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EXPERIMENTAL ARTICLES

Intensity of the Microbiological Processes of the Methane Cycle in Different Types of Baltic Lakes

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Abstract—The intensity of the microbiological processes of methane formation (MF) and methane oxidation (MO) was determined in the sediments and water of different types of Baltic lakes. The emission of methane from the lake sediments and methane distribution in the water column of the lakes were studied as functions of the lake productivity and hydrologic conditions. During summers, the intensity of MF in the lake sediments and waters varied from 0.001 to 106 ml CH_4/(dm^3 day) and from 0 to 3.2 ml CH_4/(l day), respectively, and the intensity of MO in the sediments and water varied from 0 to 11.2 ml CH_4/(dm^3 day) and from 0 to 1.1 ml CH_4/(l day), respectively. The total methane production (MP) in the lakes varied from 15 to 5000 ml CH_4/(m^2 day). In anoxic waters, the MP comprised 9–18% of the total PM in the lakes. The consumption of organic carbon for methanogenesis varied from 0.03 to 9.7 g/(m^2 day). The role of the methane cycle in the degradation of organic matter in the lakes increased with their productivity.

Key words: microbiological processes, methane formation, methane oxidation, degradation.

The finding that, in freshwater ecosystems, methane is the major terminal product of the anaerobic degradation of organic matter has stimulated increasing interest of researchers in the study of the methane cycle. Most of the investigations into this problem were carried out for the bodies of water situated in different climatic and landscape zones [1–3], which intricates the comparative analysis of experimental results.

The aim of the present work was to evaluate the intensity of the microbiological processes of the methane cycle in Baltic lakes with different hydrologic characteristics and productivity levels and to determine the main ecological factors that influence these processes under different conditions.

MATERIALS AND METHODS

Investigations were carried out during the summers of 1986 and 1987 on some Baltic lakes, which, in spite of their geographic closeness, considerably differed in the area, depth, surrounding landscapes, as well as in the hydrologic, hydrochemical, and biological characteristics. These were small forest lakes in southern Estonia (Lakes Tivera, Mustyarv, and Linoyarv); Lakes Dridzas, Vishki, Stropu, and Dotkas on the Latgalian Upland in southeastern Latvia; and Lake Drukshyai, or Drisvyaty, in northeastern Lithuania, at the border with Belarus and Latvia.

Water samples for microbiological analysis were taken using a Franzev sterile bottle-type sampler. Water samples for chemical analysis were taken using a Ruttner bathometer. The lake sediments were sampled using a box-type dredge, which allowed the structure of the sediment to be retained. Sediment subsamples for chemical and microbiological analyses were taken from the dredge using sterile tubes.

The physicochemical and productivity characteristics of the lakes were determined by standard techniques [4] using a KL-115 oxygen meter, a Radelkis ion meter, an Ergoval microscope, and a Mark-2 scintillation counter. Organic matter (OM) in the lake sediments was evaluated as organic carbon (C_{org}). C_{org} and the total nitrogen content (N_{total}) were measured using a CNH-1 gas chromatographic analyzer. An easily hydrolyzable, or labile, fraction of OM (C_{lab}) was determined with 5% H_2SO_4. Sulfates (S) were analyzed by titrating them with alizarin. The primary production of phytoplankton and the consumption of O_2 associated with the degradation of organic matter in the lake waters were measured by the oxygen method. Bacteria were enumerated by direct count on 0.17-μm Synpor filters. Aerobic heterotrophic bacteria were grown on fish peptone agar (FPA); butyric acid bacteria, on media with glucose and starch; and sulfate-reducing bacteria, on Postgate medium B. Methanogenic bacteria were counted using the method elaborated by Belyaev *et al.* as described by Kuznetsov and Dubinina [4]. The content of methane in the lake sediments and water was determined by the method of partial proportions [5], using a Chrom-5 chromatograph equipped with a flame ionization detector and a 2.4-m column packed with Porapack-Q (35°C; the carrier gas helium).

Table 1. General characteristics of the Baltic lakes in the summer of 1987

Lake	Country	Area, km^2	Depth*, m	Physicochemical and biological characteristics of lakes								
				Water transparency, m	Temperature, °C		O_2, mg/l		Color intensity, degree	Trophic parameters**		
					0.5 m	bottom	0.5 m	bottom		PPP	OCR	TBC
Dridzas	Latvia	7.40	50(65)	4.2	19.5	5.0	9.4	6.6	10	0.16	0.36	0.6–1.1
Stropu	″	4.19	5(7)	1.5	21.3	17.8	8.5	7.6	20	0.23	0.68	1.4–3.5
Vishki	″	3.60	12(20)	2.2	19.2	15.2	9.2	5.5	20	0.31	0.41	0.7–1.9
Dotkas (June)***	″	0.23	3(3.5)	1.1	17.0	15.8	8.1	6.7	40	0.79	2.15	2.3–7.6
Dotkas (July)	″	0.23	3(3.5)	0.5	24.6	15.0	16.2	0	–	1.39	2.93	5.1–12.8
Tivera	Estonia	0.04	5(6)	2.2	19.2	14.1	8.9	3.2	45	0.24	0.68	2.7–3.9
Mustyarv	″	0.22	7(9)	1.2	22.9	6.7	8.2	0.5	300	0.45	0.21	1.8–6.1
Linoyarv	″	0.03	9(11)	0.9	21.2	5.2	10.0	0	20	2.29	4.12	3.91–6.5
Drukshyai	Lithuania	44.8	30(35)	3.7	18.4	8.8	9.1	0	10	0.56	0.79	0.9–7.8

Note: The symbol ”–” stands for “not measured.” * Lake depths are given for the central station; parenthesized are the maximum depths of the lakes. ** The primary production of phytoplankton (PPP) is given in mg C/(l day); the oxygen consumption rate (OCR) by phytoplankton is expressed in mg O_2/(l day); and the total bacterial count (TBC) expressed in 10^6 cells/ml is given as the range of minimal and maximal values observed throughout the water column. *** Data for Lake Dotkas are given for June 16–19 and July 3–5.

The overall degradation (both aerobic and anaerobic) of organic matter in the surface layer of the lake sediments was calculated from the amounts of oxygen consumed and carbon dioxide produced in the hermetically sealed stratometric tubes containing a mud monolith and bottom lake water. The rates of the dark assimilation (DA) of CO_2 and bacterial sulfate reduction were measured by the isotope method using the standard solutions of [^{14}C]-bicarbonate and [^{35}S]sulfate [4].

The intensity of the microbiological processes of the methane cycle was evaluated from the difference in the methane concentrations in the control and experimental samples [4]. The concentration of methane was determined by gas chromatography. The formation and consumption of methane in the lake sediments were studied in stratometric flasks using the necessary inhibitors [6]. The rate of methane emission from the lake sediments was determined simultaneously with the analysis of the degradation of organic matter. Experiments with the lake waters were carried out using 60-ml flasks sealed with silicone stoppers and perforated caps. All manipulations, such as sampling and sample fixation, were performed aseptically in a flow of an inert gas using sterile syringes and needles. The experimental flasks were incubated in lightproof bags for 8–24 h at temperatures typical of particular lakes. The samples were fixed with the saturated solution of $HgCl_2$. The intensities of the formation and oxidation of methane were determined as described by Kuznetsov and Dubinina [4] and Naguib [5].

RESULTS AND DISCUSSION

The morphological and hydrologic characteristics of the Baltic lakes studied were very different (Table 1). About half of the lakes were dimictic because of the presence of basins on their bottoms, and others were holomictic. By mid-summer, when the temperature stratification and the trophic parameters of the lakes were maximum, the content of dissolved oxygen in deep waters decreased. The decrease was different in different types of the lakes. In most of the stratified lakes, except for deep oligotrophic Lake Dridzas, the hypolimnion in July was completely anoxic. At the same time, in holomictic lakes Stropu, Vishki, and Tivera, whose productivity was intermediate, the concentration of dissolved oxygen near the bottom did not drop below 3.2–5.5 mg O_2/l. Specific ecological conditions were observed in shallow-water eutrophic Lake Dotkas, which has bottom springs. Most of the vegetation period, this lake represented a holomictic body of water fairly aerated down to the bottom. However, during the periods of hot windless weather, water in this lake drastically stratified to become completely anoxic near the bottom. These changes were favored by intense productive processes in the lake (Table 1) and by the income of cold spring waters.

The sediment structure and the physicochemical characteristics of the lakes under study, as well as the composition of their organic matter, corresponded to the typological features of these lakes (Table 2). Judging from Eh values, the littoral sands and the surface layer of the mineralized clayey detrital muds of the less

Table 2. Physicochemical characteristics of sediments in the Baltic lakes

Lake	Depth, m	General sediment characteristic	Eh, mV		Mean content in 1 dm^3 wet sample (0–5 cm)				C/N
			0–2 cm	2–5 cm	C_{org}, g	C_{lab}, % C_{org}	S/SO_4^{-2}, mg	CH_4, ml	
Dridzas	3	Sand with plant debris	180	20	7.8	20	–	0.1	20
″	50	Clayey mud	120	60	9.8	10	16	0.3	18
Stropu	2	Sand	180	–	6.2	21	–	0.3	15
″	6	Coarse detrital mud	55	0	14.8	26	35	11.2	12
Vishki	2	Fine detrital mud	90	–30	12.1	14	–	25.1	15
″	12	Black detrital mud	80	10	10.3	13	18	3.5	12
Dotkas (June)***	3	Fine detrital mud	10	–60	16.4	21	70	26.8	9
Dotkas (July)	1	Black detrital mud	40	–20	7.8	14	40	1.4	16
″	3	Black detrital mud	–60	–115	18.3	26	75	31.1	7
Tivera	5	Gray clayey mud	60	–10	13.1	15	11	4.7	14
Mustyarv	7	Peaty mud	–	–	14.3	10	–	2.0	18
Linoyarv	10	Dark green gyttja	220	–	21.8	33	8.5	64.2	8
Drukshyai	2	Sand	210	–	2.8	–	–	0.1	–
″	5	Black clayey mud	60	–110	10.4	14	120	2.2	12
″	30	Black liquid mud	–40	–140	9.8	21	30	26.5	9

productive lakes in summer were characterized by oxidative conditions. However, at a depth of 2–5 cm, sediments even in the well-aerated regions of the lakes were characterized by reductive conditions. The redox potential of dark gas-producing muds in the profundal zones of the eutrophic lakes was always low.

The lake sediments greatly differed in the total C_{org} content and the C/N ratio, whereas the content of labile organic matter (C_{lab}) was relatively high in all of the lakes studied. The concentration of soluble sulfates in most of the lakes did not exceed 30 mg S/dm^3 of wet mud, except that the black mud of Lake Dotkas, which is strongly polluted by agricultural wastes, and the black clayey mud of Lake Drukshyai at the site of the inflow of wastes from the Ignalina Nuclear Power Plant (NPP) contained 75–120 mg S/dm^3. The methane content varied from 0.1–0.3 ml CH_4/dm^3 in sandy silts to 25–64 ml CH_4/dm^3 in the profundal muds of the eutrophic lakes, being in agreement with the redox conditions of these environments (Table 2).

The total density of bacteriobenthos, as well as the population density of its particular groups, corresponded to the ecological conditions (primarily, to the C_{org} content) of their habitats. The distribution of different bacterial groups strongly depended on the redox potential: the bacterial communities of littoral sandy and oxidized muds were dominated by aerobic heterotrophs, whereas the profundal muds (which are characterized by reductive conditions) were dominated by anaerobic fermentative bacteria, methanogens, and, in some cases, sulfate-reducing bacteria (Table 3).

Due to the high content of labile organic matter, the total activity of bacteriobenthos, which was evaluated by the intensity of CO_2 emission from mud and its dark assimilation, was high in all of the lakes investigated (Table 4). The estimation of the oxygen consumption rate showed that organic matter in the oxidized muds was degraded aerobically. The anaerobic mineralization of organic matter was observed not only in the bottom basins of the productive stratified lakes (which is not surprising, taking into account the reductive conditions of these environments) but also in some shallow-water regions, namely, in the littoral zones of lakes Vishki and Dotkas overgrown by macrophytes and in the bay of Lake Drukshyai polluted by wastes from the Ignalina NPP.

The intensity of methanogenesis in the lake sediments varied depending on their ecological conditions. In the aerated mud, the methane formation rate varied from 0.005–0.45 ml $CH_4/(dm^3$ day) in the surface layer to 1.2–6.7 ml $CH_4/(dm^3$ day) in deeper layers. These values are comparable with those observed for oligo- and mesotrophic lakes [3, 7, 8]. In the muds of the bottom basins of the productive stratified lakes, the methane formation rate reached 21–106 ml $CH_4/(dm^3$ day) (Table 4), being comparable with the values observed for eutrophic lakes in other climatic and geographic areas [1, 2, 9]. Unlike Sorrell and Boon [9], we did not observe a direct relationship between methanogenesis

Table 3. Concentrations of various bacteria in the sediments of the Baltic lakes in the summers of 1986 and 1987 years

Lake	Depth, m	Total bacteria, 10^9 cells/cm^3	Heterotrophs, 10^6 cells/cm^3	Butyric acid bacteria, 10^6 cells/cm^3		Methanogens, 10^3 cells/cm^3	Sulfate reducers, 10^3 cells/cm^3
				C. pasteurianum	*C. butyricum*		
Dridzas	3	1.2–1.6	0.1–0.4	0.05–0.1	0.1–0.3	–	–
″	50	0.9–1.4	0.09–0.2	0.2–0.7	0.5–1.1	0.1	<0.1
Stropu	2	0.9	0.3	0.007	0.01	–	–
″	6	2.1	0.4	0.17	0.47	–	–
Vishki	2	1.6–2.2	3.7–7.4	0.25–0.7	0.7–1.1	0.3–21	18
″	12	2.8–4.9	0.8–5.2	0.5–0.7	0.5–0.7	0.1–1.7	0.1
Dotkas (June)***	3	2.2–4.6	0.8–12	0.7–7.0	1.1–3.7	1.1–7.0	–
Dotkas (July)	1	2.6	22	1.1	1.8	1.3	7
″	3	3.2–5.8	2.6–17	1.7–11	0.7–4.4	11–40	50
Tivera	5	1.9	0.2			–	–
Mustyarv	7	3.1–4.8	0.2–0.5	0.01–0.05	0.1–0.7	–	–
Linoyarv	10	4.9–9.2	0.3–0.4	0.7–11	1.7–4.4	100	1
Drukshyai	2	0.6	0.05	0.001	0.005	–	–
″	5	4.3	6.7	0.4	7.1	0.9	100
″	30	1.9–3.1	0.7–2.6	0.9–1.1	4.4–7.0	1.3–25	7

Table 4. The intensity of microbiological processes in the surface layer (0–5 cm) of the Baltic lake sediments

Lake	Depth, m	O_2 consumption, mg/(m^2 day)	CO_2 production, mg C/(m^2 day)	DA of CO_2, mg C/(dm^3 day)	CH_4 production ml/(dm^3 day)				Sulfate reduction, μg S/(dm^3 day)
					CH_4 production		CH_4 oxidation, 0–2 cm	CH_4 emission, m^2	
					0–2 cm	2–5 cm			
Dridzas	3	480	560	0.58	<0.01	1.15	1.35	<0.1	–
″	50	145	270	0.43	0.02	0.40	0.33	3	13
Stropu	2	–	–	0.09	<0.01	0.34	0.12	<0.1	–
″	6	380	220	0.48	0.32	2.35	2.85	17	65
Vishki	2	1290	1690	6.79	0.01	16.2	6.52	140	–
″	12	320	710	1.23	0.35	0.64	3.17	35	20
Dotkas (June)***	3	840	1180	10.4	14.8	4.14	9.12	220	90
Dotkas (July)	1	1800	1700	6.88	0.67	14.7	11.2	100	42
″	3	0	2640	5.52	21.2	15.7	0	820	110
Tivera	5	570	820	1.22	0.45	6.72	4.87	80	–
Mustyarv	7	0	210	–	1.55	3.02	0	115	–
Linoyarv	10	0	6600	–	106	70.5	0	3400	7
Drukshyai	2	80	30	0.01	<0.01	–	0.01	<0.1	–
″	5	620	2580	3.20	1.82	0.54	1.48	11	280
″	30	0	860	0.87	20.6	15.7	0	280	27

and environmental temperature. For instance, the methane formation rate in the profundal mud of warm eutrophic Lake Dotkas was lower than in Lake Linoyarv, where the temperature of the bottom mud in summer did not exceed 5°C (Table 1). At the same time, the intensity of methanogenesis directly depended on redox conditions and the C_{lab} content (Table 2).

The intensity of methane oxidation in the oxic lake sediments varied from 0.01 to 11.2 ml CH_4/(dm^3 day). In the coastal sands and clayey mud of Lake Dridzas, where methanogenesis was found to be minimal, up to 90% of methane produced was oxidized. This value is comparable with that observed for oligotrophic Lake Boden [10]. The oxidation of methane in the coarse

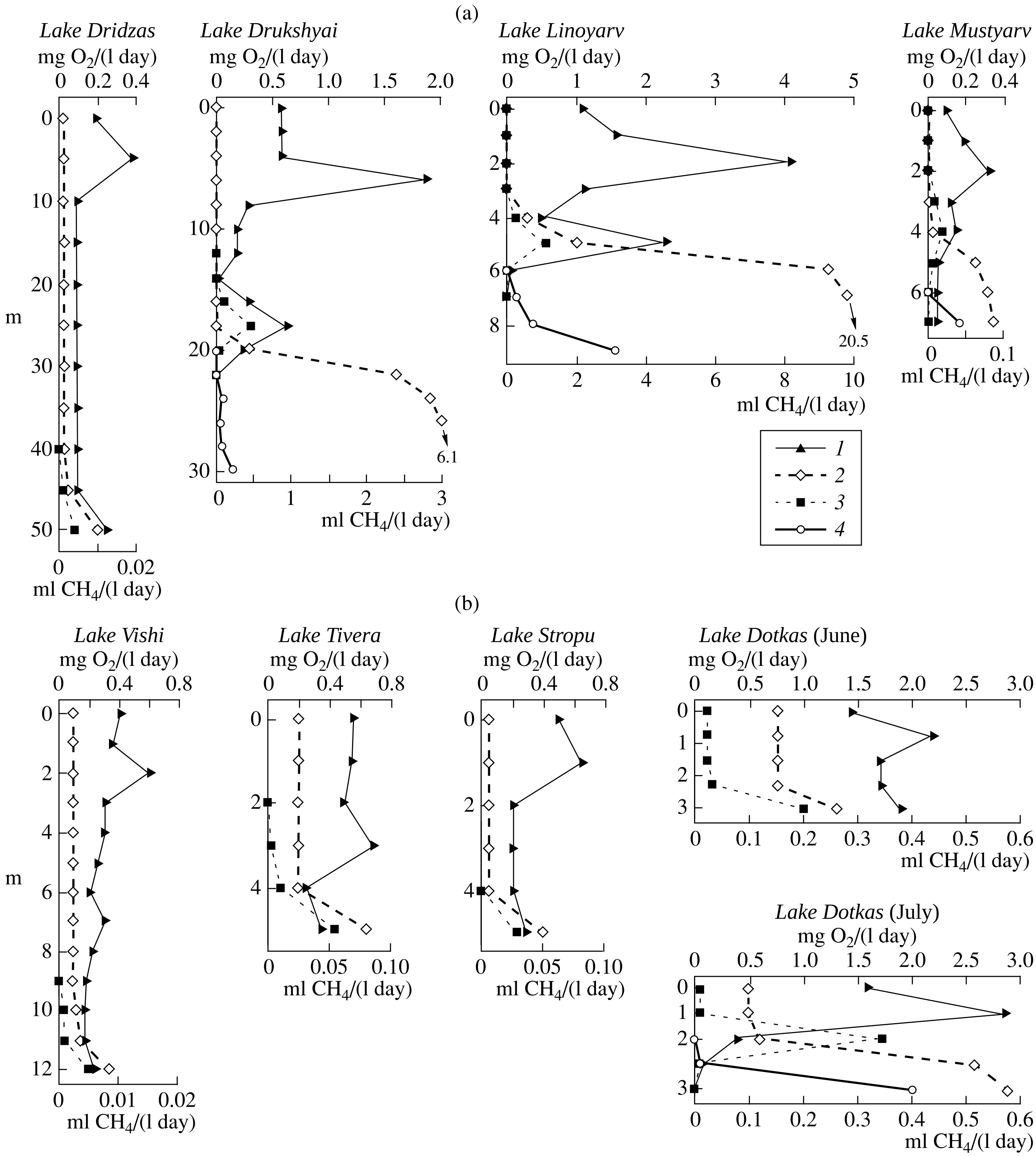

Fig. 1. Distribution of methane and the intensity of its transformation in the (a) dimictic and (b) holomictic Baltic lakes: (*1*) oxygen consumption rate; (*2*) methane concentration; (*3*) methane oxidation rate; and (*4*) methane production rate. The upper abscissa shows the oxygen consumption rate in mg O_2/(l day). The lower abscissa shows the concentration of methane in ml CH_4/l and the intensities of methane formation and oxidation in ml CH_4/(l day). The ordinate represents depth in m.

detrital silt and macrophyte thicket, where the methane formation processes were intense, did not exceed 50%, i.e., value typical of eutrophic lakes [11, 12]. In the highly anoxic muds of lakes Drukshyai and Linoyarv with stable hypolimnion, methane was anaerobically consumed at a rate of 3.6–9.4 ml CH_4/(dm^3 day). The daily upflow of methane from the lake bottoms varied from 0.1–140 ml CH_4/m^2 in the littoral zones of the lakes to 220–3400 ml CH_4/m^3 in their profundal basins (Table 4).

Table 5. The intensity of various processes of the methane cycle in the Baltic lakes (ml $CH_4/(m^2$ day))

Lake	Trophic level	Mud (0–5 cm)			Water				Consumption of C_{org} for MP, mg $C/(m^2$ day)	
		methane production (MP)	methane oxidation	methane emission	methane production (MP)	% of the sum	methane oxidation	% of the sum	mud	water
Lakes with oxic conditions at the bottom										
Dridzas	Oligomesotrophic	15	11	3	0	0	1	8	30	0
Stropu	Mesotrophic	80	60	17	0	0	10	14	150	0
Vishki		110	65	35	0	0	15	19	180	0
Tivera	Mesoeutrophic	210	100	80	0	0	40	30	330	0
Dotkas (June)	Eutrophic	410	180	220	2	0.5	100	35	765	5
Lakes with anoxic conditions at the bottom										
Mustyarv	Chthonoeutrophic	120	0	115	<1	<1	90	100	220	<1
Drukshyai	Eumesotrophic	780	0	280	110	14	370	100	1450	200
Dotkas (July)	Eutrophic	970	0	820	90	9	320	100	1810	170
Linoyarv	Hypereutrophic	420	0	3400	800	18	1180	100	8230	1550

The intensity of sulfate reduction, another important terminal process of the anaerobic decomposition of organic matter, in the lake muds was low, except for the black mud of the bay of Lake Drukshyai polluted with wastes from the Ignalina NPP, where it reached 280 μg S/(dm^3 day). In geochemical consequences, such intense sulfate reduction is comparable with methanogenesis (Table 4). According to Capone and Keine [13], the high rates of sulfate reduction may be due to an increased content of sulfates in the lake muds (Table 2).

In most of the dimictic lakes, methane concentrated in the hypolimnion, where its concentration reached 6–20 ml CH_4/l. The narrow microoxic metalimnion at the thermocline bottom is characterized by the presence of a specific methanotrophic "blocking" horizon, where the intensity of methane oxidation reached 0.45–1.1 ml CH_4/(l day) [12, 14]. Due to this horizon, the methane content in the epilimnion decreased to 3–20 μl CH_4/l, i.e., by several orders (see Fig. 1a). In the anaerobic hypolimnion of the productive lakes, the intensity of methanogenesis varied from 0.2 to 3.2 ml CH_4/(l day).

Knowing the intensities of the particular processes of the methane cycle in the lake sediments and the water column, I calculated the overall rates of the summer methane production and oxidation in the lacustrine ecosystems (Table 5). The calculations, which took no account of the littoral zones of the lakes as they comprise only insignificant fractions of the lake areas and volumes [15] showed that the production of CH_4 in the lakes with aerated water was due to the activity of the bacterial community of mud and amounted to 15–210 ml $CH_4/(m^2$ day). Such intensities of methanogenesis are typical of oligotrophic and mesotrophic bodies of water [3, 7, 8]. Most of the methane produced in mud was oxidized by the mud bacterial community, so that the emission of methane from the profundal zone varied from 3 ml $CH_4/(m^2$ day) in oligomesotrophic Lake Dridzas to 80 ml $CH_4/(m^2$ day) in mesoeutrophic Lake Tivera. The consumption of methane in the water column of the lakes varied, depending on the lake productivity, from 8 to 35% of the total methane oxidized in a given lake.

In the dimictic lakes with the anaerobic hypolimnion, methane was produced not only by benthic bacterial communities but also by bacterioplankton (the latter produced from 0.5 to 18% of the total methane). The overall production of methane in such lakes was 120–5000 ml $CH_4/(m^2$ day); these values are typical of hypereutrophic lakes and fish ponds [1, 16]. The methane produced in and released from the profundal mud was mainly oxidized in the metalimnion (Table 5). The oxidation of methane in the metalimnion reached 95% (see Fig. 1a) of its total oxidation in the lakes, which varied from 90 to 1180 ml $CH_4/(m^2$ day).

The consumption of C_{org} for methanogenesis may reach 50–65% of the total decomposition rate of organic matter [11, 17]. In the lakes with aerobic conditions at the bottom, in which methanogenesis occurred only in the bottom mud, the consumption of C_{org} varied from 30 to 765 mg $C/(m^2$ day), comprising from 11 to 64% of the total decomposition rate of organic matter in the muds (Tables 4 and 5). These values corresponded to the trophic status of the lakes. In the eutrophic lakes with the anaerobic bottom basins, the consumption of C_{org} for methanogenesis in the mud and water column varied from 220 to 9780 mg $C/(m^2$ day), comprising 67–100% of the decomposition rate of organic matter in the mud and 35–70% of the total decomposition rate of organic matter in the lake.

Thus, the microbiological processes of the methane cycle play an important part in the functioning of lacustrine ecosystems in the Baltic region. The intensities of the processes of methane formation and oxidation, as well as the proportion between them, depend on various ecological factors, such as the surrounding landscape, the lake morphology, the availability of easily metabolizable organic matter, redox conditions, and water stratification, or, in other words, on the productivity and hydrologic characteristics of the lakes.

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