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EXPERIMENTAL ARTICLES

Structure of Microbial Communities of the Sediments of Alkaline Transbaikalia Lakes with Different Salinity

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Abstract—The goal of the work was to reveal the differences in the structure of microbial communities of Transbaikalia alkaline lakes stemming from the differences in their salinity and hydrochemical parameters. The lakes studied were Verkhnee Beloe (Buryat Republic, Russia), as well as Khilganta, Gorbunka, and Borzinskoe (Transbaikal krai, Russia) with salinity from 12.3 to 430 g/L, which differed in the mineral composition of the sediments and hydrochemical parameters. Lake sediments were found to contain 47 prokaryotic phyla (42 bacterial and 5 archaeal ones). The phyla *Proteobacteria*, *Euryarchaeota*, *Bacteroides*, *Chloroflexi*, *Actinobacteria*, and *Firmicutes* were predominant, comprising over 95% of the classified sequences. Comparative abundance of archaea increased with salinity from below 1% in Lake Verkhnee Beloe to 35% in Lake Borzinskoe. The most numerous bacterial OTUs belonged to gammaproteobacteria of the genus *Halomonas* (up to 15% of the number of classified sequences). The most numerous archaeal OTUs were identified at the genus level as members of the genera *Halorubrum* and *Halohasta* belonging to the family *Halorubraceae*, which comprises extremely halophilic *Euryarchaeota*.

Keywords: microbial diversity, saline lakes, high-throughput sequencing, 16S rRNA
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Saline and brackish shallow lakes typical of the landscapes and arid climatic conditions of North Asia are characterized by an unstable water regime, complete freezing in winter, and significant fluctuations in salinity and water temperature (Namsaraev et al., 2015). Studies of the functional diversity of microbial communities of Transbaikalia and Mongolian soda and salt lakes revealed active production and decomposition of organic matter (Gorlenko et al., 1999; Sorokin et al., 2004, 2011). The metabolic and phylogenetic diversity of microbial communities in the water column and sediments of soda lakes was studied using molecular biology techniques (Foti et al., 2006 2008; Wu et al., 2009; Sorokin et al., 2011; Xiong et al., 2012; Baatar et al., 2016; Zhong et al., 2016). Bottom sediments of saline lakes are a models for studying the spatio-temporal processes of microbial ecology due to a clear vertical structure, significant chemical gradients, and the presence of oxic microzones (La Cono et al., 2013). Microbiological studies of alkaline Transbaikalia lakes resulted in isolation of a number of bacterial and archaeal cultures, including halophilic cyanobacteria (Tsyrenova et al., 2011a, 2011b), moderately halophilic cellulolytic bacteria (Kozyreva et al., 2014), halophilic alkaliphilic sulfate-reducing bacteria (Foti et al., 2007; Sorokin et al., 2012; Zakharyuk et al., 2015), and extremely halophilic archaea (Sorokin et al., 2017). *Alkaliphilus namsaraevii*, a novel species of alkaliphilic spore-forming bacteria, capable of iron and sulfur reduction under highly alkaline conditions (pH 10.7), was isolated from the bottom sediments of Lake Khilganta (Zakharyuk et al., 2017). In our previous works, we determined the rates of microbial production and degradation of organic matter and studied the taxonomic diversity in slightly mineralized lakes (Zaitseva et al., 2012; Namsaraev et al., 2015).

The goal of the present work was to reveal the differences in the structure of microbial communities stemming from the differences in salinity and hydrochemical parameters by the example of Transbaikalia lakes located in similar geographical and climatic conditions. The lakes studied were Verkhnee Beloe (Buryat Republic, Russia), as well as Khilganta, Gorbunka, and Borzinskoe (Transbaikal krai, Russia) with salinity from 12.3 to 430 g/L. It was shown that salinity affected the diversity of bacteria and archaea in the sediment microbial communities under highly alkaline conditions.

MATERIALS AND METHODS

Physicochemical parameters of the near-bottom water and sediments were determined directly at the sampling sites using portable tools: temperature and pH were measured using a PH-200 pH-meter (HM Digital, South Korea); redox potential (Eh) was determined using an ORP-169B ORP-meter (Kelilong, China); dissolved oxygen content was measured using an Oxi 315i handheld oxygen meter (WTW, Germany); water salinity was determined using a TDS-4 conductivity meter (Singapore). The major and minor ionic components in the samples were determined under laboratory conditions. The contents of ammonium, nitrate, and nitrite ions were determined by the photometric methods with the Nessler reagent, salicylic acid, and the Griess reagent, respectively; sulfate ions were determined turbidimetrically; chloride ions were measured by the argentometric method; carbonates and bicarbonates were determined by titration with hydrochloric acid using phenolphthalein and methyl orange as indicators (Namsaraev et al., 2005). X-ray phase analysis (XRD) enabling to reveal and identify minerals in the sediment samples was performed using a Phaser 2D diffractometer (Bruker, United States) (Cu$K_{\alpha 1}$ radiation). After identification of minerals in the bottom sediments, quantitative X-ray phase analysis was performed using the ICDD PDF Realase 2012 database by the superposition method based on comparison of the X-ray diffraction patterns of the test sample and those of the individual components using the Diffrac.Eva v. 3.0 interface. The accuracy and sensitivity of the analysis were 2–3 and 1–2%, respectively (Vasil'ev, 1986).

Determination of the rates of the main microbial processes was performed using a radiotracer method (Namsaraev et al., 2015). Measurement of the rate of light and dark CO_2 assimilation was performed using ^{14}C-labeled mineral carbon (carbonate).

To perform molecular biological studies, 5–10 g of the sediments from the surface layer (0–1 cm) of the coastal zone of the lakes were collected in 50-mL BD Falcon TM plastic tubes (Greiner Bio-One, Germany), which were stored in a refrigerator at 4°C prior to analysis.

Amplification and sequencing of the 16S rRNA genes. DNA was isolated from the sediment samples according to the method described by Lever et al. (2015). Amplification of the V3–V4 variable regions of the 16S rRNA genes and preparation of the libraries were performed according to previously described techniques with minor modifications (Fadrosh et al., 2012).

Amplification was performed using the forward primer (5'-CAAGCAGAAGACGGCATACGAGAT-GTGACTGGAGTTCAGACGTGTGCTCTTCCG-ATCT XXXXXXXXXXXX ZZZZ CCTAYGGGDB-GCWSCAG-3') containing 5' Illumina Linker Sequence, Index 1, Heterogeneity Spacer (Fadrosh et al., 2012), and Pro-mod-341F Primer Sequence and a reverse primer (5'-AATGATACGGCGAC-CACCGAGATCTACACTCTTTCCCTACACGAC-GCTCTTCCGATCT XXXXXXXXXXXX ZZZZ GACTACNVGGGTMTCTAATCC-3') containing 3' Illumina Linker Sequence, Index 2, Heterogeneity Spacer, and Pro-mod-805R Primer Sequence (Merkel et al., 2017). Fragments of the 16S rRNA gene were performed using 5× TaqRed buffer and *Taq* polymerase (Evrogen, Russia). The reaction mixture contained 5 μL of each primer (6 μM), 5 μL of the template DNA, and 15 μL of the PCR mixture, and the total volume of the reaction mixture was 30 μL. Each sample was amplified in duplicate, pooled, and analyzed by electrophoresis in 2% agarose gel. The amplicons were extracted from the gel using the Standard Cleanup Gel Extraction Kit (Evrogen, Russia). DNA concentrations were measured on Qubit® 2.0 fluorometer using the dsDNA HS (High Sensitivity) Assay Kit (Life Technologies, United States). DNA libraries were prepared and sequenced according to Illumina Sample Preparation Guide. DNA libraries sequencing was performed on Illumina MiSeq platform. Bioinformatic analysis was carried out using the QIIME (version 1.9.1) and SILVA software packages (Quast et al., 2013). The data obtained in this study are available in the BioProject database under ID PRJNA270559.

Multidimensional data analysis. *S*tatistical and mathematical processing of multidimensional data of the hydrochemical parameters of the studied lakes was carried out for visualization of the results and determination of the parameters most characteristic for the ecosystem of each lake. The data were analyzed using the principal component method, calculations were performed using MatLab 11 software package (The MatWorks, Inc., United States). Preliminary processing for standardization of the data was carried out according to recommendations by Groth et al. (2013).

RESULTS AND DISCUSSION

Physicochemical characteristics of the sampling sites. Microbial communities of the sediments of saline lakes Verkhnee Beloe (Buryat Republic, Russia), as well as Khilganta, Gorbunka, and Borzinskoe (Transbaikal krai, Russia) were studied in September 2015 (Fig. 1). The salinity varied between 12 g/L in the Verkhnee Beloe Lake and 430 g/L in Borzinskoe Lake, while it was 36 and 58 g/L in the lakes Khilganta and Gorbunka, respectively. Lakes Gorbunka and Khilganta were characterized by shallowness, sharp fluctuations in the total salinity and content of the main ions, and were strongly affected by seasonal and annual fluctuation of water levels (up to complete drying of Lake Khilganta). Long-term observations demonstrated that water salinity in Lake Khilganta varied from 30 to 230 g/L, while in Lake Gorbunka it ranged from 56 to 350 g/L. All lakes were characterized by shallowness with a maximum water depth of 2 m and alkaline pH values. The lakes differed in chemical composition of the water and mineralogical composition of the sediments. Lakes Borzinskoe, Khilganta, and Gorbunka were characterized by a high chloride content (of 73 to 84% of the total anion content) and low contents of carbonate (not more than

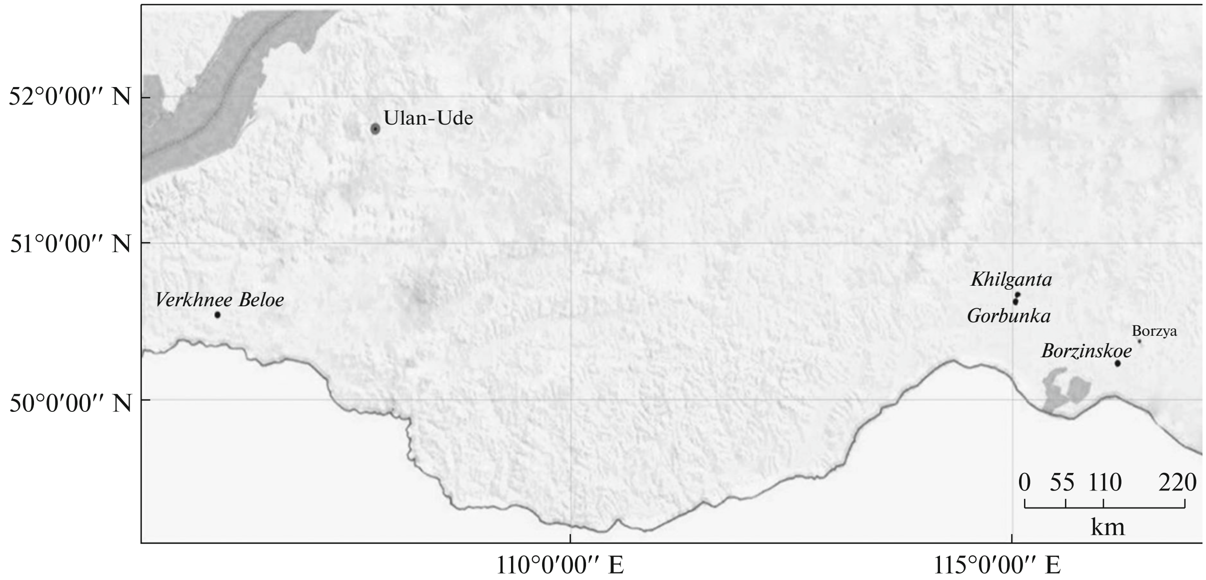

Fig. 1. Schematic maps of sampling sites.

12% of the total anion content) and sulfates (up to 17%). According to hydrochemical characteristics, Verkhnee Beloe is a soda lake with carbonate predominance in the anionic composition. Sodium cation was predominant in the water of lakes Borzinskoe, Khilganta, and Verkhnee Beloe (99% of total cation content). The water of Lake Gorbunka contained a significant amount of Mg^{2+} ions (more than 40% of the total cation content). Significant differences were revealed in trace element compositions of the near-bottom water (Table 1). Bottom sediments of the lakes were represented by sludges dark gray to blue-black in color, up to 15–20 cm in thickness, with gas breaks and plant residues, gray greasy sludge occurred lower at a depth of 70 to 100 cm. The results of solid phase analysis showed that mineral composition of the sediments of the lakes differed. Silicates, aluminosilicates, and quartz were predominant in Borzinskoe and Gorbunka. More than 40% of the mineral phase in Khilganta Lake were represented by zirconium phosphate; significant contents of sodium aluminosilicate and quartz were also found. Aluminosilicates and chromates were predominant in the solid phase from Lake Verkhnee Beloe, but comparatively rare minerals containing tellurium (telluride, tsumoite) and arsenic (tennantite) were also detected.

Principal component analysis of hydrochemical data demonstrated that salinity and chloride content made a major contribution to the first principal component (PC1), which determined 34% of variation in the studied parameters and distribution of the studied lakes on the diagram of the principal components (Fig. 2). A significant contribution was also made by the content of sulfates, sodium, calcium, some trace elements, and, to a lesser extent, by carbonates, potassium, and magnesium. These parameters determined the distribution of the samples on the diagram and the similarity in hydrochemical characteristics between the lakes Khilganta and Gorbunka. Trace elements Mo, Sn, Cs, Bi, Cr, Mn, Ni, Cd, Zn, and La, high concentrations of which were detected in Lake Verkhnee Beloe, were the most important for determination of the second component (PC2), which explained 19% of variations observed in the hydrochemical data.

Diversity of microbial communities in the bottom sediments of the lakes. In total, 120 953 sequences of the 16S rRNA gene were obtained by high-throughput sequencing. Sequence number in each sample varied from 23094 to 47976 (Table 2). In the samples from the highly mineralized Lake Borzinskoe (with salinity of 430 g/L), 1794 OTUs were revealed, whereas decrease in salinity in the lakes Khilganta (36 g/L) and Gorbunka (58 g/L) led to an increase in microbial diversity and the number of revealed OTUs increased to 3037 and 2847, respectively. All samples contained numerous OTUs represented by single sequences (less than 10) and their number varied from 78.7 to 87% of total OTU number.

In general, 47 prokaryotic phyla (42 bacterial and 5 archaeal ones) were revealed in the sediments of alkaline lakes. The phyla *Proteobacteria*, *Euryarchaeota*, *Bacteroidetes*, *Chloroflexi*, *Actinobacteria*, and *Firmicutes* were predominant, comprising over 95% of the classified sequences (Fig. 3). Comparative abundance of archaea increased with salinity from below 1% in the sediment from Lake Verkhnee Beloe to 35% in the microbial community of the sediment of Lake Borzinskoe. Representatives of the phylum *Euryarchaeota* comprised more than 30% in the microbial communities of the lakes Khilganta and Borzinskoe.

Table 1. Physicochemical and mineralogical characteristics of the studied lakes

	Verkhnee Beloe	Khilganta	Gorbunka	Borzinskoe
Sampling date	20.08.2015	25.09.2015	25.09.2015	25.09.2015
Coordinates	50°38′ N 105°43′ E	50°42′ N 115°06′ E	50°39′ N 115°04′ E	50°24′ N 116°27′ E
Temperature, °C	19	10.8	9.8	13.7
pH	10.1	10.0	9.98	9.51
Salinity, g/L	13	36	58	430
Area, km^2	4.5	0.3	1.5	3.8
Depth, m	2	0.6	0.6–0.8	1.5
Minerals (>20%)	Anorthoclase, lopezite	Pretulit, zircon	Quartz	Albite, quartz
Cations, g/L				
Na^+	4	5.3	12.3	129.6
Ca^{2+}	0.008	0.018	0.034	0.04
Mg^{2+}	0.021	0.68	0.92	0.012
K^+	0.03	0.04	0.09	0.175
Anions, g/L				
CO_3^{2-}	4.5	0.335	0.405	27.4
Cl^-	1.8	8.5	19.0	155.1
SO_4^{2-}	2.1	1.9	3.3	32.6
NO_3^{2-}, mg/L	0.13	0.52	0.46	0.35
NO_2^-, mg/L	ND	0.00	0.10	0.00
Trace elements, μg/L				
Co	2.27	1.33	1.39	2.88
Ni	106.87	18.9	25.44	35.79
Zn	306.98	42.77	94.79	204.2
Fe	574.73	77.55	203.94	626.35
Mn	79.96	6.11	5.12	19.59
Cr	43.8	5.55	6.7	8.48
Cs	0.866	0.06	0.069	0.221
Bi	0.753	0.026	0.068	0.17
Sn	30.68	1.2	1.69	6.98
As	94.68	6.94	59.78	879.26
B	2093	1328	1543	21948
Be	0.85	0.135	0.944	6.665
U	512.82	191.78	140.02	2254
Sr	1054	2831	3063	185.1
Ba	101.4	88.2	115.63	116.29
Pr	0.235	0.059	0.278	0.43
Mo	516.99	151.36	19.31	109.33

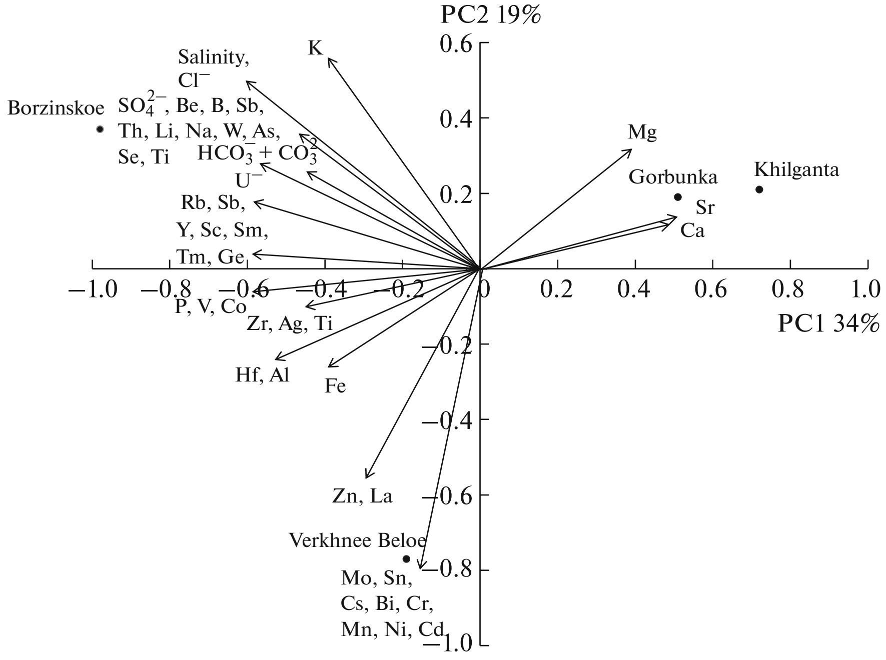

Fig. 2. Distribution of the studied lakes based on the principal component analysis of hydrochemical data.

In the microbial communities of the sediments of Lake Borzinskoe with a mineralization of 430 g/L, 28 bacterial and 3 archaeal phyla were found.

The most numerous bacterial OTUs were represented by haloalkaliphilic gammaproteobacteria of the genus *Halomonas* (up to 15% of the number of classified sequences). Haloalkaliphilic purple nonsulfur bacteria of the genus *Rhodobaca* were the most numerous in the microbial community of Lake Verkhnee Beloe, haloalkaliphilic actinobacteria of the genus *Nitriliruptor* were predominant in Lake Gorbunka with 58 g/L salinity.

The most numerous archaeal OTUs were identified at the genus level as members of the genera *Halorubrum* and *Halohasta* belonging to extremely halophilic *Euryarchaeota* of the family *Halorubraceae*. The number of their OTUs exceeded 21% of the total prokaryotic diversity of Lake Borzinskoe. OTUs representing the phyla *Nanohaloarchaeota* and *Woesearchaeota* were detected in sediment samples with mineralization 58 and 430 g/L. Representatives of the phyla *Thaumarchaeota* and Miscellaneous Crenarchaeotic Group detected only in the microbial community of Lake Gorbunka were not numerous and comprised 0.2 and 0.9% of the total archaeal diversity.

The share of *Proteobacteria* in the communities varied from 21–30% (lakes Khilganta and Borzinskoe) to 47–53% (lakes Gorbunka and Verkhnee Beloe) of the total number of classified sequences (Fig. 3). In all samples, the greatest number of sequences was represented by γ-proteobacteria, while the composition of predominant genera in different lakes varied. Halophilic bacteria of the genus *Halomonas* were predominant in microbial communities of the sediments at different salinity values ranging from 2% (Lake Khilganta) to 15% (Lake Borzinskoe) of the total number of sequences. The genera *Marinospirillum*, *Marinicella*, and *Nitrincola* were also abundant in the sediments of Lake Verkhnee Beloe; *Thioalkalivibrio* and *Aliidomarina* were abundant in the sediments of Lake Borzinskoe. Lithoautotrophic sulfur-oxidizing bacte-

Table 2. Effect of salinity on quantitative characteristic of OTUs

Sampling site	M, g/L	Total number of sequences	Total number of OTUs	OTUs represented by single sequences (less than 10)
Verkhnee Beloe	13	47976	2266	1783
Khilganta	38	24952	3036	2644
Gorbunka	56	23094	2847	2492
Borzinskoe	430	24931	1793	1496

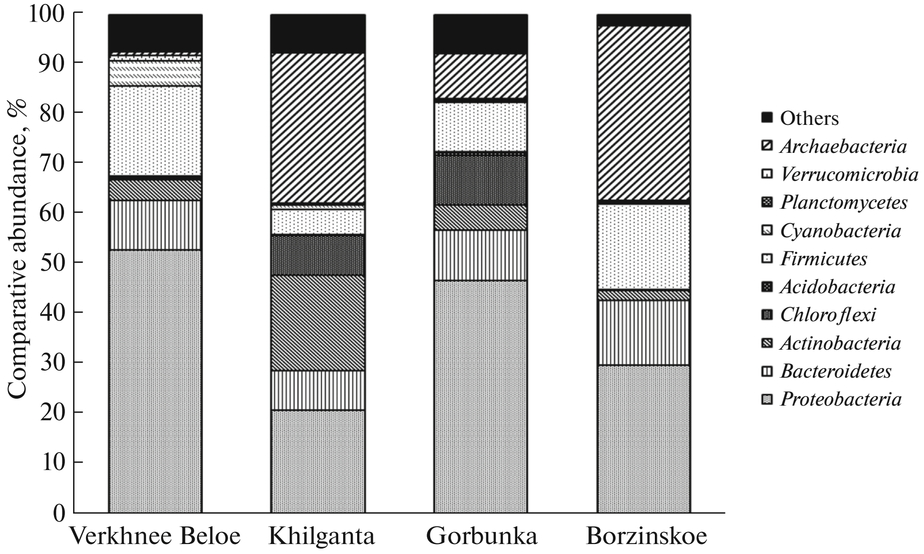

Fig. 3. Comparative abundance of predominant phyla in the sediments of alkaline lakes.

ria of the genus *Thioalkalispira*, which were originally isolated from the sediments of the soda lake Fazda (Wadi Natrun, Egypt) (Sorokin et al., 2002), were predominant in the sediments of Lake Khilganta (more than 1% of the total number of sequences).

Representatives of the class α-*Proteobacteria* were found in all sediments and the number of sequences of these bacteria significantly decreased in the samples with high salinity (Fig. 4). The sequences mainly belonged to the order *Rhodobacterales*, with the exception of the sediments of Lake Khilganta, where bacteria of the order of *Rhizobiales* were predominant. In samples from Lake Verkhnee Beloe, 41% OTUs of the class α-*Proteobacteria* belonged to alkaliphilic bacteria of the genus *Rhodobaca*, 6% of the reads of the class belonged to alkalitolerant and bacteriochlorophyll-*a*-producing bacteria of the genus *Roseibaca*, the only representative of which, *Roseibaca ekhonensis*, was isolated from the hypersaline Lake Ekho.

The phylum *Firmicutes* in all lakes was represented mainly by the class *Clostridia* with a very large proportion of uncultured bacteria (Fig. 4). In the microbial community of Lake Verkhnee Beloe, moderately halophilic bacteria of the genus *Anoxinatronum* (4% of all sequences) were predominant, while in lakes Khilganta and Gorbunka, the number of bacterial sequences of the genus *Alkaliphilus* increased (up to 1–2%). Only in Lake Borzinskoe, primary anaerobes were represented by extremely halophilic bacteria of the orders *Halanaerobiales* and *Natranaerobiales* (4 and 0.5% of the total number, respectively). Representatives of the order of *Halanaerobiales* (60 OTUs) belonged to the genera *Halanaerobium*, *Halarsenatibacter*, *Halocella*, and *Natroniella* with similarity level of 93 to 100%.

The composition of the phylum *Bacteroidetes* varied depending on the salinity (Fig. 4). In the sediments of the lakes Verkhnee Beloe and Gorbunka, representatives of the class *Bacteroidia* were predominated among bacteroids, while the share of the sequences belonging to the class *Flavobacteriia* varied from 8 to 46% in the lakes sediments, with the exception of highly mineralized Lake Borzinskoe (Fig. 4). The share of uncultured bacteria of this phylum was 25–30%. Moreover, a significant number of sequences, from 5–9 (lakes Khilganta and Gorbunka) to 36–71% (lakes Verkhnee Beloe and Borzinskoe), belonged to the group of aquatic organisms ML635J-40 involved in the degradation of polymeric compounds (Nolla-Ardevol et al., 2015).

In all the studied lake sediments, a significant number and variety of microorganisms involved in the sulfur cycle were detected, including sulfate reducers (representatives of *Deltaproteobacteria*) and sulfur oxidizers (representatives of *Chromatiales*). The methane cycle in the lake sediments was carried out by *Methanomicrobia* methanogenic archaea (0.3 to 2% of the archaeal diversity in the lakes Borzinskoe and Gorbunka, respectively). Methylotrophic *Gammaproteobacteria* (*Methylonatrum* sp.) were detected in the microbial communities of the sediments of lakes Verkhnee Beloe and Borzinskoe.

In all studied lake sediments, the activity of production processes was determined. The greatest total photosynthetic activity was detected in the sludge from Lake Verkhnee Beloe (up to 300 mg C/dm^3 day). These results of radiotracer studies were in agreement with the analysis of the taxonomic diversity of microbial communities. In Lake Verkhnee Beloe, the number of sequences belonging to the phylum *Cyanobacteria* was significant (5% of the total number of classified

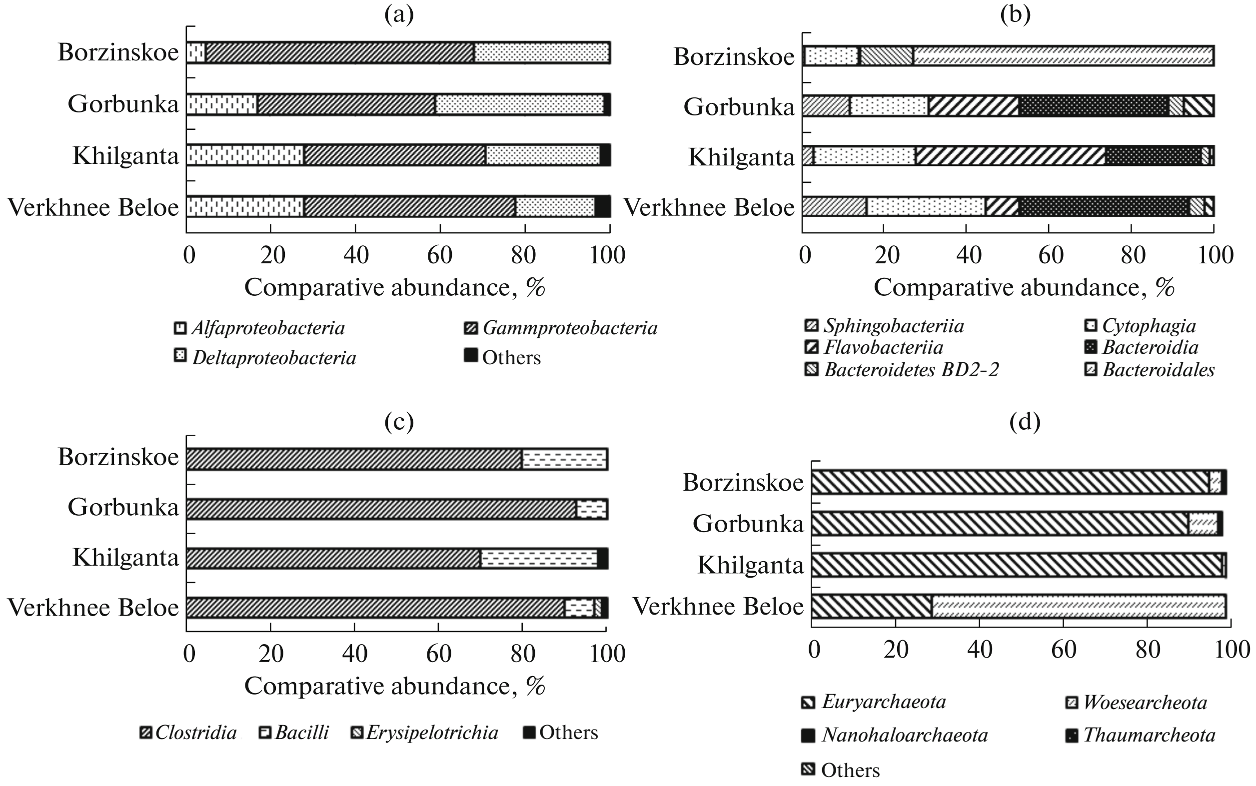

Fig. 4. Diversity of predominant phyla at the class level: *Proteobacteria* (a), *Bacteroidetes* (b), *Firmicutes* (c), and phyla of the *Archaea* domain (d).

sequences). The most numerous OTUs corresponded to the genera *Prochlorococcus*, *Lyngbia*, *Oscillatoria*, *Cyanobacterium*, and *Anabaenopsis*. The genera *Phormidium*, *Merismopedia*, *Synechococcus*, *Spirulina*, *Chloroplast*, and *Nodularia* were represented by single sequences and were detected in microbial communities of all studied lakes, including the highly mineralized Lake Borzinskoe.

Phylogenetic analysis revealed significant diversity of sulfate-reducing bacteria. The leading role of sulfate- and sulfur-reducing bacteria in the microbial communities of soda lakes was previously demonstrated (Foti et al., 2007; Sorokin et al., 2004, 2011, 2015). In the sediments of soda lakes, lithotrophic sulfate-reducing bacteria of the orders *Desulfovibrionales* (including haloalkaliphilic representatives of the genera *Desulfonatronum*, *Desulfonatronovibrio, Desulfonatronospira*) and *Desulfobacterales* were predominant. In the studied microbial communities, extremely haloalkaliphilic bacteria of the genus *Desulfonatronospira* were detected only in the microbial community of the highly mineralized Lake Borzinskoe, their comparative abundance was 36% of the representatives of the order *Desulfovibrionales*; haloalkaliphilic bacteria of the genus *Desulfonatronovibrio* (11% of *Desulfovibrionales*) were also detected. In less mineralized lakes Gorbunka, Borzinskoe, and Verkhnee Beloe, haloalkaliphilic bacteria of the genus *Desulfonatronum* were predominant among lithotrophic SRB (12–92%) (Sorokin et al., 2015). The number of heterotrophic SRB of the order *Desulfobacterales* including representatives of the genera *Desulfonatronobacter*, *Desulfobulbus*, and *Desulfobotulus* oxidizing VFA also varied depending on mineralization (Foti et al., 2007). For example, sulfate-reducing bacteria of the genus *Desulfonatronobacter* with a similarity of 97 to 99.65% and the type species *D. acidivorans* (Sorokin et al., 2012) were predominant in the sediments from Lake Borzinskoe (6% of the number of classified sequences), while in less saline lakes their shares did not exceed 0.2–0.6% of the total number of sequences. Sulfate reducers of the genus *Desulfobotulus* were detected only in the sediments of Lake Verkhnee Beloe, while the share of bacteria of the genus *Desulfobulbus* varied from 1 to 6% of *Deltaproteobacteria* in lakes Khilganta, Gorbunka, and Verkhnee Beloe. Data on the analysis of phylogenetic diversity reflected a significant role of SRB in microbial degradation in lake sediments. Determination of the rates of terminal processes demonstrated that the rate of sulfate reduction varied from 16 to 887 mg S/dm^3 day, and the greatest rate of sulfate reduction was detected in the sediments of Lake Borzinskoe.

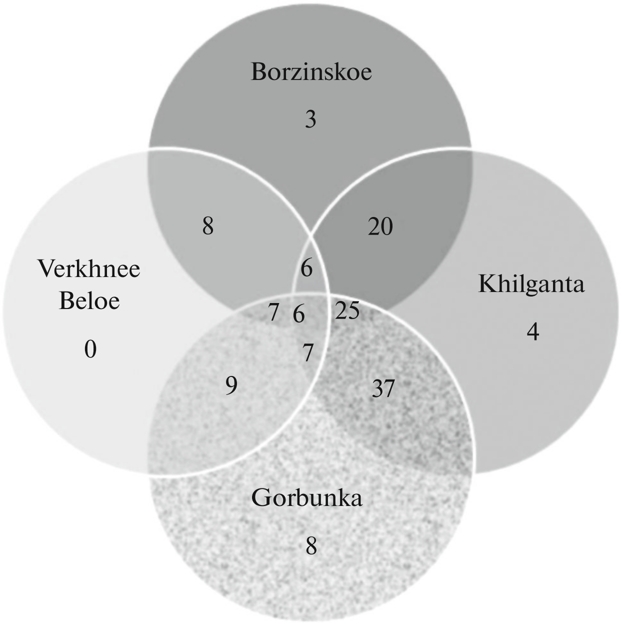

Fig. 5. Venn diagram of unique and common archaeal genera in microbial communities.

Distribution of archaea in microbial communities. Dependence of the distribution of archaea in the microbial communities of the lakes on their salinity was studied. In the presence of 12 g/L salts, the archaeal diversity was represented by 111 OTU and the representatives of the phylum *Woesearchaeota* were predominant (Fig. 4). Increased salinity resulted in an increase in archaeal diversity, and 1039 archaeal OTUs were detected in Lake Khilganta (with salinity of 36 g/L), with the most numerous OTUs represented by uncultured archaea, as well as by the genera *Natronococcus*, *Halovivax*, and *Haloterrigena*. In the microbial community of the sediment from Lake Gorbunka with a salinity of 58 g/L, 531 archaeal OTUs mainly represented by uncultured archaea were detected, and only 49 OTUs were represented by more than 10 sequences. The maximum diversity and predominance of archaea in the microbial community of the surface sediment was determined in the microbial community of Lake Borzinskoe (Fig. 4). The most represented OTUs were assigned to uncultured archaea of the genera *Halorubrum*, *Natronomonas*, and *Halohasta*. Sequences representing the class *Methanomicrobia* were revealed in all studied lakes. In the sediments of Lake Gorbunka, the greatest diversity and abundance of methanogens was found (7 genera: *Methanoculleus*, *Methanogenium*, *Methanosarcina*, *Methanohalophilus*, *Methanolobus*). Methanogenic archaea in the surface sediments of Lake Borzinskoe were mainly represented by halophilic and alkaliphilic archaea of the genus *Methanosalsum* (87% of *Methanomicrobia*, 0.3% of *Archaea*), which were previously isolated from hypersaline lakes Wadi Natrun and Magadi, as well as from Kulunda Steppe (Kevbrin et al., 1997; Sorokin et al., 2015). Methylotrophic methanogens of the genus *Methanolobus* were represented by single sequences in all samples. Moderately halotolerant representatives of this genus were previously observed in the sediments of the hypersaline lakes Fazda and Tanatar (Mesbah et al., 2007; Vavourakis et al., 2016). Venn diagram demonstrates the number of archaeal genera common and unique for microbial communities of the lakes (Fig. 5). Archaeal communities of lakes Gorbunka, Khilganta, and Borzinskoe very highly similar at the genus level.

Microbial diversity in the water of saline lakes of the Tibet Plateau was previously studied using high-throughput sequencing. Water samples had salinity from below 1 to 344 g/L. It was shown that the salinity and content of the main ions (Mg^{2+}, K^+, Cl^-, Na^+, SO_4^{2-}, Ca^{2+}) determined the diversity of prokaryotes (Zhong et al., 2016). Bacteria were predominant in the water of the lakes with mineralization up to 100 g/L. Microbial communities with predominance of archaea (79–89% of the total diversity), among which most of the sequences belonged to the family *Halobacteriaceae* of the phylum *Euryarchaeota*, were observed at salinity of 317 to 344 g/L. It should be noted that in the water of most lakes of the Tibet Plateau, the number of extremely halophilic archaea did not exceed 0.1–0.5% of the total diversity even at high salinity values (92–99 g/L).

In the microbial communities of sediments of hypersaline Laguna Tebenquiche (Chile), archaea were predominant in all samples in the gradient of salinity of 62 to 150 g/L, the representatives of the phylum *Euryarchaeota* comprised from 62 to 97% of the total diversity of prokaryotes at salinity of 150 and 117 g/L, respectively (Fernandez et al., 2016). Bacterial diversity in the sample with mineralization of 150 g/L was mainly represented by the phyla *Planctomycetes*, *Acetothermia, Chloroflexi,* and *Firmicutes*. Sequences of the 16S rRNA genes belonging to these phyla comprised 2 to 7% of the total diversity of prokaryotes.

Based on the studies of saline lakes of different geographic location and more than 100 strains of the genus *Thioalkalivibrio*, it was shown that most genomic species of this genus occur in the same geographic region, including Central Asia (Mongolia and the South Siberian steppes) and Africa (Kenya or Egypt) (Foti et al., 2006; Ahn et al., 2017). The genotypes represented by the cultures isolated from different habitats had similar physiological and biochemical characteristics, including relation to salinity, chloride concentration,and oxygen content, which shows the importance of local geographical features of each lake (Foti et al., 2006). According to our data, gammaproteobacteria *Thioalkalivibrio* are widespread in the studied lakes, and their comparative abundance varied from 0.1% in Khilganta to 1% in Borzinskoe. The greatest diversity represented by 17 OTUs was revealed in the sediment from Lake Gorbunka, while the lowest diversity was observed in the lakes Verkhnee Beloe and Khilganta (6 and 8 OTUs, respectively). Most of the sequences were assigned to the genotype characteristic of the Mongolian (*Thioalkalivibrio* sp. ALMg11) and Kulunda Steppe lakes (*Thioalkalivibrio* sp. AKL3), which confirms endemic tendencies. Single sequences related to the isolates from the Egyptian Lake Wadi Natrun (*T. nitratireducens* and *Thioalkalivibrio* sp. ALE19) were also revealed.

Thus, high taxonomic diversity of bacteria and archaea was revealed in the microbial communities of the surface sediments of shallow-water alkaline lakes of Transbaikalia, the effect of salinity on the composition of the dominant and minor groups of microorganisms was shown, and hydrochemical and mineralogical characteristics that reflect the possible features of the ecosystem of each lake were analyzed.

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