	0	5
	Enrichment cultures	pH 9.5	60	60	80	100	20	40	0	60	0	7
	Enrichm cultures	pH 10.5	80	0	20	0	0	20	0	0	40	4
Lakes with water mineralization from 5 to 40 g/l	Sample	pH 9.5	100	17	83	83	67	100	0	67	0	7
	nt	pH 7	0	0	100	0	0	100	0	0	0	2
	Enrichment cultures	pH 9.5	100	17	33	17	33	83	0	17	0	7
	Enrichm cultures	pH 10.5	100	0	0	0	0	33	0	0	0	2

Table 2. Occurrence (%)* of various APB groups** in microbial films sampled from the studied lakes, as well as in enrichment cultures obtained at various pH values

* The percentage of the studied lakes where microbial films or enrichment cultures obtained from them contained representatives of a particular APB group.

** Some columns report on several APB genera which cannot be distinguished without special studies.

*** Data from [6].

southeastern Transbaikal Region are best adapted to these conditions.

It has been previously demonstrated that the APB inhabiting the soda lakes of the southeastern Transbaikal Region are represented by both alkaliphilic and alkalitolerant species [6]. Alkalitolerant microorganisms are represented by purple sulfur bacteria of the *Allochromatium–Thiocystis* and *Amoebobacter–Thiocapsa* morphotypes, as well as by purple nonsulfur bacteria of the family *Rhodobacteraceae*; alkaliphilic bacteria are represented by *Ectothiorhodospira*, *Thiorhodospira* sibirica, *Thioalkalicoccus* limnaeus, and heliobacteria.

The obligately alkaliphilic species of the genera *Thiorhodospira*, *Thioalkalicoccus*, and *Heliorestis*

were not detected in the enrichment cultures from the lakes with a water mineralization lower than 1 g/l (irrespective of the pH values), as well as from the lakes with a higher mineralization at pH 7.

Purple sulfur bacteria of the *Amoebobacter–Thio capsa* morphotype preferred a low water mineralization (up to 5 g/l) and pH 9.5. The range of conditions favorable for the growth of bacteria belonging to the *Allochromatium–Thiocystis* morphotype was wider. In the enrichments grown at a low water mineralization, these bacteria were detected at various pH values, whereas, in media with salinity more than 5 g/l, they grew mainly at pH 7. According to our preliminary results, in freshwater and saline lakes these bacteria represent different taxa.

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Rhodobacteraceae were found in most samples collected in both freshwater, brackish, and saline lakes at various pH values, as well as in the enrichment cultures obtained from these samples. Under laboratory conditions, isolates of Rhodobacteraceae turned out to be alkalitolerants growing within a broad pH range with an optimum at about 8.5 [6]. It is obvious that their active development at pH 7 is associated with the lack of strong competition with purple sulfur bacteria, rather than with their preference for neutral conditions. It is also likely that there exist different taxa growing under either neutral or alkaline conditions. For example, members of the family *Rhodobacteraceae* were found in the enrichment cultures obtained from Lakes Gonzogor and Ilim-Torom at pH 7 and 10.5; they were not hovever detected at pH 9.5. The fact that bacteria of the family *Rhodobacteraceae* are present and even predominant under extreme alkaline conditions is of particular interest, and these bacteria are currently under study.

Purple nonsulfur bacteria of the genus *Rhodo-pseudomonas* were not detected during the APB enumeration in natural samples. They were detected only in enrichment cultures at pH 7 and water mineralization lower than 2 g/l and were represented by a typical neutrophilic freshwater microorganism, which is eurybiotic and probably allochthonous and enters the lake with runoff from the land surface. Its presence indicates that freshwater soda lakes are in a position between ordinary freshwater lakes and true soda lakes.

Members of the genus *Oscillochloris* grew in enrichment cultures at a mineralization lower than 1 g/l and pH values of 7 and 9.5; in the cultures with mineralization higher than 1 g/l, they grew only at pH 9.5. Evidently, freshwater bacteria of the genus *Oscillochloris* are better adapted to neutral conditions than the strains from brackish lakes.

Heliobacteria were detected in the samples and enrichment cultures obtained at pH 10.5 from two lakes, Barun-Torei and Ostozhe (water mineralization higher than 1 g/l). These microorganisms are probably distributed more widely, but remain underestimated, since they show poor growth under laboratory conditions.

Members of *Ectothiorhodospiraceae* developed only at high pH and mineralization levels. They were not detected in freshwater enrichments at pH 10.5 or in any of the cultures obtained at pH 7, including saline ones. Their proportion in APB communities increased with an increase in the pH and salinity levels.

We have previously demonstrated [6] that members of the family *Ectothiorhodospiraceae* inhabiting the studied lakes may be considered indicators of the water mineralization level. Their paucity or absence corresponded to the water mineralization level of lower than 1 g/l; their presence as a constant although not predominant component was observed at a water mineralization from 1 to 5 g/l, whereas they were predominant at a water mineralization higher than 5 g/l. According to the results of the present work, *Ectothiorhodospira* may also be considered indicators of water alkalinity in soda lakes with a mineralization higher than 5 g/l. They were not detected at pH 7 and were predominant at pH 9.5; at pH 10.5, they monopolized the community (alone or together with *Rhodobacteraceae*).

The water level in shallow water bodies is subject to considerable fluctuations. It may rise during periods of snow thawing or rainfall or decrease to the point of water body drying. Ectothiorhodospira are the most competitive microorganisms, both under the conditions of increased mineralization and a pH increase to extreme values. Obviously, with the periodic increases in mineralization or pH, the domination of Ectothiorhodospira among the APB should increase. On the contrary, some alkalitolerant members of the families Chromatiaceae and Rhodobacteraceae gain an advantage from water dilution and the subsequent decrease in the pH and salinity levels. Freshwater bacteria of the genus *Rhodopseudomonas* were detected as the levels of pH and mineralization decreased further. The most eurybiotic microorganisms are the representatives of the family *Rhodobacteraceae*, which were detected in samples and enrichments at all pH and salinity levels. High adaptability to the unstable conditions of the habitat is the characteristic trait of most representatives of this group. When the lakes dry up, spore-forming heliobacteria gain an advantage. Under laboratory conditions, they dominated the cultures obtained from dry microbial mats. It is noteworthy that no APB growing at both low water mineralization (lower than 5 g/l) and extremely alkaline pH were detected. It is possible that these conditions may be most favorable for halotolerant and alkaliphilic heliobacteria [6]. These microorganisms were found in the enrichment cultures obtained from two lakes with a water mineralization of approximately 2 g/l and pH 10.5. The distribution area of heliobacteria is probably wider, but they cannot be easily detected due to the fact that they are strict anaerobes and, therefore, cannot tolerate even transient contacts with oxygen.

The APB communities of the soda lakes of the southeastern Transbaikal Region consist of microorganisms that differ in their physiological properties, have different pH and salinity optima, and are adapted to different types of habitat. At the pH level of 9.5, which was average for the studied lakes, considerable diversity and evenness of the species composition were observed in the APB communities. The shift of the pH to either neutral or extremely alkaline values was the limiting factor that usually restricted the species diversity within the APB community, resulting in marked predominance of the most adapted forms.

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