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EXPERIMENTAL ARTICLES

Bacterioplankton and Bacteriobenthos of Three Floodplain Lakes in the Lower Course of the Amur River

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Abstract—The main structural and functional characteristics of bacterioplankton and bacteriobenthos of three lakes in the lower course of the Amur River are presented: the total number of bacteria (TNB), biomass, the numbers of bacteria of certain aerobic and anaerobic groups; the intensities of methanogenesis (MG), methane oxidation (MO), assimilation of ^{14}C-compounds, sulfate reduction (SR); and gross estimate of organic matter decomposition (D). Depending on the reservoir type and the anthropogenic load, TNB constituted (2.27 to 16.1) $\times 10^6$ cells/ml in water and (1.06 to 10.35) $\times 10^9$ cells/cm^3 in sediments; MO was 0 to 0.28 ml CH_4/(l day) in water and 0 to 8.4 ml CH_4/(dm^3 day) in sediments; MG in sediments was 0.001 to 40 ml CH_4/(dm^3 day); SR varied from 0.001 to 24.8 mg S/(dm^3 day); D was 0.3 to 25 g C/(m^2 day) in water and 0.2 to 4.9 g C/(m^2 day) in sediments. The role of anaerobic microbial processes of organic matter decomposition was shown to increase with an increase in the anthropogenic load, attaining 95% of the total D in the ecosystem of an accumulating pond.

Key words: number of bacteria, microbial processes, methane cycle, decomposition of organic matter.

The Amur, one of the largest rivers of Russia, has a complex and branched system of channels, eriks (shallow channels), and various floodplain lakes [1]. However, the ecological investigations of these reservoirs are scarce [2], and no data on the bacterial population is available. The aim of this work was to provide a microbiological characteristic of some lakes that are part of the Lower Amur system and to assess the role of the plankton and benthic bacterial communities in the organic matter turnover in these reservoirs under conditions of different anthropogenic loads.

SUBJECTS AND METHODS

The research was carried out in autumn periods in 1989 through 1991 on three lakes situated on the left bank of the lower course of the Amur River on a stretch from the town of Amursk to the village of Bogorodskoe (Fig. 1). The largest of them (Lake Udyl’) is in the forbidden zone at the spurs of the Sikhote Alin Range, and two small lakes (Lake Ommi and an accumulating pond) are situated within the industrial complex of the Amursk Paper and Cardboard Combine (APCC).

The water and sediment sampling stations were in the deep area of the lakes and in the littoral areas. The water for microbiological analyses was taken with a sterile Frantsev’s bottle; for chemical analyses, water was taken with a Rutner’s bathometer. Bottom sediments were sampled with a dredge that enabled their structure to be preserved; therefrom, using sterile tubes, samples of the superficial layer (0 to 5 cm) were obtained for hydrochemical analyses and microbiological inoculations and experiments.

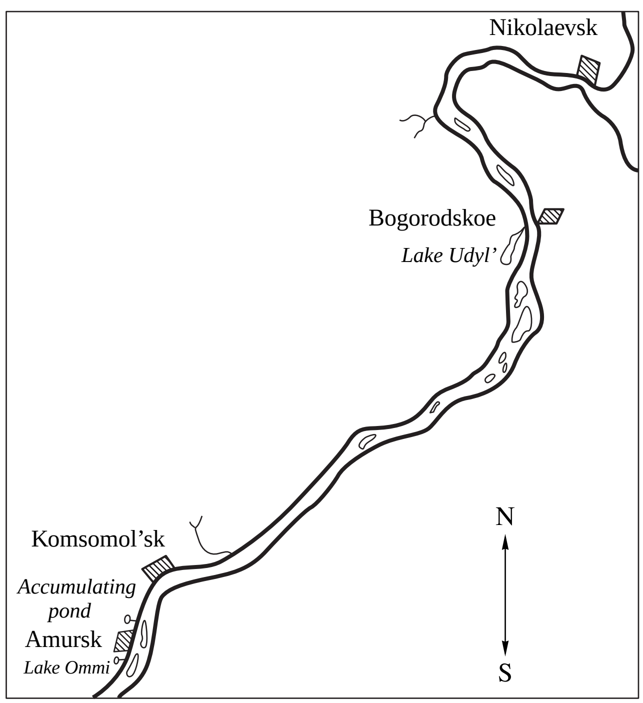

Fig. 1. Scheme of the location of the lakes studied in the lower course of the Amur River.

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Table 1. Physicochemical and production characteristics of Lake Udyl' waters

Station no.	Depth, m	Temperature, (T), °C	O_2, mg/l	pH	Carbonates, mg C/l	Methane, μl CH_4/l	Photosynthesis (P), mg C/(l day)
1	1.6	14.1/14.1	11.2/10.8	8.2/–	3.0/–	3.9/3.9	0.25/–
2	3.5	14.2/14.2	10.8/10.8	7.9/7.9	4.2/4.2	3.6/3.6	0.13/–
3	4.8	14.2/14.3	10.8/10.5	7.9/7.9	4.2/4.4	10.3/13.7	0.14/–
4	2.0	13.1/13.1	9.7/9.7	7.6/–	8.7/–	0.8/–	0.08/–

Note: The numerator shows the results of the analysis of superficial (0 to 0.5 m) waters; the denominator shows data for near-bottom waters. The dash (here and in the other tables) denotes the absence of data.

Table 2. Microbiological characteristics of Lake Udyl' waters

Station no.	Bacterioplankton, cells/ml		Fungi (F), diaspo-res/ml	B, mg/l	Assimilation, μg C/(l day)			BP, mg C/(l day)	MO, μl CH_4/(l day)	
	TNB, $\times 10^6$	SB, $\times 10^1$			CO_2	acetate	hydro-lysate		0.5 m	near the bottom
1	4.86	200	1.5	0.69	4.7	0.4	0.5	0.08	0.38	0.30
2	4.68	280	1	0.56	–	–	–	–	0.12	0.11
3	4.73	820	3.5	0.71	5.1	0.6	0.6	0.09	1.46	3.55
4	2.27	50	<1	0.22	2.1	0.1	0.1	0.03	0.01	–

Note: TNB is the total number of bacteria; SB is the numer of saprophytic bacteria; B is wet biomass of bacteria; BP is bacterial biomass production; MO is methane oxidation.

The physicochemical and production characteristics of the lakes were investigated by generally accepted methods [3] using the following instruments: a KL-115 oxygen meter with a thermistor, a Radelkis ionometer, an Ergoval microscope, and a Mark-2 scintillation counter. The organic matter (OM) of the sediments was determined on a CNH-1 gas chromatographic analyzer, separating readily hydrolyzable OM fractions (C_{rh}) by treating the samples with 5% H_2SO_4; sulfates (S) were determined by titration with alizarin. The methane content in water and bottom sediments was analyzed by the partial ratios method [4] using a Chrom-5 chromatograph equipped with a flame-ionization detector and 2.4-m columns with Porapak-Q; the temperature was 35°C; helium was the carrier gas. The intensity of plankton photosynthesis was measured by the radiocarbon method. The total number of bacteria (TNB) was counted on Synpor membrane filters (pore diameter, 0.17 μm) after staining them with erythrosin. Saprophytic bacteria were grown on fish–peptone agar (to create anaerobic conditions, Na_2S was added); sulfate-reducing bacteria were grown on Postgate-B medium; methanogens, were grown according to the Belyaev' method [3]; fungi and yeasts were grown on wort agar.

The intensity of the microbial processes of the methane cycle was assessed by the gas chromatographic method from the difference in methane concentrations between the control and test vessels [3] with the use of inhibitory analysis [5, 6]. All the manipulations with the samples were carried out using the syringe technique and inert gas. The vessels were incubated for 8 to 24 h in the dark at the temperature of the pond. Further calculations were made according to [3, 4]. The rates of CO_2, acetate, and protein hydrolysate assimilation, as well as the rate of sulfate reduction to H_2S, were measured by the radiocarbon method [3] by adding corresponding ^{14}C or ^{35}S preparations and incubating in the dark for 12 h. The bacterial production was determined from dark assimilation of CO_2, using different coefficients, depending on the oxidation conditions [7]. The gross value of the aerobic and anaerobic OM destruction in the sediments was calculated from O_2 consumption and CO_2 release [3], taking into account CO_2 reassimilation [8] and the expenditure of C_{org} on methanogenesis and sulfate reduction.

RESULTS AND DISCUSSION

Lake Udyl', one of the largest (330 km^2) in the Lower Amur basin, has an oblong form and a maximal depth of 6 m. The water alimentation is mixed: in the high-water period, it is supplied by the Amur waters; in the low-water period, it is replenished by the tributaries flowing in the taiga (coniferous forest) area not interfered with by economic activities.

Microbiological investigations carried out in September 16–19, 1989, at a transverse semisection in the

Table 3. Physicochemical characteristics of the bottom sediments of Lake Udyl'

Station no.	Appearance	Eh,* mV	pH	Content in 1 dm^3 of wet ground				
				CO_3^{-2}, g C	SO_4^{-2}, mg	C_{org}, g	C_{rh}, g	CH_4, ml
1	Clayey silt	75/40	7.2	0.8	15	5.2	0.6	0.21
2	Sandy silt	80/60	7.4	0.7	10	4.4	0.5	0.08
3	Detritus clayey silt	40/–20	7.4	1.2	12	9.5	1.9	3.17
4	lightly silted sand	180/–	7.6	1.5	21	1.8	–	0.01

* The numerator shows the measurement results for the 0- to 2-cm layer; the denominator, for the 2- to 5-cm layer.

Table 4. Microbiological characteristics of the bottom sediments of Lake Udyl'

Station no.	Bacteriobenthos, cells/cm^3				Microbial processes, dm^3/day					
	TNB, $\times 10^9$	SB, $\times 10^4$	MGB, $\times 10^3$	SRB $\times 10^3$	methane conversion, ml CH_4		assimilation, mg C			sulfate reduction (SR), mg S
					MG	MO	CO_2	acetate	hydrolysate	
1	4.93	44	0.1	0.02	0.11	0.09	132	0.12	0.05	0.04
2	2.42	28	0.1	0.01	0.19	0.21	0.76	0.06	0.03	0.02
3	6.35	278	10	1.7	5.75	2.90	1.45	0.23	0.11	0.08
4	1.06	11	0.01	<0.01	0.05	0.05	0.18	0.02	0.01	<0.01

Note: MGB, methanogenic bacteria; SRB, sulfate-reducing bacteria; MG, methanogenesis. The rest designations are as in Table 2.

Table 5. General and microbiological characteristics of Lake Ommi waters

Depth, m	*T*, °C	O_2, mg/l	CH_4, µl/l	P, mg C/(l day)	Bacterioplankton total number (cells/ml) and activity (l/ day)			
					TNB, $\times 10^6$	SB, $\times 10^1$	CO_2 assimilation, µg	MO, µl CH_4
1.5	19.5/19.5	10.1/10.1	22/21	0.48	5.21	660	12.6	7.6/6.8
4.5	19.1/19.0	10.2/10.2	64/92	0.67	6.35	840	17.4	18/22

Note: The designations are the same as in Tables 1 and 2.

middle of the reservoir (stations 1–3) and in the upper part of the lake (station 4) revealed the vertical homogeneity of its water thickness, determined by permanent mixing (Table 1). However, in certain zones, the waters were markedly different in both physicochemical and biological characteristics. In cooler, mineralized, and low-production head waters directly influenced by the tributaries, the density and the physiological activity of bacterioplankton appeared to be low (Table 2). In the central part of the lake, where the phytoplankton development was abundant (especially in the waters of the right-bank bay at station 1), the TNB and the main trophic characteristics of bacterioplankton increased by a factor of 2 or 3 as compared with the head water region; the number of saprophytic bacteria and fungi was higher by an order of magnitude. An increase in the content of methane in the water and sharp activation of its oxidation processes, attaining 1.5 µl CH_4/(l day) in the superficial layers of the deepest lake zone was noted, which is characteristic of mesoeutrophic reservoirs not exposed to anthropogenic load [6, 9].

The physicochemical properties of bottom sediments in the zones of Lake Udyl' studied and the availability of C_{org} in them varied significantly, reflecting the productivity and other ecological peculiarities of the reservoir. The Eh values in the sediments of the central part of the lake, despite the saturation of the near-bottom layers of water with oxygen, appeared to be low, and strictly aerobic conditions were recorded only in the

Table 6. Physicochemical and microbiological characteristics of the bottom sediments of Lake Ommi

Eh, mV	C_{org}, g/dm^3	CH_4, ml/dm^3	SO_4^{-2}, mg	Total number (cells/cm^3) and activity (dm^3/day) of bacteria					
				TNB, $\times 10^9$	SB, $\times 10^4$	MO, ml CH_4	CO_2 assimilation, µg C	MG, ml CH_4	SR, mg S
80/20	8.8	1.23	63	4.71	440	–	2.35	1.53	0.04
60/–40	14.2	7.45	92	7.22	680	8.43	3.87	9.85	0.18

Note: The designations are the same as in Tables 2–4.

Table 7. General and microbiological characteristics of the superficial waters of the accumulating pond

Station no.	Depth, m	T, °C	O_2, mg/l	CH_4, ml/l	Microbial plankton total number (cells (diaspores)/ml)				B, mg/l	Assimilation, µg C (l day)			Total bacterioplankton activity		
					TNB, $\times 10^6$	SB, $\times 10^1$	F, $\times 10^1$	Yeasts		CO_2	acetate	hydrolysate	MO, µl CH_4/(l day)	G, h	BP, mg C/(l day)
1	2	14.3	1.4	3.6	16.1	80	50	80	5.2	140	11.3	3.6	220	60	0.75
2	5	14.1	1.3	2.7	12.9	60	40	120	5.4	162	–	4.8	282	45	0.82
3	9	14.0	1.4	2.7	10.8	50	10	1	3.1	114	17.2	2.6	110	80	0.56
4	6	14.0	1.5	2.4	10.6	50	10	<1	2.9	104	–	2.3	95	90	0.52

Note: G is the time of TNB doubling. The rest designations are the same as in Tables 1 and 2.

sandy sediments of the upper part of the lake (Table 3). Methane concentration varied from 0.01–0.8 ml CH_4/dm^3 in the sandy grounds to 3.17 CH_4/dm^3 in the detritus silts of the deepest lake zone (station 3).

The spatial distribution of bacteriobenthos was on the whole similar to the bacterioplankton distribution: the minimal number and activity of microorganisms were observed in the head water sandy sediments; the maximal occurred in the center of the lake (Table 4). This heterogeneity manifested itself more sharply when anaerobic communities were analyzed. In mineralized sediments, with a sufficient abundance of aerobic saprophytes, the number of methanogenic and sulfate-reducing bacteria was extremely low (<10cells/cm^3); methanogenesis did not exceed 0.01 to 0.19 ml CH_4/(dm^3 day); the sulfate reduction rate was a low as 0.005 to 0.04 mg S/(dm^3 day). In the reduced detritus silts of the central part of the reservoir, where the C_{rh} content attained 20% of OM, the community structure appeared to be complex: both aerobic and anaerobic groups of bacteria developed actively; the intensity of methanogenesis increased by an order of magnitude, as compared with the head water and littoral regions; however, the main part of the CH_4 formed was oxidized here; sulfate reduction remained low due to the obvious lack of the required electron acceptor [9]. On the whole, the OM decomposition in the mesoeutrophic Lake Udyl' occurred with the predominance of aerobic processes, and the dominant terminal stage of the anaerobic decay of C_{org} was methanogenesis.

Lake Ommi is a small (0.9 km^2) shallow lake near the town of Amursk, and it is used for recreation and fish breeding. The investigations carried out in September 9–11, 1989, in the littoral waters and at the maximal depth showed that, due to vigorous phytoplankton photosynthesis and permanent mixing, the water thickness was uniformly warmed and saturated with oxygen. The methane concentration, with an insignificant gradient, was 64 µl CH_4/l even near the surface, which is inherent in eutrophic reservoirs [6, 11]. The density and physiological activity of bacterioplankton give evidence of the high saprogeneity of the lake waters (Table 5), i.e., of the noticeable anthropogenic load on its ecosystem.

The bottom bed of Lake Ommi is covered with homogeneous clay sediments strongly reduced in the 2- to 5-cm layer. The number and the activity of bacteriobenthos, by virtue of a large supply of C_{org} and a good warm-up, appeared to be high everywhere. Despite the small depth of the reservoir and the presence of oxygen in the water, not only aerobic but also anaerobic processes of OM decomposition occurred in its sediments. Among them, methanogenesis appeared to be the most significant ecologically, as in Lake Udyl' (Table 6); however, the role of sulfate reduction here increased substantially. The latter may be determined by the increased content of sulfates [12] accumulating

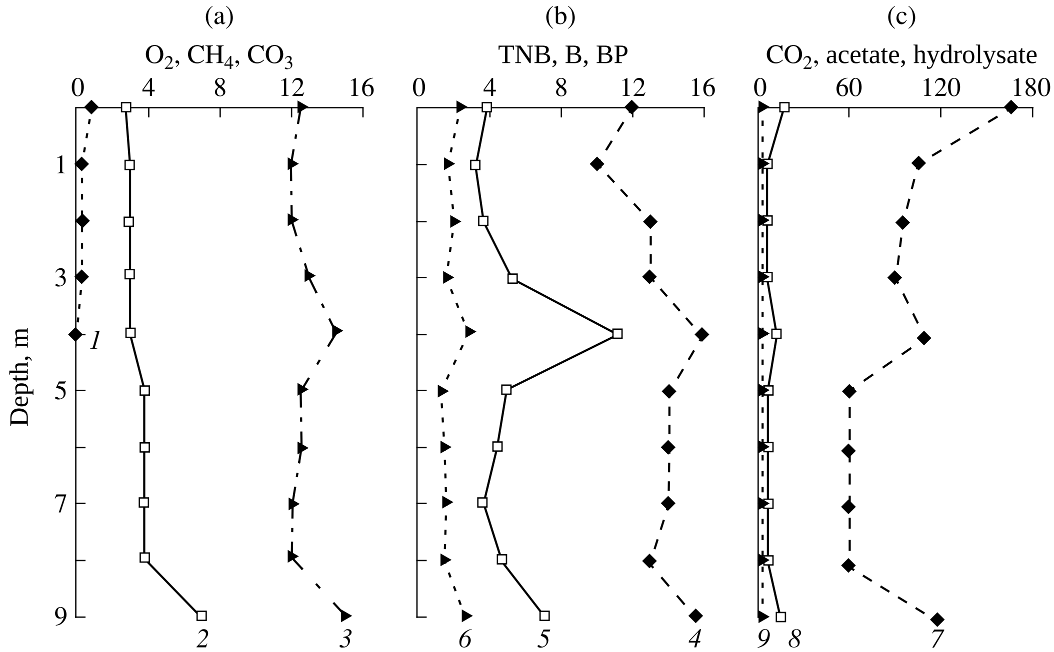

Fig. 2. Distribution of (a) dissolved gases and carbonates, (b) bacterioplankton, and (c) microbial assimilation of ^{14}C-compounds in the water thickness of the accumulating pond: (*1*) O_2, mg/l; (*2*) CH_4, ml/l; (*3*) CO_3-C, mg/l; (*4*) the total amount of bacterioplankton (TNB), million cells/ml; (*5*) bacterial biomass (B), mg/l; (*6*) bacterial production (BP), mg C/(l day); assimilation of (*7*) CO_2, (*8*) acetate, and (*9*) hydrolysate, μg C/(l day).

due to the anthropogenic load on the ecosystem of the lake.

The accumulating pond for processed sewage of the Amursk industrial enterprises (mainly APCC) was built in 1968 by banking up the gully with the Bolotnyi stream and represents a stable specific lacustrine ecosystem. Its area, depending on the filling, constitutes 1.2 to 1.7 km^2; it maximal depth is 10 to 16 m.

The studies conducted in September 26–October 23, 1991, showed that, under conditions of density stagnation and homothermy, the waters of the accumulating pond are sufficiently homogeneous by physicochemical criteria. Its high-color and C_{org}-rich waters (700 and 470 mg C/l, respectively, according to Bikbulatov's data), contained methane across the entire vertical profile (2.7 to 4.5 ml/l) and were virtually devoid of oxygen. Only near the surface, was the O_2 concentration 1.3 to 1.5 mg/l. The physicochemical properties of the waters of individual zones were also similar; however, their microbiological characteristics differed considerably (Table 7). A high TNB and biomass level was noted throughout the pond area, but in the littoral waters (station 1)—near the collector of the processed effluents flowing into the pond—these trophic values reached the maximum. Here and in the adjacent region (station 2), aquatic fungi and yeasts were especially numerous, while the amount of saprophytic bacteria was low. The estimates of the bacterioplankton activity also testify to its spatial heterogeneity. The APCC wastes entering the accumulating pond contain, in addition to lignin and cellulose, a large amount of readily hydrolyzable substances, which, as judged by the assimilation rate of ^{14}C-compounds, vigorously undergo decomposition in close proximity to the collector (stations 1, 2). Other functional characteristics of the bacteria also reached their maximum here (Table 7).

The vertical structure of the bacterioplankton in the main crater of the accumulating pond appeared to be rather complicated, despite the apparent homogeneity of the water mass (Fig. 2a). In the water thickness of the pond, as judged by the distribution of bacteria and their physiological activity, three ecological zones were formed, conditionally corresponding to the hypo-, meta-, and epilimnion of natural lakes (Figs. 2b, 2c). The first of them is the zone of contact with silts, the second is the zone of transition from anaerobic conditions to microaerobic ones, the third is the zone of contact with the atmosphere.

The bottom of the pond is covered with black, strongly reduced silts with a strong odor of hydrogen sulfide. Nearer to the collector (stations 1, 2), the sediments are continuously replenished with an organic suspension, contain a large amount of woody fibers, and are liquid and gas-emitting; further towards the opposite bank (stations 3, 4), warp-free and more dense grounds occur. The C_{org} content (in the 0- to 5-cm layer) is high throughout the whole bottom, but, in the young methane-saturated sediments, the C_{rh} content is twice as high (Table 8). A distinctive feature of the silts in the accumulating pond is their high sulfate concentration, attaining 680 mg SO_4^{2-}/dm^3 in the old dense silts.

Table 8. Physicochemical characteristics of the bottom sediment of the accumulating pond

Station no.	Appearance	Eh, mV	Eh, mV; Content in 1 dm^3 of the wet ground				
			CO_3^{-2}, g C	SO_4^{-2}, mg	C_{org}, g	C_{rh}, g	CH_4, ml
1	Black gas-emitting silt with woody fibers	–90/–100	2.2	480	27.8	2.9	110
2	Black gas-emitting silt	–90/–100	2.4	540	23.2	2.3	133
3	Black viscous silt	–100/–100	6.0	620	21.2	1.2	26
4	Black silt with a white film	–110/–110	7.8	680	21.5	1.1	12

Table 9. Microbiological characteristics of the bottom sediments of the accumulating pond

Station no.	Bacteriobenthos, cells/cm^3				Microbial processes, dm^3/day				
	TNB, $\times 10^9$	SB, $\times 10^4$	MGB, $\times 10^3$	SRB, $\times 10^3$	MG, ml CH_4	assimilation, mg C			Sulfate reduction (SR), mg S
						CO_2	acetate	hydrolysate	
1	6.42	128	100	70	39.2	270	130	30	2.9
2	10.35	276	100	–	40.1	220	40	170	6.7
3	7.93	24	25	280	5.8	390	70	20	24.3
4	8.06	11	25	260	5.0	120	20	240	16.8

Note: The designations are the same as in Tables 2 and 4.

The studies of four typical regions of the pond bottom (preliminary analyses were performed at nine points) revealed certain specific features of the bacteriobenthos spatial distribution and functioning, reflecting the heterogeneity of the bottom sediments. The TNB and the total activity of bacteria (judged from the assimilation rates of ^{14}C-compounds) were high at all the sites of the basin; however the anaerobic communities proved more heterogeneous. Predominantly anaerobic saprophytic and methanogenic bacteria developed in gas-emitting sediments rich in labile OM (stations 1, 2). The methanogenesis in these zones attained the level recorded in hypereutrophic lakes [13]—40 ml CH_4/(dm^3 day)—and was the main terminal stage of the anaerobic OM decomposition. In the silts of the zone remote from the sewage, which had the maximal SO_4^{2-} content but were C_{rh}-depleted, sulfate-reducing bacteria dominated, and the ratio of the terminal anaerobic processes was changed, i.e., methanogenesis declined, and the main role in the C_{rh} decay was taken over by sulfate reduction that increased several times, as compared with the first region (Table 9). The simultaneous occurrence of these processes, especially in marine sediments, is known to be possible [13]; however, such a high level is not typical of freshwater reservoirs, although it was noted in meromictic lakes [15, 16] and in local areas of the water storage basins exposed to industrial pollution [17].

Based on the experimental data obtained and the stoichiometric calculations, general estimates of the aerobic and anaerobic pathways of OM decomposition in the water and bottom sediments in various zones of the lakes were made (Fig. 3). The gross C_{org} decomposition in the water thickness constituted 0.28 to 25 g/(m^2 day); in the sediments, this value varied from, 0.18 to 4.9 g/(m^2 day). In Lake Udyl', where these values are minimal, aerobic processes predominated, and methanogenesis was the main anaerobic process. In Lake Ommi, the decomposition processes were, on the whole, balanced, and an increase in the sulfate reduction rate was noted. In the accumulating pond, decomposition was the most intense, and it was mainly anaerobic (95% of the total D); the sulfate reduction process was predominant.

Thus, this study provided general microbiological characterization of different types of lakes of the Lower Amur basin, as well as quantitative estimation of the activities of the plankton and benthic bacterial communities. The share of each of them in the total OM decomposition depends not only on the provision of the ecosystem with available C_{org} but also on the biotope type. In the littoral zone of all the reservoirs, the ratio of the decomposition processes in the water and sediments was almost the same, ranging between 0.81 and 0.89; in the deep-water zones, this ratio was between 0.65 and 1.8; the contribution of anaerobic processes to the total OM decomposition varied from 28% in Lake Udyl' to 95% in the accumulating pond.

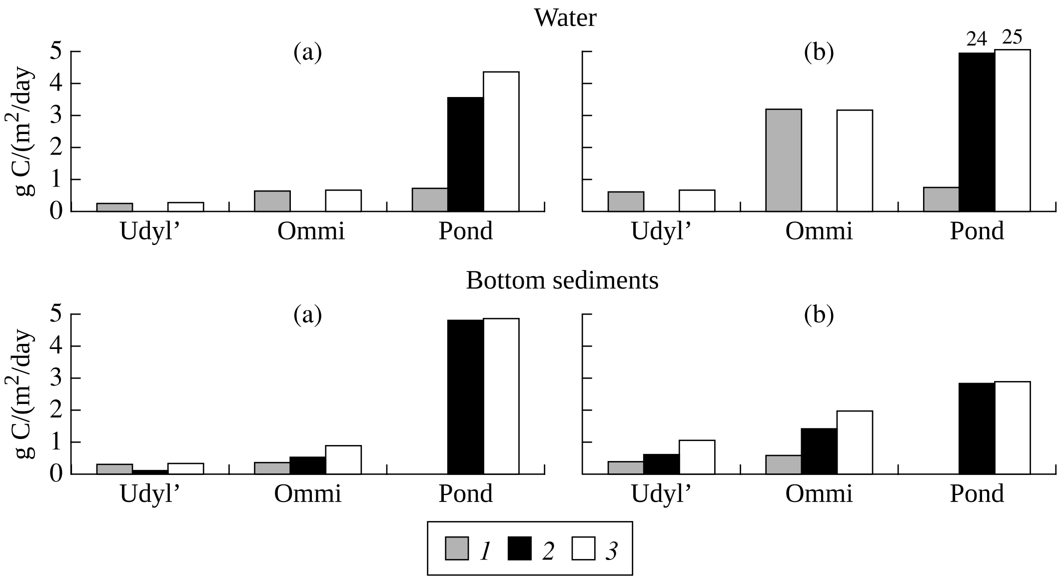

Fig. 3. Gross estimates of the microbial processes of organic matter decomposition in the water and bottom sediments of the floodplain lakes of the Lower Amur: (*1*) aerobic; (*2*) anaerobic; (*3*) total; (a) littoral area; (b) deep-sea zone.

In addition, the comparison between the data obtained and the data of similar works [5, 6, 8–13, 15–18], made it possible to reveal some general ecological tendencies. In low-production lakes and in the littoral areas of most other inland reservoirs, the turnover of organic matter is mainly driven by the aerobic communities of the water and bottom sediments. With the enhancement of the trophic status of a lake, the role of benthic bacterial cenoses increases, including the anaerobic ones, in which methanogens become more numerous and active. An increased anthropogenic load on freshwater ecosystems leads to considerable changes in the structure of bacterial communities, primarily benthic ones, where the population of sulfate-reducing bacteria increases dramatically. With a further increase in the anthropogenic (especially technogenic) load, anaerobic microbial processes, including sulfate reduction, become predominant.

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