ISSN 0026-2617, Microbiology, 2009, Vol. 78, No. 5, pp. 643–649. © Pleiades Publishing, Ltd., 2009.
Original Russian Text © E.I. Kompantseva, A.V. Komova, I.I. Rusanov, N.V. Pimenov, D.Yu. Sorokin, 2009, published in Mikrobiologiya, 2009, Vol. 78, No. 5, pp. 709–715.

EXPERIMENTAL ARTICLES

Primary Production of Organic Matter and Phototrophic Communities in the Soda Lakes of the Kulunda Steppe (Altai Krai)

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Received December 9, 2008

Abstract—The rates of photosynthesis and dark CO_2 fixation were determined in 12 soda lakes of the Kulunda steppe. Characterization of the phototrophic communities was given, and the cell numbers of anoxygenic phototrophic bacteria (APB) were determined. The photosynthetic production in different lakes was substantially different, constituting from 0.01 to 1.32 g C m^{-2} day^{-1}. The main part of carbon dioxide was assimilated in the process of oxygenic photosynthesis. Anoxygenic photosynthesis was recorded only in 5 of the 12 lakes studied. Its values varied between 0.06 and 0.42 g C m^{-2} day^{-1}, constituting from 8 to 34% of the total photosynthetic activity. Anoxygenic photosynthesis was revealed in the lakes where the number of APB reached 10^7–10^9 CFU cm^{-3}. Dark CO_2 fixation constituted 0.01–0.15 g C m^{-2} day^{-1}. Positive correlation was observed between the primary production value and water alkalinity. No relationship between productivity and water mineralization was revealed in the 30–200 g l^{-1} range, whereas an increase in salinity above 200 g l^{-1} suppressed the photosynthetic activity. The mechanisms of influence of the environmental factors on the rate of photosynthesis are discussed.

Key words: primary production, soda lakes, oxygenic and anoxygenic photosynthesis, water alkalinity, mineralization.

DOI: 10.1134/S002626170905018X

Soda lakes attract the attention of microbiologists from many laboratories of the world. Due to increased mineralization and alkalinity, the biota of soda lakes predominantly consists of prokaryotic organisms whose metabolism is distinguished by a number of features determined by the specifics of the conditions of existence. Of the soda habitats, many new taxa of virtually all known physiological groups of microorganisms have been revealed and described [1]. An increasing interest in extremely alkaliphilic microbial communities is connected with the hypothesis considering them as a relict analogue of the terrestrial biota of the early Proterozoic era [2].

Despite the extreme conditions (high mineralization and alkalinity), many soda lakes are among the most productive natural ecosystems. First and foremost, this concerns the soda lakes of the East African Rift, which are the best-studied in this respect and where the rate of photosynthesis may exceed 10 g C m^{-2} day^{-1} [3, 4]. The meromictic soda lakes of North America [5, 6], also studied in detail, appear to be slightly less productive (up to 3 g C m^{-2} day^{-1}).

The soda lakes of the cryoarid zone of Central Asia have been studied less thoroughly. The physicochemical characteristics of this region, such as the geological structure, the relief of the area, the poorly developed river network, the extremely continental dry climate, permafrost, and seasonal frozen ground are conducive to the formation of numerous small shallow soda lakes. By their physicochemical characteristics, these lakes differ significantly from the African and North American reservoirs. One of the most characteristic features of the lakes of the cryoarid zone is the extreme instability of their water and chemical regimes. Despite the wide spread and multiplicity of Central Asian soda lakes, the data on their productivity is restricted to several works pertinent to the lakes of the Transbaikal Region (Chita oblast, Buryat Republic) and Mongolia [7, 8].

This work was designed to study the production processes in the soda lakes situated in the cryoarid zone of southern Siberia, in the Kulunda steppe (Altai krai). Apart from determining the primary production, we were to characterize the phototrophic communities, to analyze the influence of the environmental factors on productivity, and to compare the Kulunda lakes with the soda reservoirs in other regions.

MATERIALS AND METHODS

The primary production was determined by the radioisotopic method. Pieces of the bacterial mat or upper sediment layer (2 cm^2) containing phototrophic

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microorganisms were sampled and placed into 20-ml glass flasks, to which lake water was added. Lake Iodnoe, from which water samples were taken, was an exception. In order to determine the primary production, 0.2 ml of sodium ^{14}C-bicarbonate (10 μCi) was introduced into the flasks with a sample and closed hermetically. Diuron (3-(3,4-dichlorophenyl)-1,1-dimethylurea) at a concentration of 7 μM was used as an inhibitor of oxygenic photosynthesis. The flasks intended for determining dark CO_2 fixation were wrapped in foil. All the samples were incubated for 6–12 h at the sampling site and then fixed by introducing 1 ml of a 40% formaldehyde solution into the flask. Further sample treatment was carried out at a laboratory. The samples were filtered through Millipore filters. The filters were placed into the reaction flask, 100 ml of water was added, and a reflux condenser was attached; the samples were acidified through a dropping tube with dilute orthophosphoric acid. The acidified sample was bubbled with air with constant heating for 1–1.5 h to completely remove the ^{14}C-bicarbonate that had not been assimilated. Then, 25 g of potassium persulfate was added to the flask, and the carbon dioxide formed as a result of chemical oxidation of organic compounds (wet burning) was sublimed with constant boiling for 1.5 h. The $^{14}CO_2$ that had been incorporated from ^{14}C-bicarbonate into the bacterial biomass was trapped with an absorbing fluid. A RackBeta scintillation counter (LKB, Sweden) was used to measure the radioactivity of the sample. The rate of carbon dioxide assimilation by the bacteria was calculated by the standard method [9] with taking into account the content of bicarbonate ion in the water.

Anoxygenic phototrophic bacteria (APB) were enumerated by agar shake dilution series method. The mineralization and alkalinity of the media corresponded to the parameters of the lakes studied. In addition to NaCl, $NaHCO_3$, and Na_2CO_3, the media contained (g l^{-1}) the following: KH_2PO_4, 0.5; NH_4Cl, 0.5; $MgCl_2 \cdot 6\ H_2O$, 0.2; sodium acetate, 0.5; sodium malate, 0.5; yeast extract, 0.1; $Na_2S \cdot 9\,H_2O$, 0.2; as well as 1 ml l^{-1} of trace element solution and 20 μg l^{-1} of vitamin B_{12}; the pH of the was 9.5. The inoculated media were incubated in a luminostat at 25°C and light intensity of about 2000 lx.

RESULTS AND DISCUSSION

17 saline soda lakes of the Kulunda steppe (Altai krai), different in their physicochemical characteristics, were studied by us in the course of the expedition in July 2006 (table). The lake depth in the period of the field works was small, 10–30 cm on average. Only Lake Iodnoe was several meters deep. The total mineralization in the lakes varied between 30 and 280 g l^{-1}; the total alkalinity, between 0.01 and 2.8 g-equiv l^{-1}. The pH values varied between 8.1 and 10.3. On the whole, the lakes studied are characterized by small sizes, shallowness, a wide range of salinity and alkalinity, as well as by an extreme instability of the water and chemical regimes.

Characterization of the Phototrophic Communities

In most lakes, phototrophic microorganisms were part of the benthic communities, developing in the form of thin (0.5–3 mm) cyanobacterial mats or a stained loose layer on the surface of sediment deposits. Filamentous cyanobacteria of the family *Oscillatoriaceae* formed the mat basis. Filamentous green algae occurred in moderately mineralized lakes (less than 100 g $^{-1}$). Mass development of the planktonic forms of unicellular green algae (presumably *Chlorella* sp.), the so-called water blooming, was observed only in one lake (Iodnoe), which was several meters deep and where industrial effluents were discharged. In some lakes with highly mineralized water, the chlamydomonads *Dunaliella viridis* and halobacteria were also present; however, no green or red staining of water as a result of mass development of these organisms was observed. In many lakes, a high number of the crustaceans *Artemia* sp. was noted.

Visually noticeable accumulations of anoxygenic phototrophic bacteria (APB) in the form of lilac–pink layers in bacterial mats were noted only in several lakes (Petukhovo, Gorchina-1, and Gorchina-2) with the water mineralization of 60–200 g l^{-1}, alkalinity of 0.9–2.8 g-equiv l^{-1}, and active sulfate reduction in the sediments. However, the enumeration of APB showed their presence in all the lakes studied. The number of APB in 17 Altai krai soda lakes, determined by inoculating nutrient media with serial dilutions, varied between 10^3 and 10^9 CFU cm^{-3} (table). In all the lakes, purple sulfur bacteria of the family *Ectothiorhodospiraceae* were present and dominated among the anoxygenic phototrophs. Their number in the cyanobacterial mats and in the upper layer of loose benthic deposits reached 10^7–10^9 CFU cm^{-3}. In 14 of 17 lakes with the water mineralization not greater than 200 g l^{-1}, spheroidene-containing nonsulfur purple bacteria of the family *Rhodobacteraceae* were also revealed (10^3–10^8 CFU cm^{-3}). Purple sulfur bacteria of the family *Chromatiaceae* were less widespread: *Halochromatium* sp. (10^4–10^7 CFU cm^{-3}) were found in six lakes with a salinity of 60–160 g l^{-1}; *Thiocapsa* sp. (10^4 CFU cm^{-3}) was found in one lake (40 g l^{-1}). At a higher salinity (200–300 g l^{-1}), *Ectothiorhodospiraceae* were the only APB in the benthic microbial community. In lakes with different mineralization and alkalinity values, *Ectothiorhodospiraceae* and *Rhodobacteraceae* were represented by different morphotypes. Their taxonomic status is currently under study; genetic analysis is to be carried out. According to the preliminary data, at least eight APB species were found in the lakes studied. Thus, the communities of APB in the Kulunda lakes bear much similarity to the communities of the slightly mineralized soda lakes of the Transbaikal Region described by us earlier [10], differing from them by a

Physicochemical conditions, CO_2 fixation rate, and number of anoxygenic phototrophic bacteria (APB) in the studied soda lakes of Altai krai

Station no.	Lake name*	Mineralization, g l^{-1}	H_2S in sediments	pH	Alkalinity, g-equiv l^{-1}		CO_2 fixation rate, g C m^{-2} day^{-1}				APB number, log CFU** cm^{-3}
					Total	CO_3^{2-}	Oxygenic photosynthesis	Oxygenic photosynthesis	Anoxygenic photosynthesis	Dark CO_2 fixation	
2KL-06	Lomovoe	280		8.1	0.01	0	0.04	0.04	0	0.05	3
3KL-06	Kochkovoe	240		8.5	0.01	0	0.01	0.01	0	0.01	3
8KL-06	Pechatnoe	200		9.5	0.17	0.10	0.12	0.12	0	0.06	5
9KL-06	Bezymyannoe-1	30		10.2	0.20	0.15	0.25	0.25	0	0.04	3
14KL-06	Bezymyannoe	40		10.2	0.21	0.15	0.12	0.12	0	0.04	6
7KL-06*	Iodnoe	120		9.6	0.35	0.20	0.50	0.50	0	0.08	5
10KL-06	Zhivopisnoe	90		10.1	0.50	0.45	0.80	0.80	0	0.04	6
1KL-06	Petukhovo	60	+	10.3	0.90	0.85	0.74	0.62	0.12	0.05	8
6KL-06	Tanatar-3	112	+	10.1	1.13	0.90	0.67	0.60	0.07	0.06	7
17KL-06	Gorchina-2	80	+	10.3	1.25	1.05	1.32	1.04	0.28	0.12	9
4KL-06	Tanatar-1	200	+	10.0	1.57	1.30	0.76	0.70	0.06	0.06	8
15KL-06	Gorchina-1	200	+	10.2	2.83	2.25	1.22	0.80	0.42	0.15	9

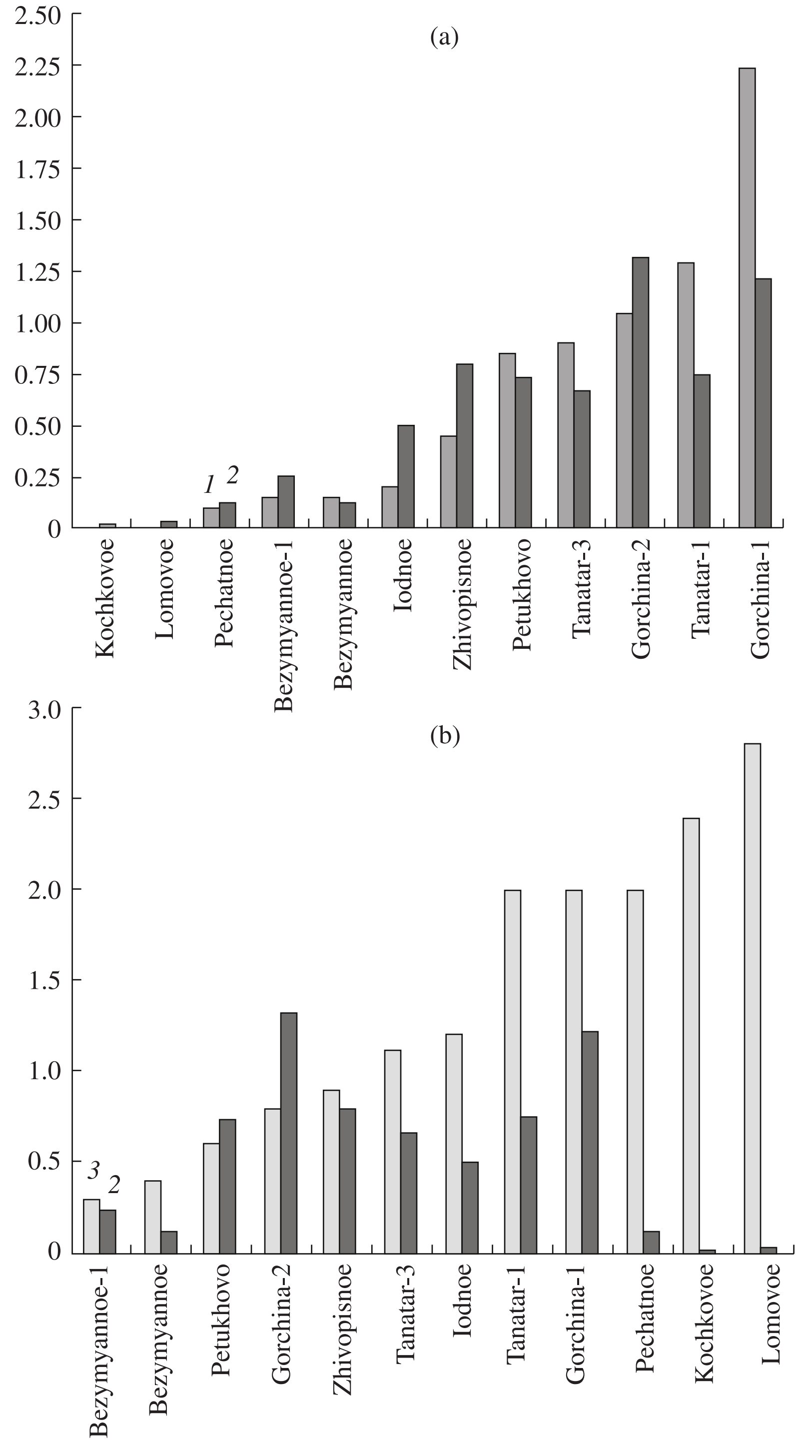
Notes: * The list of lakes is arranged according to increasing alkalinity.
** CFU, colony-forming units.

smaller species diversity and a more marked dominance of ectothiorhodospiras, which is due to the higher mineralization of the Kulunda lakes.

Productivity of the Lakes Studied

In 12 soda lakes of the Kulunda steppe, the rates of photosynthesis and dark CO_2 fixation were determined (table). Photosynthetic production was substantially different in different lakes, constituting from 0.01 to 1.32 g C m^{-2} day^{-1}. Most of the carbon dioxide was assimilated in the process of oxygenic photosynthesis. Anoxygenic photosynthesis was recorded only in 5 of the 12 lakes studied. Its value varied between 0.06 and 0.42 g C m^{-2} day^{-1}, constituting 8 to 34% of the total photosynthetic activity. The data obtained correlate with the results of the enumeration of APB. Anoxygenic photosynthesis was revealed in the lakes where the number of APB attained 10^7–10^9 CFU cm^{-3} (table). In the lakes where the APB number was below 10^7 CFU cm^{-3}, the photosynthetic activity of APB was lower than the sensitivity limit of the method used. Dark CO_2 fixation constituted 0.01–0.15 g C m^{-2} day^{-1}.

The maximum rate of photosynthesis (total photosynthesis of 1.22–1.32 g C m^{-2} day^{-1}) was noted in Lakes Gorchina-1 and Gorchina-2 with different mineral content of the water (200 and 60 g l^{-1}) and high alkalinity (1.25–2.83 g-equiv l^{-1}). The photosynthetic activity in Lake Tanatar-1, Lake Tanatar-3, and Lake Petukhovo with a water alkalinity of 0.9–1.57 g-equiv l^{-1} was somewhat lower (0.67–0.76 g C m^{-2} day^{-1}). A similar productivity (0.5 and 0.8 g C m^{-2} day^{-1}) was characteristic of Lake Iodnoe and Lake Zhivopisnoe (alkalinity of 0.35–0.5 g-equiv l^{-1}) subject to anthropogenic contamination (industrial effluents and a cow-shed). In Lake Pechatnoe, Lake Bezymyannoe-1, and Lake Bezy-



Rates of photosynthesis in the Kulunda soda lakes at different (a) water alkalinity and (b) water mineralization: (*1*) alkalinity, g-equiv l^{-1}; (*2*) photosynthesis rate, g C m^{-2} day^{-1}; (*3*) mineralization, 100 g l^{-1}.

myannoe with a moderate alkalinity (0.2 g-equiv l^{-1}), the rate of light CO_2 fixation constituted 012–025 g C m^{-2} day^{-1}. The least productive (0.01–0.04 g C m^{-2} day^{-1}) were the hypersaline lakes Lomovoe and Kochkovoe with a low water alkalinity. On the whole, we observed a positive correlation between alkalinity and the rate of photosynthesis in the lakes studied (Fig. 1a). The variations in water salinity between 30 and 200 g l^{-1} were not accompanied by regular changes in the primary production value; however, in hypersaline (more than 200 g l^{-1}) lakes, a decrease in the photosynthetic activity was noted (Fig. 1b).

The Influence of the Environmental Factors on the Productivity of the Soda Lakes

The relationship between productivity and alkalinity was also recorded in one of the East African soda lakes (Lake Nakuru). It was established that the phytoplankton abundance, including the abundance of the main producer, *Spirulina platensis*, and some diatoms, increases with an increase in water alkalinity [4].

The positive effect of alkalinity on the rate of photosynthesis can be explained by several reasons. For highly mineralized lakes, this may be a decrease in osmotic pressure. D.Yu. Sorokin showed that the osmotic pressure of a soda solution is twice as low as that of a NaCl solution at the same concentration [11]. Hence, the larger the proportion of carbonates among the anions (alkalinity), the lower the osmotic pressure of the brine. In this sense, it is interesting to compare Lakes Gorchina-1, Tanatar-1, and Pechatnoe with different water alkalinity and the same water mineralization (200 g l^{-1}). The rate of photosynthesis in these lakes increased with their alkalinity. The NaCl concentration higher than 200 g l^{-1} (3.5 M) prevents many phototrophic organisms from developing; however, if carbonates and/or sulfates are present among the anions, the total salt concentration favoring photosynthesis may be significantly higher.

The mechanism of influence of alkalinity on productivity may be linked to the increase in the available bicarbonate (at pH below 10.5), as well as to other changes in the salt composition. A considerable content of biogenic elements is usually considered to be one of the factors contributing to the high productivity of soda lakes. However, this is not true of all the lakes. Thus, limitation of photosynthesis by phosphorus was shown for the East African soda Lake Sonachi [12], but it turned out that what is of primary importance is the nitrogen to phosphorus ratio, and not their concentrations, which are usually used for predicting lake productivity. If the N/P ratio is within 10–17, the limitation by nitrogen, phosphorus, or both elements is possible, but if it exceeds 17, the limitation by phosphorus will be observed irrespective of the element concentrations. Unfortunately, we do not know the content of biogenic elements in the Kulunda lakes studied; however, we may suggest that it increases with the increase in alkalinity and the decrease in the calcium concentration.

The differences in the productivity of lakes whose water mineralization below 15% might also be connected with grazing of photosynthetic organisms by the alkaliphilic crustaceans *Artemia* sp., which are widely spread and whose number often attains very high values in the Kulunda lakes. This may be one of the causes of the lower productivity of Lake Tanatar-3 (with a high density of artemias) compared to similar lakes. In hypersaline lakes, high mineralization prevents artemias from developing, although a considerable number of their eggs, likely to have been laid in the previous period of freshening, occur there. In many Kulunda lakes, artemian eggs are collected to be used as fish feed and raw material for medicine production.

The influence of redox conditions. It should be noted that, among the Kulunda lakes studied by us, those with maximum alkalinity were characterized by the most markedly pronounced reductive conditions in the sediments (table). These lakes also exhibited the highest productivity. The main role in creating the reductive conditions in the sediments of the soda lake belongs to biogenic sulfate reduction, which influences the proceeding of the biogeochemical processes in several ways. Sulfate reduction as the final stage of destruction of organic matter aids in recycling of elements. Abd-el-Malek showed that biogenic sulfate reduction is the mechanism of the establishment and maintenance of alkaline conditions in the Wadi Natrun soda lakes (Egypt) [13]. In addition, sulfate reduction plays an important part in establishing anaerobiosis in the near-bottom zone. It was shown that the reductive conditions in the near-bottom layers of water promote the transfer of biogenic elements from the sediments to the water column, and, on the contrary, the presence of oxygen in the near-bottom region makes the sediments a “storage of elements” [14]. And, finally, the sulfide formed upon sulfate reduction serves as an electron donor for anoxygenic photosynthesis. Thus, positive feedback is established between the production and destruction of organic matter.

The lake depth and the strength of wind are also of vital importance for establishment of the reductive conditions in the near-bottom water layers. The deeper the lake, the easier the anaerobic conditions are established near the bottom. Wind and shallowness promote mixing of the water and establishment of oxidative conditions in the sediments. The level of water in the Kulunda lakes in the period of our studies was very low. It may be suggested that the rate of photosynthesis in the periods of greater flooding is higher in the lakes studied.

Comparison of the Kulunda Steppe Lakes with Other Soda Lakes

On the whole, soda lakes are considered to be the most productive natural ecosystems. It is often mentioned in the literature that the rate of photosynthesis in some soda lakes of the East African Rift exceeds 10 g C m^{-2} day^{-1} ([3, 4]). However, such high values are obtained using the free water method, when oxygen concentrations are measured directly in the lake, and these results usually exceed several-fold the values obtained when oxygen is measured in isolated samples [4]. Since most of the works used the latter method, it is more adequate to use for comparisons the data obtained with it. These values for eastern African lakes are not so high and vary within a wide range, but, nevertheless, they are also high. The productivity of a number of moderately mineralized eastern African lakes (Nakuru, Sonachi, Bogoria, Elmenteita, Magad, Manyara, Big Momela, and Reshitani) was studied by many authors and such studies are continuing. In different lakes and in different seasons, the productivity constituted from 0.5 to 7.5 g C m^{-2} day^{-1} [4, 15, 16] (in the works cited, the rate of photosynthesis is expressed in g O_2 m^{-2} day^{-1} and it was converted by us to g C m^{-2} day^{-1}). The highly mineralized soda lakes of Wadi Natrun (Egypt) supplied with sulfide- and biogen-enriched ground waters inflowing from the Nile delta are the subject of many microbiological studies. No data on the rates of photosynthesis for these lakes are available; however, judging from the mass development of cyanobacteria, green algae, and APB, discovered there both in plankton and in benthos [17], the Wadi Natrun lakes appear to be also highly productive.

Among the American soda lakes, the moderately mineralized (3–10%) stratified Mono Lake and Big Soda Lake have been most thoroughly studied. In Mono Lake (California, United States), the main primary producer is the alga *Picocystis* sp., which occupy the APB niche, developing below the oxycline in the anaerobic reductive surroundings and carrying out exclusively oxygenic photosynthesis [5]. The oxygenic photosynthesis rate constitutes 270–1060 g C m^{-2} per year, which is 0.7–3 g C m^{-2} day^{-1} on average. No anoxygenic photosynthesis was recorded in this lake. In Big Soda Lake (Nevada, United States), the total photosynthesis constituted 0.27–2.8 g C m^{-2} day^{-1}. The anoxygenic photosynthesis rate is from 0 to 0.21 g C m^{-2} day^{-1}, or from 0 (in the holomixis period, at maximum total productivity) to 70% (in the period of stratification, at minimum total productivity) of the total rate of photosynthesis [6]. Thus, as it could be expected, the productivity of the above-mentioned lakes significantly exceeds that of most of the Kulunda soda lakes studied by us. However, the rate of photosynthesis in the most productive Kulunda lakes is comparable with the productivity of African and American lakes.

The above-mentioned African and American lakes differ substantially from the Central Asian ones: they do not freeze, are usually large and deep, and, although some of them sometimes dry out, they are on the whole much more stable than the lakes of the cryoarid zone. The prevalence of the planktonic forms of photosynthetic organisms is one of the most characteristic features of these lakes, the water column being the main zone of photosynthesis. This is true in relation of both stratified and holomictic reservoirs. In meromictic lakes, phototrophs mainly develop in the mixolimnion and chemocline; and in holomictic lakes, intense development of phytoplankton occurs, the so-called blooming of water, which results in shading of the near-bottom layers and suppression of the benthic phototrophic community. Only in some soda lakes, e.g., Wadi Natrun (Egypt), do photosynthetic organisms develop both in the water column and on the surface of sediment deposits [17]. The development of benthic photosynthetic organisms is usually accompanied by a lesser abundance of phytoplankton [14].

On the contrary, in the central Asian lakes of the cryoarid zone, the benthic type of phototroph development prevails. In this work, primary production was determined in mats and upper phototroph-containing sediment layers; however, the values obtained virtually reflect the total photosynthesis per 1 m^2, because in the Kulunda lakes (except for Lake Iodnoe), phototrophic organisms were concentrated in the near-bottom layer with a water column height being as small as 5–30 cm. Therefore, our data may well be compared with data on production in the water column for the lakes with a predominantly planktonic type of development of photosynthetic organisms.

The primary production of organic matter in the soda lakes of the cryoarid zone is little studied. However, data are available on the soda lakes of Mongolia and Transbaikal Region. In the Mongolian lakes, which are similar to the Kulunda lakes in the degree of water mineralization and alkalinity, the total photosynthesis constituted 0.002–0.018 g C kg^{-1} day^{-1}; anoxygenic photosynthesis made up 0.0003–0.012 g C kg^{-1} day^{-1} [8]. These values are impossible to be converted to g C m^{-2} day^{-1} to be compared to the data on other lakes, because the thickness of the mats or sediments in which the measurements were made is unknown. However, it is evident from these data that the productivity of the Mongolian lakes is low. This may be due, among other things, to the fact that the studies were conducted in autumn.

In the low-mineralization Transbaikal Region soda lakes, the productivity of cyanobacterial mats in the summer time constituted 0.03–1.2 g C m^{-2} day^{-1}; the share of anoxygenic photosynthesis varied between 3 and 92% [7]. The authors note the presence of two peaks of productivity in the lakes, at salinities of 3–12 and 165–215 g l^{-1}. A special case among Transbaikal lakes is Lake Khilganta (Agin Buryat Autonomic District), where the development of thick (10–15 mm) layered cyanobacterial mats was observed and the rate of photosynthesis in the summer period attained 3.6–3.86 g C m^{-2} day^{-1} (85% was accounted for by anoxygenic photosynthesis); this is likely due to the inflow of underground waters with a high content of biogenic elements. Earlier (1995–1996), we determined a still higher photosynthesis rate in the Lake Khilganta mats, about 5 g C m^{-2} day^{-1}, and 75–95% of the organic matter was formed in the process of anoxygenic photosynthesis carried out by both APB and cyanobacteria [18]. On the whole, the primary production values in the Kulunda and Transbaikal Region lakes (except Lake Khilganta) are in the same range. However, when studying the Kulunda lakes, we did not find any correlation between productivity and salinity in the range of 30–200-g l^{-1}.

Thus, by the rate of photosynthesis, the soda lakes of the Kulunda steppe studied by us are close to the slightly mineralized soda lakes of the Transbaikal Region and much inferior to the eastern African and American soda lakes. Positive correlation between the primary production value and the water alkalinity was observed in the lakes studied. No relationship between productivity and water mineralization in the range of 30–200 g l^{-1} was revealed, whereas an increase in salinity above 200 g l^{-1} suppressed the phototrophic community. Anoxygenic photosynthesis was recorded only in several lakes with reductive conditions in the sediments and near-bottom water.

ACKNOWLEDGMENTS

The work was supported by the Russian Foundation for Basic Research (RFBR), project no. 07-04-00651a; NVO-RFBR, project no. 047.011.2004.010; and the programs of the Presidium of the Russian Academy of Sciences "Molecular and Cell Biology" and "The Origin and Evolution of the Biosphere."

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