Microbiology, Vol. 72, No. 2, 2003, pp. 221–229. Translated from Mikrobiologiya, Vol. 72, No. 2, 2003, pp. 259–267.

EXPERIMENTAL ARTICLES

Microbial Processes of the Carbon and Sulfur Cycles in Lake Shira (Khakasia)

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Received August 19, 2002

Abstract—Microbiological and biogeochemical studies of the meromictic saline Lake Shira (Khakasia) were conducted. In the upper part of the hydrogen-sulfide zone, at a depth of 13.5–14 m, there was a pale pink layer of water due to the development of purple bacteria (6×10^5 cells/ml), which were assigned by their morphological and spectral characteristics to *Lamprocystis purpurea* (formerly *Amoebobacter purpureus*). In August, the production of organic matter (OM) in Lake Shira was estimated to be 943 mg C/(m^2 day). The contribution of anoxygenic photosynthesis was insignificant (about 7% of the total OM production). The share of bacterial chemosynthesis was still less (no more than 2%). In the anaerobic zone, the community of sulfate-reducing bacteria played a decisive role in the terminal decomposition of OM. The maximal rates of sulfate reduction were observed in the near-bottom water (114 μg S/(l day)) and in the surface layer of bottom sediments (901 μg S/(dm^3 day)). The daily expenditure of C_{org} for sulfate reduction was 73% of C_{org} formed daily in the processes of oxygenic and anoxygenic photosynthesis and bacterial chemosynthesis. The profile of methane distribution in the water column and bottom sediments was typical of meromictic reservoirs. The methane content in the water column increased beginning with the thermocline (7–8 m) and reached maximum values in the near-bottom water (17 μl/l). In bottom sediments, the greatest methane concentrations (57 μl/l) were observed in the surface layer (0–3 cm). The integral rate of methane formation in the water column and bottom sediments was almost an order of magnitude higher than the rate of its oxidation by aerobic and anaerobic methanotrophic microorganisms.

Key words: Lake Shira, anoxygenic photosynthesis, purple sulfur bacteria, sulfate reduction, production and oxidation of methane.

The meromictic Lake Shira (90°14' E, 54°30' N) is situated in the northern part of Khakasia 17 km to the east of the regional center Shira within a large synclinal structure made up of red sandstone, aleurolite, argillite, and grit-stone of the oidan suite of the Upper Devonian. The lake's length is 9.35 km; its maximal width is 5.3 km; the coastline is 24.5 km long; the maximal depth is 23 m; and the average depth is 11 m. The water supply is provided by the Son River, rains, and anthropogenic contributions. The unique sulfate-chloride–sodium–magnesium mineral composition of the lake water has no analogues in composition and therapeutic properties.

Detailed hydrochemical studies of Lake Shira conducted in the summer period showed that, beginning at a depth of 13–14 m, this reservoir is characterized by a stable anaerobic zone containing dissolved hydrogen sulfide. In the near-bottom layers at a depth of 22 to 23 m, the hydrogen sulfide content was estimated to be from 15 to 20 mg/l [1]. The high content of sulfate ions (about 10 g/l), the appearance of hydrogen sulfide in the water column, as well as the high number of sulfate-reducing bacteria [2], give evidence in favor of a possible active role of sulfate reduction in the degradation of organic matter (OM) in this reservoir.

In August 2001, a joint expedition of researchers from the Institute of Microbiology (Russian Academy of Sciences), Tomsk State University, and the Institute of Biophysics, Siberian Division (Russian Academy of Sciences), was organized. Complex microbiological and biogeochemical investigations were carried out to qualitatively assess the rates of oxygenic and anoxygenic photosynthesis and sulfate reduction in Lake Shira. In addition, methane distribution was studied in the water column and bottom sediments, and the rates of its microbial oxidation and production were determined.

MATERIALS AND METHODS

The work on Lake Shira was carried out in August 23–29, 2001. Water and bottom sediments were sampled in the deepest zone (depth, 22.5 m) of the lake at 54°30.334' N, 90°11.418' E.

0026-2617/03/7202-0221$25.00

Table 1. Some physicochemical characteristics of Lake Shira water and surface layer of the bottom sediments (August 2001)

Depth, m	*T*, °C*	pH*	Turbidity, arb. units*	Suspension/ C_{org}**, mg/l	Salinity, ‰*	Alk, mg-equiv/l	Content of certain compounds		
							O_2, mg/l	H_2S, mg/l	CH_4, μl/l
0	21.46	8.80	4.4	15.3/0.755	11.33	16.67	7.4		0.73
2	20.28	8.80	5.0		11.39	16.55	6.9		0.47
3	20.14	8.80	4.5		11.38		5.2		0.71
4	20.01	8.80	4.8	28.8/1.551	11.40	16.64	6.5		0.73
6	19.72	8.80	4.4		11.40		6.5		0.50
7	13.29	8.76	5.5	43.5	12.84	18.52	9.8		1.84
8	6.69	8.73	6.0	52.5/3.452	13.24	18.74	10.2		2.26
9	4.46	8.71	6.9		13.42	18.81	8.2		2.17
11	2.28	8.70	5.7	42.0/2.824	13.49	19.13	3.9		2.88
12	1.85	8.68	5.7		13.55	19.15	2.0	0	3.25
13	1.36	8.66	5.2		13.61	19.19	0.4	0.013	3.56
13.5	1.18	8.65	9.8	20.0/2.118	13.65	19.22	0.15	0.033	2.66
14	1.14	8.64	9.6	45.3/2.518	13.68	19.24	0	0.592	3.60
15	1.13	8.64	7.4	37.7/2.674	13.77	19.29		1.446	6.44
16	1.16	8.59	7.5		13.76			7.100	8.32
18	1.26	8.54	6.0	32.3/1.689	13.80	19.46		7.100	10.91
22.5	1.29	8.52	9.8	37.8/2.444	13.84	19.65		15.78	17.28
Bottom sediments (horizon, cm; the component content per dm^3 of wet silt)									
0–3						19.00			57.04
3–5						19.65			50.77
5–10						12.05			46.59
10–15						14.36			44.50
15–20						16.21			42.41
20–25						14.53			36.06

* The data obtained with the submersion probe.

** C_{org} was determined by A.I. Agatova in VNIRO.

Water samples were taken using 0.9-l Niskin plastic horizontal bathometer as well as a 1.7-l two-compartment glass bathometer, with a built-in thermometer. Bottom sediments were sampled with a limnological stratimeter with a 6-cm metallic tube.

The total number of microorganisms was determined on 0.2-μm polycarbonate membrane filters by the fluorescence method using diamidino-4.6-phenyl-2-indole dihydrochloride (DAPI) as a dye [3].

The rates of the microbial processes of sulfate reduction, methane oxidation and methane production, and carbon dioxide assimilation in the light and in the dark were determined by the radioisotope method using the following sulfur- and carbon-labeled compounds: $Na_2{}^{35}SO_4$, $NaH^{14}CO_3$, $^{14}CH_4$, and $^{14}CH_3COONa$. Labeled compounds (0.1 to 0.2 ml) were injected into 5-ml syringes (bottom sediments) or into 50-ml glass flasks (water samples) with a microsyringe and incubated under in situ conditions on capron halyards. The dark flasks were wrapped in foil. The duration of incubation for determining the rate of carbon dioxide assimilation in the light and in the dark was a light day. Upon completion of incubation with [^{14}C]-bicarbonate, water samples were fixed with glutaraldehyde and then filtered through 0.2-μm capron membrane filters.

The duration of incubation for other processes was 24 h. After completing the incubation with labeled substrate, the water and sediment samples were fixed with 0.5–1 ml of concentrated KOH. The samples were then transported to the Institute of Microbiology, where the rates of microbial processes were determined by the techniques described earlier [4–6].

The sample content of methane was determined by the phase-equilibrium degassing method [7] on a Chrom-5 gas chromatograph equipped with a flame-ionization detector. The sulfate and chlorine contents were determined with a Biotronik ionic chromatograph (Germany); the contents of oxygen and hydrogen sulfide were determined using Aquamerk standard kits of reagents (Germany). The temperature, salinity, turbid-

Table 2. Microbial numbers and rates of microbial processes in the water column and in the surface layer of bottom sediments of Lake Shira (August 2001)

Horizon*	Microbial number, cells/ml × 10^5	Rates of microbial processes				
		CO_2 assimilation, μg C/(l day)		Methane oxidation, nl/(l day)	Methanogenesis, nl/(l day)	Sulfate reduction, μg C/(l day)
		in the light	in the dark			
Water column, m						
0	1.5	38.3	8.83	15.8		
2	2.9	119	3.58	6.59		
3	4.0	125	7.91			
4	6.5	98.4	7.20	11.4		
6	7.8	44.3	6.81	8.71		
8	22	100	13.8	69.0		
9	18	36.8	4.39	31.4		
11	6.3	32.9	3.88	37.9		
13	7.5	16.4	13.8	49.4		
13.5	9.4	32.2	29.4	15.6	980(4)**	72.0
13.75	14	8.1	23.0			
14	19	56.7	27.6	15.9	550(1)	83.2
14.5	13	25.2	11.1			85.8
15	8.5	18.6	13.7	57.4	510(12)	81.3
16	6.2	11.0	17.4	63.8	620(19)	85.3
18	6.9	0	10.8	36.6	100(0)	101.1
22.5	22		12.4	67.7	230(1)	113.5
Bottom sediments (the rates of the processes are calculated per dm^3 of wet silt per day)						
0–3	23000	158		654	6410(18)	901(51)***
3–5	6800	72		134	14590(0)	401(77)
5–10	1200	174		45	1360(1)	67(82)
10–15	850	120		89	5580(0)	150(45)
15–20		13		65	11870(2)	36(57)
20–25		41		79	1670(2)	6(23)

* In meters for the water column; in centimeters for the bottom sediments.

** In parentheses, aceticlastic methanogenesis is given as a percentage of the total methanogenesis.

*** In parentheses, acid-insoluble fraction is given as a percentage of total reduced sulfur.

ity, pH, and Eh were determined using a DateSonde 4a submersion multichannel probe (HYDROLAB, United States).

Measurements of the isotopic composition of the sulfate and hydrogen sulfide sulfur were carried out on an MI-1202 V mass spectrometer (Ukraine) according to the techniques described in detail earlier [8].

The enrichment cultures of photosynthesizing bacteria were obtained by inoculating with sediment or water samples an agar (0.8%) medium of the following composition (g per 1 liter of distilled water): KH_2PO_4, 0.5; NH_4Cl, 0.5; $MgSO_4 \cdot 7H_2O$, 0.5; $CaCl_2$, 0.1; NaCl, 10; $NaHCO_3$, 1.5; Na-acetate, 0.5; Na-pyruvate, 0.5; yeast extract, 0.1; $Na_2S \cdot 9H_2O$, 0.3; $Na_2S_2O_3 \cdot 5H_2O$, 1; a solution of microelements [9], 1 ml; vitamin B_{12}, 20 μg; pH, 7.5–8.

The pigment composition of the enrichment cultures of anoxygenic phototrophic bacteria was studied in suspensions of whole cells in 50% glycerin. The absorption spectra were recorded using a LOMO SF-56 spectrophotometer (St. Petersburg) in the 350- to 1000-nm range.

To determine the pigment content in natural lake water, bacterial cells were concentrated on a membrane filter, and pigments were extracted with an acetone–methanol (7 : 2) mixture. The resulting extract was scanned spectrophotometrically at different wavelengths. The pigment content was calculated using the following absorption coefficients: for bacteriochlorophyll *a*, $k = 46.1$ (l g^{-1} cm^{-1}) [10] and for chlorophyll *a*, $k = 11.64$ (l g^{-1} cm^{-1}) [11]. The calculations were performed using the following formulas [11]:

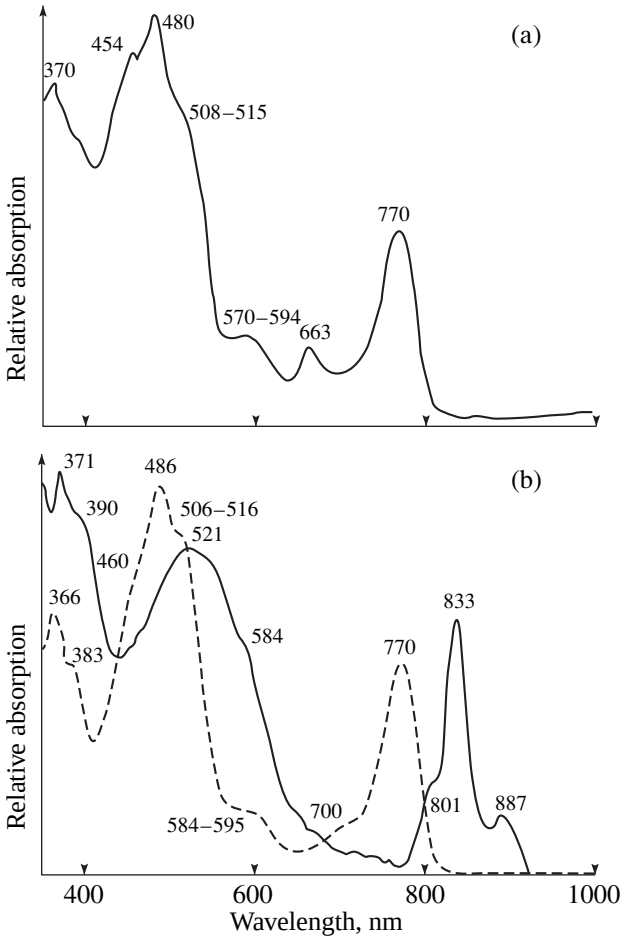

Fig. 1. Absorption spectra of bacterial pigments from the pink-colored water column of Lake Shira at a depth of 14 m: (a) absorption spectrum of an acetone–methanol extract of bacterial cells concentrated on a membrane filter and (b) absorption spectrum of whole cells (solid line) and an acetone–methanol extract (broken line) of the purple sulfur bacterium *L. purpurea.*

$$C\ (\mu g\ \text{bhcl}\ a/l) = kD_{770}\ (V_{extract}\ (ml)/V_{sample}\ (l)),$$

$$C\ (\mu g\ \text{hcl}\ a/l) = kD_{650}\ (V_{extract}\ (ml)/V_{sample}\ (l)).$$

RESULTS

Physicochemical characteristics of the water column and bottom sediments. Lake Shira is a subsaline meromictic reservoir with a marked hydrogen sulfide zone in the water column.

In the central, deepest part of the lake, which has a depth of 22–23 m, oxygen was absent below 13.5 m, and the appearance of considerable hydrogen sulfide concentrations (>0.5 mg/l) was observed at a depth of 14 m (Table 1). The content of hydrogen sulfide increased with depth and was 15.78 mg/l in the near-bottom water.

Measurements of the oxygen and hydrogen sulfide concentrations carried out with a step of 0.5 m allowed us to identify the redox zone, i.e., the zone of simultaneous existence of oxygen and hydrogen sulfide known for other meromictic reservoirs. The redox zone occurred within a narrow depth range, from 13 to 13.5 m (Table 1).

According to the data obtained using a submersion probe, the thermocline was at a depth of 6 to 10 m. In this depth range, the temperature dropped sharply from 19.7 to 2.92°C (Table 1). The absolute maximum of dissolved oxygen (Table 1), which is likely to be caused by phytoplankton activity, was observed at a depth of 7 to 8 m. Beginning at 11 m, a marked decrease in the oxygen concentration was noted (to 0.4 and 0.15 mg/l at 13 and 13.5 m, Table 1). The distribution of C_{org} of suspended matter (Table 1) was characterized by a maximum at 8 m, indicating an increased phytoplankton activity at this depth.

The alkaline pH values characteristic of the water column of the lake (8.5–8.8, as shown by the submersion probe) correlate with the high values of alkalinity (16.67 to 19.65 mg-equiv/l, Table 1), which smoothly increase with depth.

As compared to other meromictic reservoirs, the methane concentration in the water column of Lake Shira is rather low (Table 1). However, the profile of methane distribution is typical of reservoirs with a stable anaerobic zone. In the aerobic part of the water column, the methane concentration varied from 0.4 to 2 μl/l and markedly increased in the anaerobic zone. The maximum methane concentration (17 μl/l) was observed in the near-bottom layer of the water column at a depth of 22.5 m.

The upper horizons (0–25 cm) of the bottom sediments in the central part of the lake are represented by semiliquid thin-layered dark gray and black silts with a pungent hydrogen sulfide odor. As compared to near-bottom water, the methane content in them was substantially higher; its highest concentration (57 μl/dm^3 silt) was observed in the surface horizon of 0–3 cm. Deeper in the sediment, the methane concentration decreased to 36 μl/dm^3 at a depth of 20–25 cm (Table 1).

Bacterioplankton characteristics. The total number of microorganisms in the water column of Lake Shira varied from 1.5×10^5 to 22×10^5 cells/ml (Table 2); the greatest amounts of cells were noted at depths of 8 and 14 m and in the near-bottom layer. The first maximum of the number of microorganisms at 8 m coincides with the chemocline. The second maximum of the number of microorganisms at 14 m was in the upper part of the anaerobic zone, where the hydrogen sulfide content was 0.59 mg/l. The water at this depth was slightly pink in color due to the development of photosynthesizing purple sulfur bacteria that carry out anoxygenic photosynthesis. The absorption spectrum of the pigments extracted from bacterial cells collected at a depth of 14 m and concentrated on a membrane filter is shown in Fig. 1a. The peak at 770 nm indicates the presence of considerable amounts of bacteriochlorophyll *a* in the

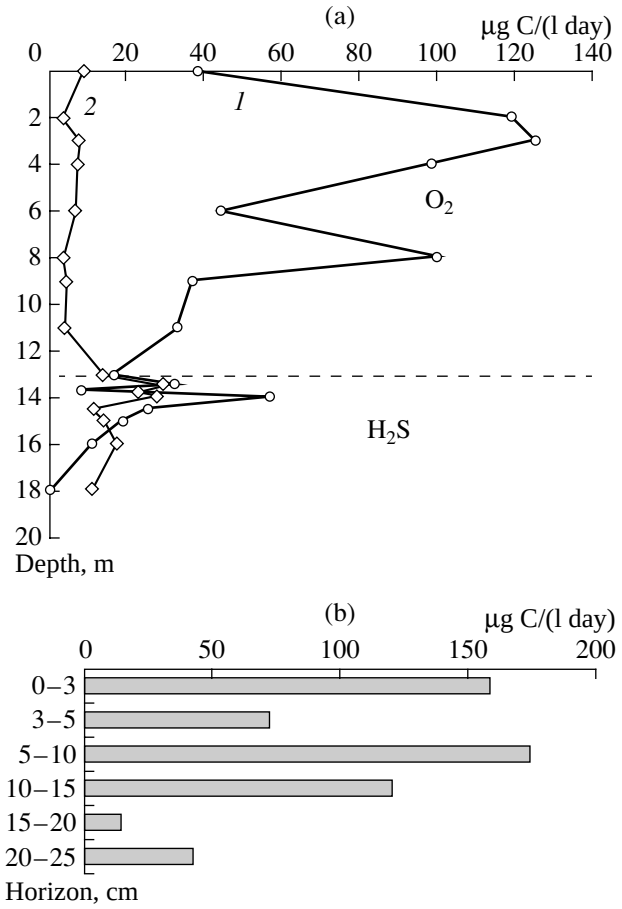

Fig. 2. Rate of carbon dioxide assimilation in the water column and bottom sediments of Lake Shira: (a) carbon dioxide assimilation rate in the water column (*1*) in the light and (*2*) in the dark; (b) carbon dioxide assimilation rate in bottom sediments.

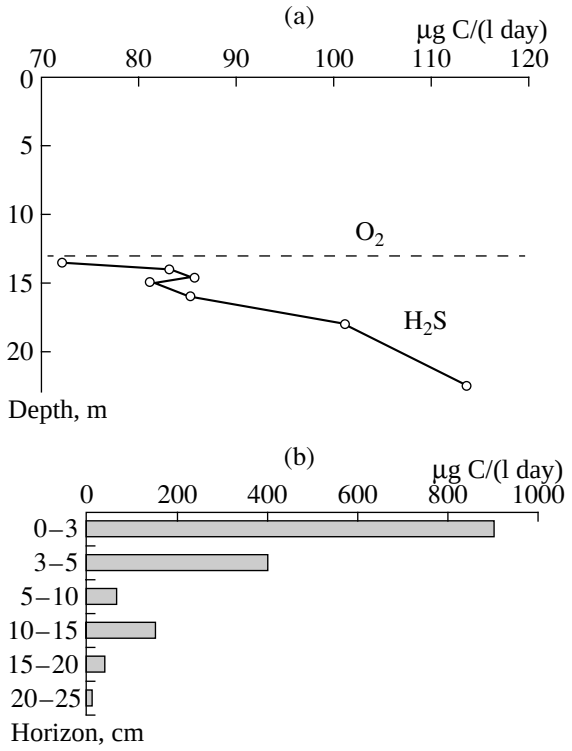

Fig. 3. Sulfate reduction rate in the (a) water column and (b) bottom sediments of Lake Shira.

sample. Its content is 30.6 μg/l, which approximately corresponds to the number of phototrophic bacteria of 6×10^5 cells/ml.

Chlorophyll *a* (3.4 μg/l) with maximum absorption at 663 nm was revealed as a minor component (Fig. 1a). This pigment is typical of phytoplankton that carry out oxygenic photosynthesis in the overlying layers of the water column.

To identify anoxygenic phototrophic bacteria under field conditions, a selective liquid medium was inoculated with water taken at a depth of 14 m. After a long period of incubation (1.5 months), a purple enrichment culture was obtained. Light microscopy revealed nonmotile bacteria morphologically similar to bacteria dominating the water samples taken from a depth of 14 m. The cells of these bacteria were round and 2 to 4 μm in size. They were arranged in pairs or in tetrads and contained inclusions of elemental sulfur and gas vacuoles. Another confirmation of the presence of gas vacuoles in the bacteria was the accumulation of cells (in the form of purple lumps or flakes) in the upper part of the vessel where the microorganisms were cultivated.

The absorption spectrum of the pigments of live bacterial cells revealed the presence of bacteriochlorophyll *a* (833 nm) and carotenoids of the okenone series (521 nm) (Fig. 1b). The absorption spectrum of the acetone–methanol extract was investigated for the additional characterization of the pigment composition of the bacteria (Fig. 1b). The spectrum obtained was virtually identical to the absorption spectrum of the natural bacterial extract (Fig. 1b), which confirmed the dominance of anoxygenic purple bacteria. By the morphological features and the characteristic absorption spectrum of the pigments, this bacterial culture can be identified as *Lamprocystis purpurea* [12] (formerly, *Amoebobacter purpurea*) [13].

Two groups of purple nonsulfur bacteria were found as minor components in the enrichment cultures. The first group was tentatively assigned to spheroidene-containing bacteria of the *Rhodobacter–Rhodovulum* morphological type. These cells were motile, oval, and measured 0.3–0.4 × 0.5–0.7 μm. The other group of purple nonsulfur bacteria was identified by its characteristic morphological properties as the exospore-forming budding bacterium *Rhodomicrobium vannielii*; these cells were oval-shaped and measured 1–1.2 μm by 2–2.8 μm [14].

Carbon dioxide assimilation. The assimilation rates of [^{14}C]-bicarbonate were determined in the light

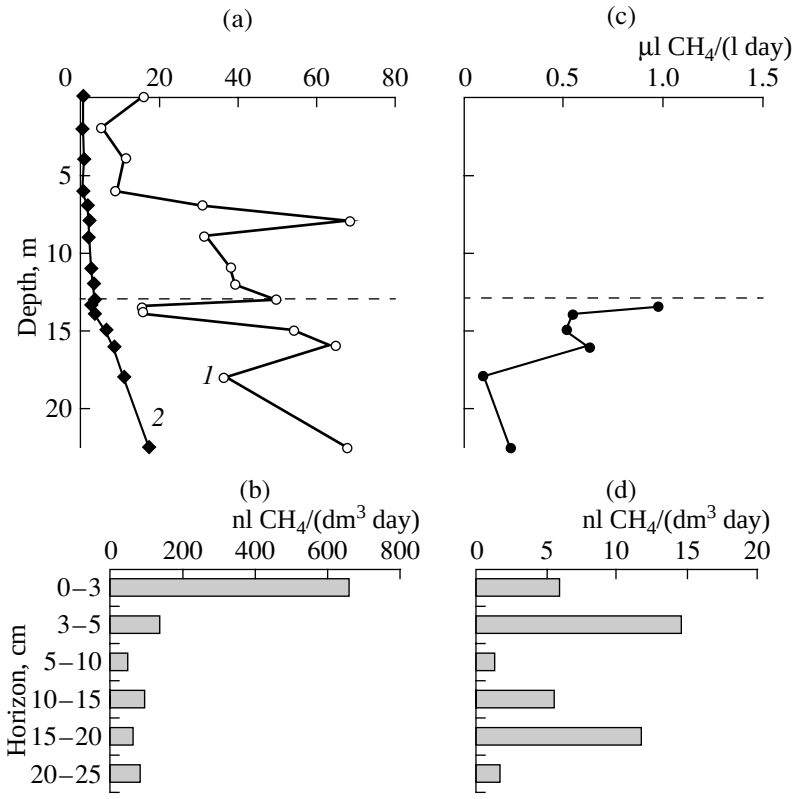

Fig. 4. Rates of methane production and oxidation in the water column and bottom sediments of Lake Shira: (a) methane oxidation rate in the water column ((*1*) methane oxidation, nl CH_4/(l day); (*2*) the methane content, μl CH_4/l) and (b) in bottom sediments; (c) methane production rate in the water column and (d) in bottom sediments.

and in the dark (Table 2, Fig. 2). The profile of the carbon dioxide assimilation rate in the light (Fig. 2) was characterized by three maxima. The first two maxima, with an intensity of light-induced CO_2 assimilation of 100–125 μm C/(l day), were in the epilimnion at depths of 2–3 and 8 m in the aerobic zone of the water column and reflected an increased phytoplankton activity. The third maximum was in the zone of development of purple bacteria at a depth of 14 m. Here, the value of carbon dioxide fixation in the light constituted 56.7 μg C/(l day).

Table 3. Isotopic composition of sulfur compounds in the water column of Lake Shira

Horizon, m	$\delta^{34}S$–SO_4^{2-}, ‰	$\delta^{34}S$–H_2S^-, ‰
0	16.8	
7	17.6	
11	17.2	
14	17.7	
16	17.5	–43.9
18	18.2	–45.8
22.5	17.5	–39.6

The distribution profile of the rates of carbon dioxide assimilation in the dark (Table 2, Fig. 2) exhibited one markedly pronounced maximum at 13–14.5 m, which could be related to the activity of both chemoautotrophic thionic bacteria (the presence of oxygen was recorded at a depth of 13.5 m (Table 1)) and phototrophs, which are able to switch over to chemoautotrophy in the dark [15]. Therefore, it may be assumed with some reservations that, in the period of our investigations, the chemosynthesis zone was in the depth range 13–14 m.

In the bottom sediments, the rate of carbon dioxide fixation in the dark reflects the aggregate activity of the microbial community. In upper layers of the sediments of Lake Shira, this value varied from 13 to 174 μg C/(dm^3 day), the maximum occurring in the 5- to 10-cm horizon.

Sulfate reduction. The sulfate reduction rate was determined in the redox zone and in the anaerobic zone in a depth range from 13 m to the bottom, as well as in the surface layer of bottom sediments (Table 2, Fig. 3a). In the water column, a regular increase in the rate of sulfate reduction with depth was observed, with a maximum of 113.5 μg S/(l day) in the near-bottom water at a depth of 22.5 m.

Table 4. Integral rates of the microbial processes in the water column and the surface layer of bottom sediments of Lake Shira (August 2001)

Process	Integral rate	
	water	sediments (per 0–25-cm layer)
CO_2 assimilation in the light, mg C/(m^2 day) in the aerobic zone (aerobic photosynthesis), 0–13 m	866	–
CO_2 assimilation in the light, mg C/(m^2 day) in the anaerobic zone (anoxygenic photosynthesis), 13.5–18 m	59	–
CO_2 assimilation in the dark, mg C/(m^2 day), 0–22.5 m*	216(18)*	48
Sulfate reduction, mg S/(m^2 day)	875	48
Methanogenesis, ml CH_4/(m^2 day)	2.94	1.48
Methane oxidation, ml CH_4/(m^2 day)	0.78	0.04

* In parentheses, the chemosynthesis value is given.

In the bottom sediments, the highest rate of sulfate reduction was noted in the surface horizon (0–3 cm). Deeper in the sediment thickness, the sulfate reduction rate decreased from 901 μg S/(dm^3 day) at the surface to 6.0 μg S/(dm^3 day) at a depth of 20–25 cm (Table 2, Fig. 3b). The result of the activity of sulfate-reducing bacteria was a regular decrease in the sediment sulfate concentration from 10 g/dm^3 at the surface to 0.75 g/dm^3 in the 20- to 25-cm horizon. Such a distribution of the rates of sulfate reduction in bottom sediments is typical of most reservoirs, with the only difference being that in Lake Shira sediments the limiting factor of the development of sulfate-reducing bacteria seems to be the availability of easily assimilable OM rather than sulfate content (a sulfate concentration of 0.75 g/dm^3 is quite sufficient for an active process).

The biogenic origin of hydrogen sulfide (due to the activity of sulfate-reducing bacteria in Lake Shira) is confirmed by the results of the study of the isotopic composition of the sulfate and hydrogen sulfide sulfur (Table 3). The isotope composition of the sulfate sulfur was almost constant along the water column profile, its $\delta^{34}S$ value varying from 16.8 to 18.2‰. As compared to sulfate, hydrogen sulfide sulfur was substantially enriched with the light isotope ^{32}S. In the range of depths from 16 to 22.5 m, the hydrogen sulfide $\delta^{34}S$ varied from –45.8 to –39.6‰. The heaviest isotopic composition of hydrogen sulfide sulfur (–39.6‰) was observed in the near-bottom horizon of the water column, where the highest rate of sulfate reduction was recorded.

The processes of methane formation and oxidation. Table 2 and Fig. 4a show the rates of methane oxidation in the water column and in the surface layer of bottom sediments. In the aerobic zone of the water column (0–13 m), the rate of methane oxidation varied from 6.59 to 49.4 nl CH_4/(l day), with a maximum at a depth of 8 m. An increased rate of methane oxidation was also observed in the chemocline zone (11–13 m), where oxygen is available.

One more peak of methane oxidation rate was in the layer of anaerobic hydrogen sulfide–containing waters at a depth of 15–16 m. In the near-bottom horizon (22.5 m), the methane oxidation rate was also increased (Fig. 4a).

In the surface layer of sediment, the rate of methane oxidation was almost an order of magnitude higher (654 nl CH_4/(l day)). Deeper in the sediment thickness, the methane oxidation rate decreased (Table 2, Fig. 4b) and varied from 45 to 134 nl CH_4/(l day).

The rates of methane formation from carbon dioxide and acetate were studied in the anaerobic part of the water column and in the surface layer of bottom sediments (Table 2). In the period of our investigations, the major part of the methane was formed from carbon dioxide, both in the anaerobic part of the water column and in the surface layer of bottom sediments. The contribution of aceticlastic methanogenesis to methane production did not exceed 19%.

Figure 4c shows the distribution profile of the rates of autotrophic methanogenesis. From 13.5 m down to the bottom, the process of methane formation was observed in all the samples of water; the highest methanogenesis rate was observed at a depth of 13.5 m.

In bottom sediments (Fig. 4d), the highest methanogenesis rate was observed in the horizons of 3–5 and 15–20 cm. In absolute values, the methanogenesis rate in bottom sediments was significantly higher than in the water column. The fact that the methanogenesis and sulfate reduction profiles in the water column and bottom sediments did not coincide merits attention. In the horizons with the minimal methanogenesis rate, the rate of sulfate reduction was close to the maximal values (Fig. 4d). Such a distribution of the rates of these anaerobic processes agrees well with the published data on the competition of sulfate-reducing and methanogenic bacteria for the substrate. In our case, it is hydrogen that seems to be such a substrate.

DISCUSSION

A detailed profile of carbon dioxide assimilation allows us to calculate OM production in Lake Shira in the processes of oxygenic and anoxygenic photosynthesis, as well as in bacterial chemosynthesis. Based on the distribution of oxygen in the water column of the lake, the aerobic zone in the period of our investigations extended to a depth of 13 m. Using the data of Table 2, we infer that the production of aerobic photosynthesis in August 2001 constituted 866 mg C/(m^2 day). This value is consistent with the earlier measurements of primary production in Lake Shira carried out by researchers from the Institute of Biophysics, Siberian Division, Russian Academy of Sciences, and from the Institute of Inland Waters Biology, Russian Academy of Sciences, who obtained values that varied in different months from 0.786 to 1.121 g C/(m^2 day) [16].

Anoxygenic photosynthesis, mainly determined by the purple sulfur bacteria *L. purpurea*, occurred in the 13.5- to 16-m range of depths and was much weaker. It was estimated to be 59 mg/(m^2 day) and constituted only 7% of the total production of photosynthesis in Lake Shira. The modest contribution of anoxygenic phototrophic bacteria is consistent with their small number (6×10^5 cells/ml), which, in turn, is connected with the low hydrogen sulfide content (0.59 mg/l) in the zone of the maximal development of phototrophic bacteria. Earlier, mass development of the purple sulfur bacterium *L. purpurea* was discovered in the meromictic Lake Mahony. A considerably greater hydrogen sulfide content in the water column of this lake (up to 320 mg/l in the near-bottom layers of water at a depth of 7.0 to 7.2 m) determines the greater number (over 10^8 cells/ml) of these bacteria and the higher rate of anoxygenic photosynthesis, which was estimated to be 304 mg C/(m^2 day) [17].

The share of chemotrophic bacteria in Lake Shira is, according to our estimates, no more than 2% of the photosynthesis production (18 mg C/(m^2 day)).

The calculations of the integral rate of sulfate reduction in the water column and in the surface layer of sediments showed the daily production of hydrogen sulfide to be 875 mg S/(m^2 day) in the water column and 48 mg S/(m^2 day) in bottom sediments. Therefore, in the period of our investigations, the main portion of hydrogen sulfide was formed immediately in the water column rather than migrating from the surface layer of bottom sediments. Using the combined equation for sulfate reduction $2[CH_2O] + SO_4^{2-} \longrightarrow H_2S + 2HCO_3^-$ and knowing the production of hydrogen sulfide, the amount of C_{org} consumed in the process of sulfate reduction in the water column and in the surface layer of bottom sediments was estimated to be 692 mg C/(m^2 day). Along with sulfate reduction, the terminal phase of OM decomposition proceeds via methane formation, which, in Lake Shira, predominantly uses hydrogen and occurs according to the equation $4H_2 + CO_2 \longrightarrow CH_4 + 2H_2O$. Considering that, in the anaerobic zone, hydrogen is formed in the processes of fermentation or anaerobic OM oxidation and given that the total (water column + bottom sediments) methane oxidation rate is 4.02 ml CH_4/(m^2 day), we conclude that the daily consumption of C_{org} in this process will amount to 12.6 mg, which accounts for less than 2% of C_{org} used for sulfate reduction. Hence, in the period of our investigations, the main terminal process of OM mineralization was bacterial sulfate reduction, due to which 73% of the C_{org} formed during oxygenic and anoxygenic photosynthesis and chemosynthesis was mineralized (we estimate the total production of C_{org} in the water column of Lake Shira to be 943 mg C/(m^2 day)). Such a high rate of sulfate reduction can be explained by the fact that, in the anaerobic zone, not only autochthonous but also allochthonous OM, arriving as a constituent of dust particles, as well as in the river water and with rain, is concentrated.

The total methane production and oxidation values obtained for the first time for the Lake Shira water column and bottom sediments (Table 4) suggest that, as in the case of sulfate reduction, the integral rates of these processes in the water column are higher than in the surface layer (0–25 cm) of bottom sediments. However, it is rather difficult to interpret the considerable excess of the methanogenesis rate (approximately fourfold) in comparison to the methane oxidation rate (Table 4). This issue calls for further investigation; apparently, special emphasis should be placed on seasonal changes in the activity of the methane cycle microorganisms.

In conclusion, it should be emphasized that the results obtained and the ensuing conclusions as to the activities and structure of the Lake Shira microbial community are based on a one-stage seasonal analysis (the end of August), whereas the annual balance and the ratio of the rates of the processes at different time intervals may be quite different.

ACKNOWLEDGMENTS

We are grateful to V.M. Gorlenko for his help in preparing this article.

This work was supported by the Russian Foundation for Basic Research (project nos. 02-04-49296 and 02-04-48196) and "The Support of the Leading Schools" (project no. 00-15-97897); INTAS, project no. 01-2333; the Program of Support of Young Scientists, project no. 01-05-06181; and a grant from the Ecological Committee of Khakasia.

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