Taxonomic diversity and functional potential of microbial communities in salt lakes Gudzhirganskoe and Nukhe-Nur (Barguzin depression, Baikal Rift Zone)

Elena Lavrentyeva[1,2], Tuyana Banzaraktsaeva[1], Vyacheslav Dambaev[1], Lyubov' Buyantueva[2], Elena Valova[2], Vladimir Ivanov[1], and Andrey Plotnikov[3]

[1]Institute of General and Experimental Biology, Siberian Branch of
the Russian Academy of Sciences, ul. Sakhyanovoy, 6, Ulan-Ude, 670047, Russian Federation
[2]Buryat State University, ul. Smolina, 24a, Ulan-Ude, 670000, Russian Federation
[3]Institute for Cellular and Intracellular Symbiosis, Ural Branch of
the Russian Academy of Sciences, ul. Pionerskaya, 11, Orenburg, 460000, Russian Federation

Address correspondence and requests for materials to Elena Lavrentyeva, lena_l@mail.ru

Abstract

On the territory of the Barguzin depression (Baikal Rift Zone) there are salt lakes, which are unique natural formations formed in exceptional natural conditions and experiencing extreme shifts in seasonal environmental conditions. This paper presents the results of the study of the microbial communities in the sulfate Lake Gudzhirganskoe and the soda Lake Nukhe-Nur in winter and summer seasons: from the assessment of the taxonomic composition to potential metabolic pathways. For the first time, based on the 16S rRNA gene sequencing data, the diversity of the microbial community of bottom sediments in summer and winter was studied. Environmental conditions such as pH, temperature and mineralization mainly determined the microbial community composition and led to noticeable shifts in the composition of the community at the level of families and genera. The change of the "summer" obligate and moderately alkalphilic and halophilic community to the "winter" alkali-, halotolerant/halophilic microbial community is observed in the winter period in Lake Gudzhirganskoe. In Lake Nukhe-Nur, a change from mesophilic-thermophilic community in summer to mesophilic-psychrophilic microbial community in winter was revealed. The totality of the obtained results gives an idea about the main trends in the seasonal dynamics of extremophilic microbial communities in the studied lakes in response to fluctuations in environmental parameters. The prediction of the metabolic pathways of prokaryotic communities using the Tax4Fun program made it possible to reveal similarities and differences in the metabolic potential of the microbial communities of the studied lakes. Potential functional genes have been found for all stages of the C, N and S cycles, with the exception of nitrification and aerobic CH_4 oxidation.Only small qualitative and quantitative variations in the relative abundance of predicted functional genes were found between the microbial communities of the studied lakes. We predicted metabolic pathways that play an important role in the adaptation of microorganisms to changing environmental conditions. In general, it has been shown that there is a change in the dominant taxa at the level of families and genera in the microbial community in the summer and winter seasons, however, the predicted functional potential of microbial communities differed slightly by season and between the studied lakes.

Keywords: extremophilic microbial communities, taxonomic diversity, seasonal dynamics, functional potential prediction, C, N and S cycles, salt lakes, Baikal Rift Zone

Sulphate Lake Gudzhirganskoe and soda Lake Nukhe-Nur located on the territory of the Barguzin depression are polyextremal systems that demonstrate alkaline pH values combined with high mineralization. The Barguzin depression belongs to the

Citation: Lavrentyeva, E., Banzaraktsaeva, T., Dambaev, V., Buyantueva, L., Valova, E., Ivanov, V., and Plotnikov, A. 2023. Taxonomic diversity and functional potential of microbial communities in salt lakes Gudzhirganskoe and Nukhe-Nur (Barguzin depression, Baikal Rift Zone). Bio. Comm. 68(2): 86–96. https://doi.org/10.21638/spbu03.2023.203

Authors' information: Elena Lavrentyeva, PhD, Senior Researcher, Associate Professor, orcid.org/0000-0002-2500-103X; Tuyana Banzaraktsaeva, PhD, Researcher, orcid.org/0000-0002-3264-9336; Vyacheslav Dambaev, PhD, Researcher, orcid.org/0000-0002-0801-1658; Lyubov' Buyantueva, PhD, Associate Professor, orcid.org/0000-0003-2942-4037; Elena Valova, PhD, Associate Professor, orcid.org/0009-0008-7025-3798; Vladimir Ivanov, PhD Student, orcid.org/0009-0004-2694-9860; Andrey Plotnikov, PhD, Director, orcid.org/0000-0001-6830-4068

Manuscript Editor: Kirill Antonets, Department of Cytology and Histology, Faculty of Biology, Saint Petersburg State University, Saint Petersburg, Russia

Received: August 31, 2022;

Revised: December 7, 2022;

Accepted: January 24, 2023.

Funding: This work was financially supported by grant of the Federal State Budget Educational Institution of Higher Education BGU No. 22-03-0502 and the state assignment of the IGEB SB RAS No. 121030100229-1.

Ethics statement: This paper does not contain any studies involving human participants or animals performed by any of the authors.

Supplementary information: Supplemental material to the article is available at https://doi.org/10.21638/spbu03.2023.203. Supplementary files are published as submitted by the authors, and are not copyedited.

Competing interests: The authors have declared that no competing interests exist.

Baikal Rift Zone, which is characterized by a cryoarid climate and significant temperature fluctuations throughout the year. The annual amplitude of absolute air temperatures reaches 90 °C, the maximum air temperature in summer is +38 °C, and the minimum in winter is −52 °C (Namsaraev et al., 2007). Despite the small catchment area, the lakes do not dry out in dry years. This is due to the fact that they are fed mainly by groundwater discharges and only partially by precipitation and land runoff (Plyusnin, Khazheeva, Sanzhanova, and Angakhaeva, 2020a). The formation of the sulfate-sodium chemical composition of water in Lake Gudzhirganskoe is due to the discharge of thermal fissure-vein waters. The supply of sulfur is associated with the dissolution of sulfate minerals, which may be present in metamorphogenic-sedimentary formations. Nitrogen thermal waters are discharged into Lake Nukhe-Nur, where, as a result of actively occurring processes of evaporation and freezing, solutions are concentrated and the chemical composition of the lake water is transformed along the soda direction (Plyusnin et al., 2020b).

In a salt lake, microorganisms are key components with their high genetic diversity playing an important role in element cycling (Sorokin et al., 2014). Microbial communities of salt lakes are able to develop in a wide range of salt concentrations and under conditions of high pH values. Microbial diversity "instantly" (for natural conditions) responds to changes in external environmental parameters under climatic extremes (summer-winter), and these conditions determine the composition, structure, and functional activity of the microbial community.

To elucidate the question of how the structure and functionality of the microbial community differ between the two seasons, we characterized the microbial communities in summer and winter using 16S rRNA gene amplicons. The study of the diversity of the microbial community and the prediction of its functional capabilities depending on environmental factors by modern molecular genetics and bioinformatic methods has not been previously carried out in the salt lakes of the Barguzin depression.

The purpose of the study is to establish the diversity of the prokaryotic community in the bottom sediments of the Gudzhirganskoe and Nukhe-Nur lakes in summer and winter and to determine the effect of environmental parameters on the composition and functionality of the microbial community.

Objects and methods

Study area

The study area belongs to the cryoarid zone, which is characterized by sharp seasonal and daily temperature fluctuations and low precipitation. The studied lakes were formed in exceptional natural conditions, and, as a rule, the lakes are frozen for 6 months per year. Sampling for physicochemical, hydrochemical, and molecular genetic studies was carried out in summer (August 2019) and winter (December 2019). In summer, at the time of sampling, the air temperature was +21.6 °C, in winter — −35 °C. In winter, the lakes were covered with ice and snow, sediments were collected using an ice drill.

Lake Gudzhirganskoe (54°01′890″ N 110°16′537″ E, altitude 493 m a. s. l.) belongs to the group of Alga lakes, is shallow and has a relatively small area — 0.3 km^2. In summer 2019, the lake was mainly covered with a dry salt crust 0.5 to 5 cm thick. Thenardite (Na_2SO_4) crystals were observed on its surface. In small depressions there was residual brine. The upper layers of sediments were represented by gray silt. Lake Nukhe-Nur (53°38′781″ N 109°56′807″E, height 479 m above sea level, water surface area about 2–2.5 km^2), is located in a depression above the floodplain on the steppe part of the valley, along the right bank of the Barguzin River. The lake consists of two reservoirs, and has the shape of an asymmetric figure "eight" elongated from north to south. Bottom sediments are represented by finely dispersed silt, evenly covering the bottom of the lake. Sampling was carried out in the northern Lake Nukhe-Nur. To determine the physicochemical and hydrochemical parameters, we used bottom water in summer and pore water extracted from thawed samples of bottom sediments in winter. We measured pH and temperature using a portable pH meter pH-200 HM Digital (South Korea) with a contact thermometer. Mineralization was determined by test conductometer TDS-4 (Singapore). The macrocomponent composition of the brine was determined using hydrochemical methods at the Research Equipment Sharing Center of the Geological Institute of Siberian Branch of the Russian Academy of Sciences, Ulan-Ude (www.geo.stbur.ru).

Molecular genetic analysis

At each lake site, bottom sediments from three randomly selected plots were selected as replicates. These three subsamples (depth of up to 10 cm) were pooled into a single bottom sediment sample. For molecular genetic analysis, the samples of bottom sediments were taken into sterile plastic 15 ml Falcon tubes and fixed with ethanol to a final concentration of 50 % (v/v). The samples were delivered to the laboratory within 24 hours and kept in a refrigerator at +4 °C until DNA extraction.

DNA isolation from sediments was carried out using the DNeasy PowerSoil Kit (Qiagen, USA) according to the manufacturer's protocol. Qualitative and quantitative assessment of the DNA preparations was carried out on a Nanodrop 1000 spectrophotometer (Thermo Fisher Scientific, United States). The V3-V4 region of the 16S rRNA gene was amplified using the primers 343F (5'-CTCCTACGGRRSGCAGCAG-3') and 806R (5'-GGACTACNVGGGTWTCTAAT-3'), containing adapter sequences (Illumina), a linker, and a barcode (Fadrosh et al., 2014). Amplification was carried out as described previously (Brouchkov et al., 2017). Sequencing was carried out in the technospark company “Biospark” (Moscow) on a MiSeq sequencer (Illumina, USA) using the Reagent Kit v3 (2 × 300, Illumina). Demultiplexing was carried out with the appropriate scripts of QIIME version 1.9.0 (Caporaso et al., 2010). The subsequent sequence processing and analysis were also performed in QIIME ver. 1.9.0. The data were passed through a filter with the minimum nucleotide read quality of 30 and the minimum read length of 350 bp. The chimerism testing of the reads was performed using the identify_chimeric_seqs.py script by the algorithm of USEARCH version 6.1544 (Edgar, 2010) and the Silva 123 reference base of 16S rRNA reads (Quast et al., 2013). The OTU table was formed using the pick_open_reference_otus.py script. The sequences were grouped in OTUs with a similarity level of 97 % (Schloss and Handelsman, 2006) using the algorithm of USEARCH version 6.1544 (Edgar, 2010) and the Silva 123 version reference base of 16S rRNA reads (Quast et al., 2013). The NCBI (https://blast.ncbi.nlm.nih.gov/Blast.cgi) and EzBioCloud (https://www.ezbiocloud.net/) servers were used to search for nearby homologues.

The DNA sequences in this study have been deposited in the National Center for Biotechnology Information (NCBI) under BioProject PRJNA903517 and BioSample accession SAMN31807139.

Statistical analyses and functional prediction

Heat map of classified taxa was created using the MicrobiomeAnalyst online resource (https://www.microbiomeanalyst.ca) (Dhariwal et al., 2017; Chong, Liu, Zhou, and Xia, 2020).

The correlation of the composition of the dominant genera in the summer and winter communities with physicochemical parameters was assessed by the principal component analysis (PCA) using Past 3.14 software (Hammer, Harper, and Ryan, 2001). Prior to the analysis, all environmental data were standardized by subtracting the mean and dividing by the standard deviation.

The Tax4Fun program was used for data annotated in the SILVA database (Aßhauer, Wemheuer, Daniel, and Meinicke, 2015). The result is a table containing relative levels of KO (KEGG ORTHOLOGY). KO profiles were used to profile functional diversity based on KEGG (EC pathways, modules or categories).

Results and discussion

Ecological conditions for microbial communities

Table 1. Hydrochemical analysis of water, mg/dm^3

Ions	Lake Gudzhirganskoe		Lake Nukhe-Nur	
	Summer	Winter	Summer	Winter
Na^+	43856.89	35440	2940.86	1963.6
Ca^{2+}	120.24	74.19	12.02	10.7
Mg^{2+}	243.2	116	42.56	36
HCO^{3-}	3050.9	2146.3	5186.53	4217.1
CO^{3-}	510.09	321.4	780.13	571.2
NO^{3-}	5.33	nd	5.1	1.7
SO_4^{2-}	86127.31	62120.0	157.07	89.4
Cl^-	2570.63	1682.5	613.41	22.4
F^-	7.49	nd	6.17	5.13
SiO_3^{2-}	3.20	nd	41.8	nd

nd stands for not determined.

The water of Lake Gudzhirganskoe in summer was characterized by a high pH value of 9.3, the water temperature in the lake was +23.1 °C, and the total mineralization of the water reached 137 g/dm^3. The studied lake is characterized by the redox potential –0.76 mV. The macrocomponent composition of the lake was dominated by sodium cation — 43856.9 mg/dm^3. In dry climate, sodium is a characteristic element of the evaporative concentration of salt lakes in the steppe regions. The content of magnesium ions was 243 mg/dm^3. The dominant ion in the anionic composition was the sulfate ion, its content was 86127 mg/dm^3. The content of carbonates did not exceed 510 mg/dm^3, hydrocarbonates — 3051 mg/dm^3. Chlorides are a constant component of water; their content in the lake was 2570 mg/dm^3. In the water of Lake Gudzhirganskoe, fluorides and silicon ions were determined (Table 1). In winter, the pH of the water in the lake was 8.76, the mineralization was 102 g/dm^3, and the redox potential was –166 mV. Determination of the cationic-anionic composition of water in winter also showed the dominance of sodium cation (35400 mg/dm^3), sulfates dominated in the anionic composition of water — 62120 mg/dm^3. In Lake Nukhe-Nur at the time of sampling in summer, the pH value was 9.62 and the mineralization was 9.8 g/dm^3. The redox potential was — 0.75 mV. In winter, the pH value of pore water was 8.8, mineralization 7 g/dm^3, redox potential was within –0.53 mV. The study of the hydrochemical composition of the water of Lake Nukhe-Nur in the summer period showed that the dominant cation was Na^+ — 2941 mg/dm^3, the concentration of Mg^{2+} ions was 42 mg/dm^3. The content of Ca^{2+} in the water of the lake in summer was 12 mg/dm^3, while in winter it decreased to 10 mg/dm^3. The alkaline pH of the lake water is created due to high concentrations of HCO_3^- and CO_3^{2-} ions, the content of which in summer reached 5186 mg/dm^3 and 780 mg/dm^3. The concentration of sulfates in the water was insignificant and amounted to 157 mg/dm^3, in winter —

89.4 mg/dm^3. The content of chloride ions was 613.0 mg/dm^3 in August 2019, while in December 2019 the content of chloride ions was 22.4 mg/dm^3. Fluorides, bromides and silicon ions were also found in the water of the lake.

Taxonomic composition of microbial communities

The Shannon, ACE, and Chao1 diversity indices were calculated (Table 2).

Table 2. OTUs and alpha diversity indices in summer and winter periods

Sample	Number of reads (n=2)	Shannon_H	Chao 1	ACE
Gudzh_summer	13453	3.2	40	40.7
Gudzh_winter	12985	2.2	48.1	42.6
Nukhe-Nur_summer	13905	2.5	49.3	54.5
Nukhe-Nur_winter	11706	2.7	46.5	46.7

The diversity index according to Shannon ranged from 2.2 to 3.2 in Lake Gudzhirganskoe in winter and in summer. The largest number of OTUs and the maximum species richness, estimated using the Chao 1 and ACE indices were found in the bottom sediments of Nukhe-Nur in summer.

The bottom sediment communities of the studied lakes were predominantly represented by the Bacteria domain. The share of the Archaea domain ranged from 0.8 to 2 %. The analysis showed that, at the phylum level, the microbial communities of the studied lakes were similar in composition and diversity (Fig. 1). The predominant phyla were *Bacteroidetes* (6–42 %), *Actinobacteria* (3–30 %), *Firmicutes* (4–25 %) and *Proteobacteria*, classes *Gammaproteobacteria* (10–24 %), *Alphaproteobacteria* (5–18 %) in the community of bottom sediments of lakes Gudzhirganskoe and Nukhe-Nur. In Lake Nukhe-Nur, *Chloroflexi* (5–12 %) was present as subdominants, its ratio slightly varied in different periods of the study. A feature of the taxonomic composition of the microbial community of the bottom sediments of the studied lakes was the dominance of OTUs classified as uncultivated clones belonging to taxa of different ranks.

Determination of taxonomic diversity at the level of families and genera showed a difference in the composition of microbial communities in the bottom sediments of lakes Gudzhirganskoe and Nukhe-Nur with changes in external environmental parameters under conditions of climatic extremes (summer-winter). Comparative analysis of the heat map of dominant bacteria (representation in the community ≥ 1 %) indicates the specificity of the microbial community of each studied lake (Fig. 2). Probably, the sulfate type of water (Lake Gudzhirganskoe) and the soda type of water (Lake Nukhe-Nur) determine the formation of a specific microbial community in the studied lakes. Similar changes in the taxonomic composition depending on ecological conditions were also observed in other aquatic ecosystems (Lew et al., 2015; Vigneron et al., 2019; Cotta et al., 2022). Characteristically, the change of seasons results in the shift of the composition of the community of the studied lakes at the level of genera and families. Thus, in summer, the microbial community of the bottom sediments of Lake Gudzhirganskoe was dominated by representatives of the genera *Rhodobaca*, *Loktanella*, *Nitrincola*, *Methylophaga*, the *Izimaplasmataceae* family, as well as uncultivated representatives of the Blvii28 wastewater-sludge group and uncultivated *Planctomycetes* of the class VadinHA49. Their proportion in winter significantly decreased and in some cases was not detected at all. In the winter microbial community of Lake Gudzhirganskoe, representatives of completely different families and genera dominated in the taxonomic structure. The sequences identified as *Actinobacteria* of the *Nitriliruptoraceae* family were the most common in winter. Sequences assigned to the genera *Roseinatronobacter*, *Paracoccus*, and nitrogen-fixing cyanobacteria *Nodularia* PCC-9350 were also widely represented. Codominants in the studied community were sequences assigned to the genera *Salinarimonas* and *Truepera*. Sequences presented exclusively in winter were assigned to the genus *Antarcticibacterium*.

An analysis of the microbial community of the bottom sediments of Lake Nukhe-Nur in the summer and winter periods also revealed significant changes in the taxonomic composition. In summer, representatives of the phylum Bacteroidetes ML635J-40 aquatic group, the genera *Azoarcus*, *Desulfurivibrio*, *Mangroviflexus*, *Dethiobacter*, *Rhodobaculum*, *Tindalia*, and other representatives dominated in the microbial community of the bottom sediments of Lake Nukhe-Nur. Characteristically, for the microbial community of the summer period, sequences with close homology to thermophilic bacteria were found among the dominants (Nepomnyashchaya et al., 2012; Zhao, Gao, Qin, and Ruan, 2012; Lee, Wong, and Adav, 2014). Probably, the discharge of underground nitrogen thermal waters in Lake Nukhe-Nur favors the spread of this ecological group of bacteria. An analysis of the taxonomic diversity of the microbial community in the winter period showed an almost complete replacement of the dominant representatives. The composition of the microbial community in winter shifted to representatives of bacteria of the genera *Arthrobacter*, *Glaciihabitans*, *Rhodoferax*, *Acetobacterium*, *Polaromonas*, *Clostridium sensu stricto* 13, *Trichococcus*, etc., whose closest homologues are psychrophilic organisms (Kotsyurbenko et al., 1995; Liu et al., 2002; Spring, 2003; Zhang

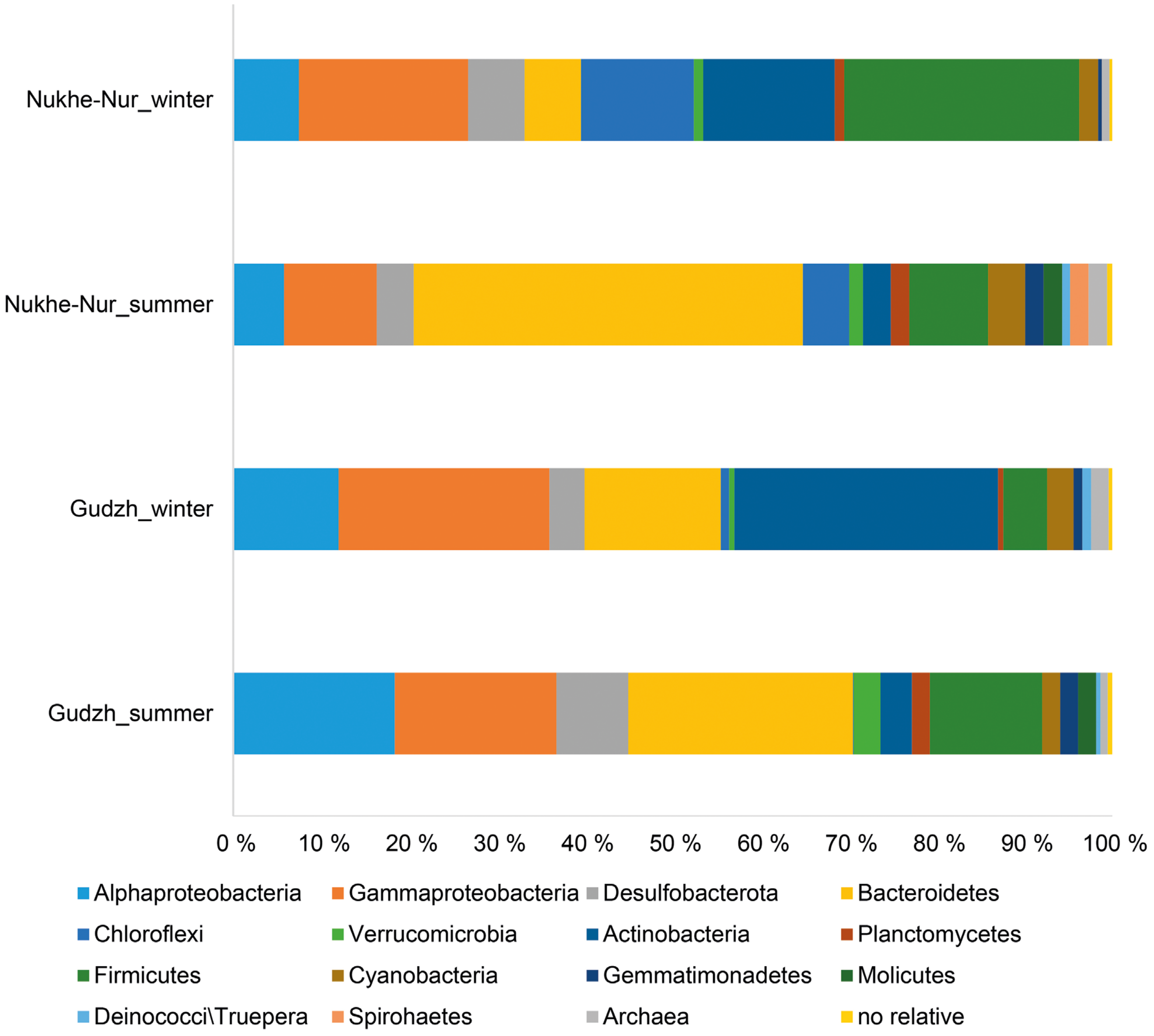

Fig. 1. Taxonomic diversity of prokaryotes at the phylum level (classes for *Proteobacteria*) in bottom sediments in summer and winter in Gudzhirganskoe and Nukhe-Nur lakes.

et al., 2008; Margesin, Spröer, Zhang, and Busse, 2012; Kaden, Spröer, Beyer, and Krolla-Sidenstein, 2014).

The physicochemical factors affecting the composition of the dominant genera of the summer and winter periods in the studied lakes were determined by using the method of principal components (PCA) (Figs S1, S2). The results demonstrated the predominance of obligate and moderate alkaline and halophilic bacteria in summer in Lake Gudzhirganskoe ($pH_{opt} > 8$ and $M_{opt} > 3\%$ NaCl). For example, the summer community was dominated by bacterial sequences whose closest homologues belonging to the genera *Methylonatrum*, *Anoxynatronum*, *Desulfonatronobacter*, *Desulfonatronovibrio*, *Mongoliibacter* had growth optima at pH > 9.5 (Alazard et al., 2007; Sorokin et al., 2007; Sorokin et al., 2011; Sorokin, Tourova, Panteleeva, and Muyzer, 2012; Wang et al., 2016). We obtained sequences whose closest homologues belonged to the bacteria *Wenzhouxiangella, Methylonatrum, Alcanivorax, Nitrincola, Anoxynatronum, Spirochaeta*. This group of bacteria was assigned to moderate halophiles (Zhilina et al., 1996; Wang et al., 2022; Borsodi et al., 2017; Liao et al., 2020). In winter, alkaliphilic bacteria were presented by the genus *Roseinatronobacter* ($pH_{opt} > 9.5$) (Sorokin et al., 2000). All other bacterial sequences of the winter period were phylogenetically close to alkali-, halotolerant bacteria (Fig. S3).

Only the temperature factor was used for the dominants of the Nukhe-Nur Lake community, since according to PCA, the strongest correlation of the composition of the bacterial community in both periods with this factor is observed (Fig. S4). An analysis of the distribution of dominant genera showed that in summer there

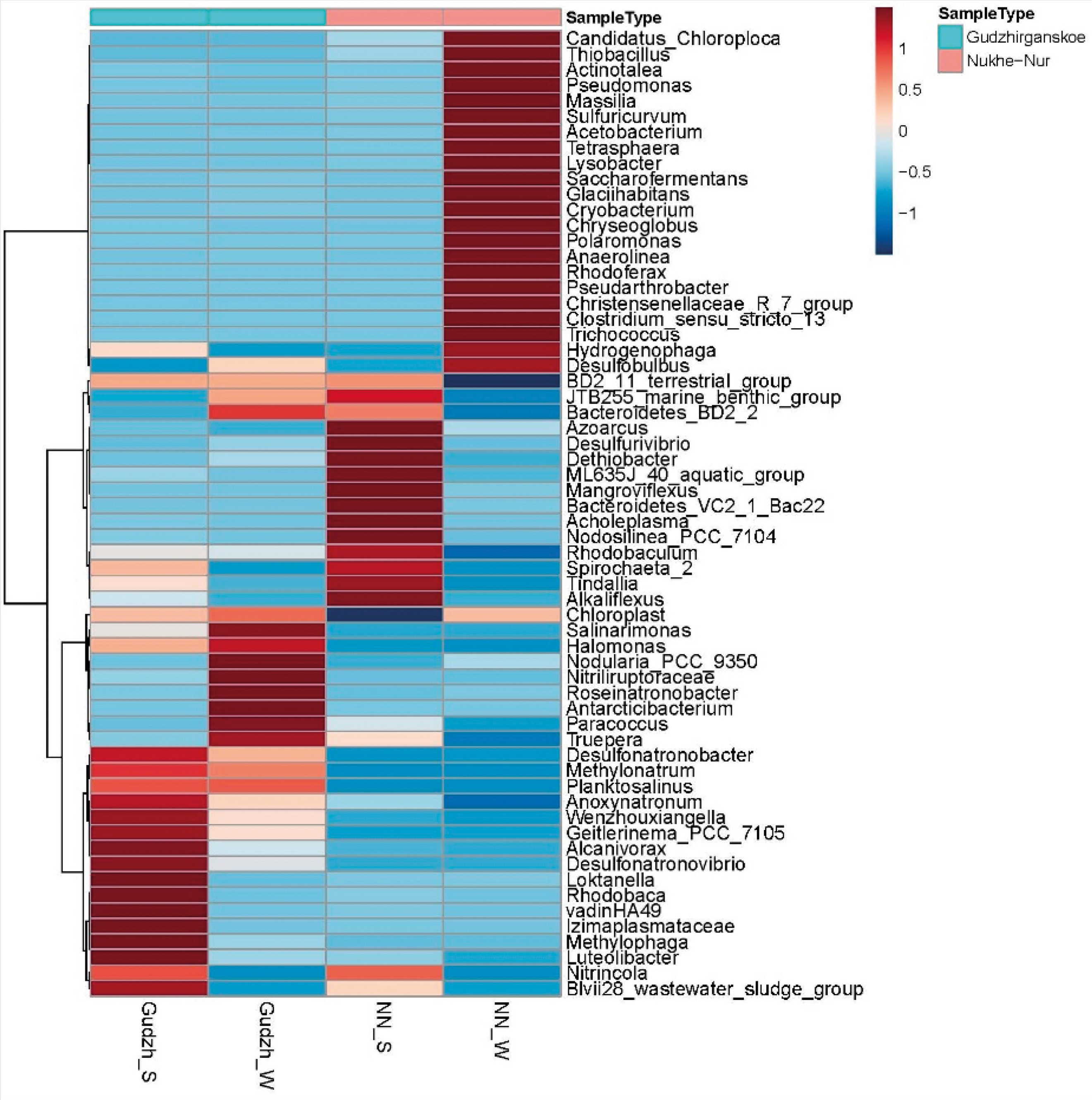

Fig. 2. Heat map of classified taxa (abundance ≥ 1 %) in bottom sediments of lakes Gudzhirganskoe and Nukhe-Nur in summer (Gudzh_S and NN_S) and winter (Gudzh_W and NN_W) periods.

was a high proportion of bacterial sequences whose closest homologues had an optimal growth temperature above 35 °C, including bacteria of the genera *Dethiobacter* and *Truepera* (T_{opt} 65 °C and 50 °C, respectively). In the winter community, a clear predominance of bacterial sequences closely related to bacteria with a temperature optimum below 20 °C was noted. However, it should be noted that representatives of thermophilic bacteria of the genus *Chloroploca*, *Anaerolinea*, and *Saccharofermentans* were also found in the winter microbial community (Pierson and Castenholz, 1974; Yamada et al., 2006; Chen, Niu, and Zhang, 2010).

Functional Prediction

Based on the Tax4Fun program, 7084 KEGG Orthology (KOs) were predicted from the 16S rRNA gene sequences in the microbial communities of the bottom sediments of the Gudzhirganskoe and Nukhe-Nur lakes in winter and summer seasons. According to the KEGG database, potential metabolic functions were classified by gene orthology (KO).

Small qualitative and quantitative variations in the predicted KOs were found between the microbial communities of the studied lakes (Fig. 3).

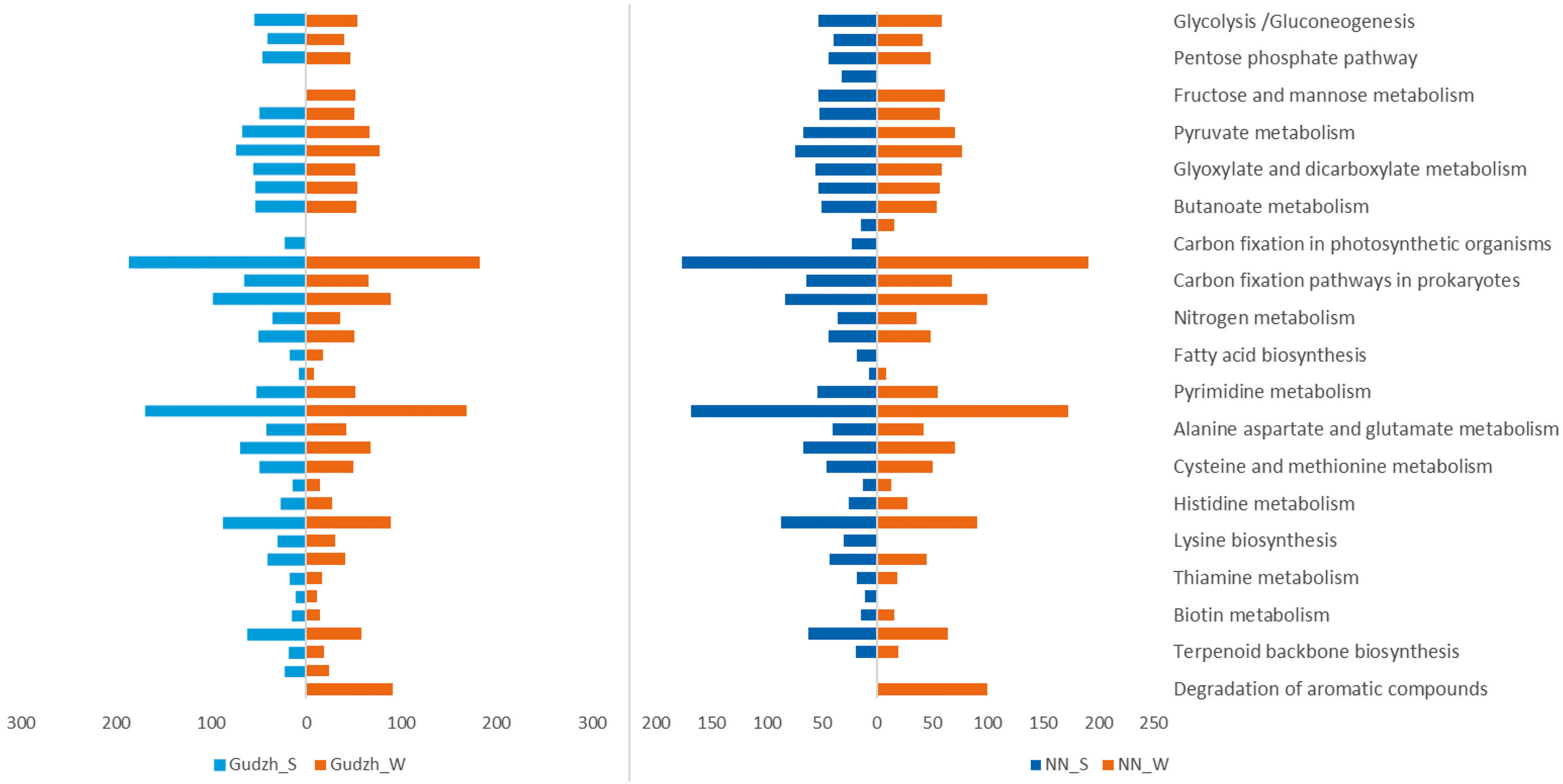

Fig. 3. Functional profile of microbial communities of Lake Gudzhirganskoe (Gudzh_S summer; Gudzh_W winter) and Nukhe-Nur (NN_S summer; NN_W winter).

Thus, we did not predict the metabolic pathways of pentose and glucuronate interconversions and C5-Branched dibasic acid metabolism in Lake Gudzhirganskoe, which are important carbohydrate metabolic pathways and play an important role in many biosynthetic pathways. In Lake Nukhe-Nur, we did not predict the pathways that provide the degradation of xylene. Interestingly, carbon fixation pathways in prokaryotes are predicted only in summer, both in Lake Gudzhirganskoe and in Lake Nukhe-Nur.

In general, the predicted functional profile of microbial communities differed slightly between lakes and seasons, in contrast to the taxonomic diversity of bacteria.

Biogeochemical cycles C, N and S are important ecological functions in salt lakes (Sorokin et al., 2014).

We analyzed the relative abundance of potential functional genes from the identified KOs and selected marker genes associated with the C, N, and S cycles (Table S1). It was shown that the expected functional differences between microbial communities in different seasons and between the studied lakes were not obvious.

The microbial communities in Lake Gudzhirganskoe had a higher relative abundance of genes associated with C, N, and S cycles. Thus, the microbial community in Lake Gudzhirganskoe in summer had a higher relative abundance of genes associated with aerobic C fixation (Calvin cycle), CO oxidation, denitrification, nitrogen assimilation, nitrogen fixation and sulfur mineralization. Greater functional potential of anaerobic C fixation, assimilatory sulfate reduction, dissimilatory sulfate reduction, sulfide oxidation and polysulfide reduction were predicted for the winter microbial community in Lake Gudzhirganskoe.

In Lake Nukhe-Nur, the predicted functions in the C-metabolism, N-metabolism, and S-metabolism pathways had a significantly higher relative abundance in winter for aerobic respiration, anaerobic C fixation, CO oxidation, fermentation, ammonification, nitrate reduction, nitrogen assimilation and nitrogen mineralization. It was shown that in the microbial communities of Lake Nukhe-Nur, the relative number of predicted genes for fermentation was higher both in summer and winter seasons than in the microbial communities of Lake Gudzhirganskoe.

Based on the dataset of the 16S rRNA gene sequences, it can be assumed that bacteria of the orders *Bacteroidales, Spirochaetales, Rhizobiales, Clostridiales, Rhodobacterales Desulfobacterales* and *Micrococcales* can potentially participate in the carbon cycle of the studied lakes. It is assumed that the nitrogen cycle pathways in the studied microbial communities can be implemented with *Pseudomonadales, Rhodobacterales, Bacillales* and *Clostridiales*. Representatives of these orders were found both in the summer and winter seasons in the studied lakes. The low prevalence of anammox genes and the lack of nitrification potential was a characteristic feature of the microbial communities of the studied lakes. In the sulfur cycle, the assimilation reduction of sulfate and sulfur mineralization were the main pathways in Lake Gudzhirganskoe both in winter and in summer. We assume that representatives of the orders *Rhodobacterales, Pseudomonales, Propionibacteriales, Clostridiales* and *Bacteroidales* are involved in these pathways. In the studied microbial communities of the studied lakes, the proportion of each order was ≤ 1 %.

Thus, we predicted the potential participation of various taxa of microorganisms in the biogeochemical cycles C, N, and S in the bottom sediments of the studied lakes.

In addition, it should be noted that the presence of metabolic pathways predicted in the microbial communities of the studied lakes referred to the ABC transporters (283 KOs) and the Two-component system (381 KOs). It is known that ABC transporters of microbial communities are able to effectively perceive and respond to environmental changes. Two-component systems play an important role in the adaptation of microorganisms to changing environmental conditions (Giuliani et al., 2011; Capra and Laub, 2012).

Bacteria in the microbial communities of the studied lakes had genes that were predicted to be involved in the synthesis of halo-adaptive compounds such as ectoine, glycine-betaine, glutamate, trehalose, and choline (Table S2). Characteristically, the largest number of genes involved in adaptation to a high salt environment was predicted in the summer in Lake Gudzhirganskoe.

Conclusion

Microbial communities are fundamental components of lake ecosystems, encompassing great diversity and playing a key role in the management of biogeochemical processes, including carbon, nitrogen and sulfur cycles (Ren et al., 2017).

This paper presents the results of the study of the microbial communities in the sulfate Lake Gudzhirganskoe and the soda Lake Nukhe-Nur in winter and summer seasons: from the assessment of the taxonomic composition to potential metabolic pathways. The studied lakes are unique natural ecosystems formed in exceptional natural conditions and experiencing extreme shifts in seasonal environmental conditions.

The taxonomic structure and functional potential of microbial communities of the sulfate Lake Gudzhirganskoe and the soda Lake Nukhe-Nur in winter and summer seasons were studied for the first time by high-throughput sequencing of the 16S rRNA gene. Our results showed that environmental conditions, such as pH, temperature and mineralization, mainly determined the composition of the community in the bottom sediments of lakes Gudzhirganskoe and Nukhe-Nur. The change of the "summer" obligate and moderately alkaliphilic and halophilic community to the "winter" alkali-, halotolerant/halophilic microbial community was observed in the winter period in Lake Gudzhirganskoe. In Lake Nukhe-Nur, a change from mesophilic-thermophilic community in summer to a mesophilic-psychrophilic microbial community in winter was revealed. Thus, the results obtained give an idea of the main trends in the seasonal dynamics of extremophilic microbial communities in the studied lakes in response to fluctuations in environmental parameters.

Prediction of the functional profiling of microbial communities using the Tax4Fun program made it possible to reveal the similarities and differences in the metabolic potential of the microbial communities in the studied lakes. Between the microbial communities of the studied lakes, only small qualitative and quantitative variations in the relative abundance of predicted functional genes were found. Potential functional genes have been found for all stages of the C, N and S cycles, with the exception of nitrification and aerobic CH_4 oxidation. In addition, we should note the presence of metabolic pathways predicted in the microbial communities of the studied lakes, which play an important role in the adaptation of microorganisms to changing environmental conditions (ABC transporters, a two-component system and genes that may be involved in the synthesis of haloadaptive compounds, such as ectoine, glycine-betaine, glutamate, trehalose and choline).

In general, it has been shown that there was a change in the dominant taxa at the level of families and genera in the microbial community in the summer and winter seasons, however, the predicted functional profile of microbial communities differed slightly between seasons and between the studied lakes. At the same time, it should be noted that the predictive nature of functional profiling based on high-throughput 16S rRNA gene sequencing data provides a preview of the metabolic functioning of microbial communities in these lakes, which should be further explored using a shotgun sequencing approach.

References

Alazard, D., Badillo, C., Fardeau, M. L., Cayol, J. L., Thomas, P., Roldan, T., Tholozan, J. L., and Ollivier, B. 2007. *Tindallia texcoconensis* sp. nov., a new haloalkaliphilic bacterium isolated from lake Texcoco, Mexico. *Extremophiles* 11(1):33–39. https://doi.org/10.1007/s00792-006-0006-5

Aßhauer, K. P., Wemheuer, B., Daniel, R., and Meinicke, P. 2015. Tax4Fun: predicting functional profiles from metagenomic 16S rRNA data. *Bioinformatics* 31(17):2882–2884. https://doi.org/10.1093/bioinformatics/btv287

Borsodi, A. K., Korponai, K., Schumann, P., Sproer, C., Felfoldi, T., Marialigeti, K., Szili-Kovacs, T., and Toth, E. 2017. "*Nitrincola alkalilacustris* sp. nov. and *Nitrincola schmidtii* sp. nov., alkaliphilic bacteria isolated from soda pans, and emended description of the genus Nitrincola." *International Journal of Systematic and Evolutionary Microbiology* 67(12):5159-5164. https://doi.org/10.1099/ijsem.0.002437

Brouchkov, A., Kabilov, M., Filippova, S., Baturina, O., Rogov, V., Galchenko, V., Mulyukin, A., Fursova, O., and Pogorelko, G. 2017. Bacterial community in ancient permafrost alluvium at the Mammoth Mountain (Eastern Siberia). *Gene* 636:48–53. https://doi.org/10.1016/j.gene.2017.09.021

Caporaso, J. G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F. D., Costello, E. K., Fierer, N., Peña, A. G., Goodrich, J. K., Gordon, J. I., Huttley, G. A., Kelley, S. T., Knights, D., Koenig, J. E., Ley, R. E., Lozupone, C. A., McDonald, D., Muegge, B. D., Pir-rung, M., Reeder, J., Sevinsky, J. R., Turnbaugh ,P. J., Walters, W. A. Widmann, J., Yatsunenko, T., Zaneveld, J., and Knight, R. 2010. QIIME allows analysis of high-throughput community sequencingdata. *Nature Methods* 7:335–336. https://doi.org/10.1038/nmeth.f.303

Capra, E. J. and Laub, M. T. 2012. Evolution of two-component signal transduction systems. *Annual Review of Microbiology* 66(1):325–347. https://doi.org/10.1146/annurev-micro-092611-150039

Chen, S., Niu, L., and Zhang, Y. 2010. *Saccharofermentans acetigenes* gen. nov., sp. nov., an anaerobic bacterium isolated from sludge treating brewery wastewater. *International Journal of Systematic and Evolutionary Microbiology* 60(12):2735–2738. https://doi.org/10.1099/ijs.0.017590-0

Chong, J., Liu, P., Zhou, G., and Xia, J. 2020. Using MicrobiomeAnalyst for comprehensive statistical, functional, and meta-analysis of microbiome data. *Nature Protocols* 15:799–821. https://doi.org/10.1038/s41596-019-0264-1

Cotta, S. R., Pellegrinetti, T. A., Andreote, A. P. D. Costa, J. S., Sarmento, H., and Fiore, M. F. 2022. Disentangling the lifestyle of bacterial communities in tropical soda lakes. *Scientific Report* 12:7939. https://doi.org/10.1038/s41598-022-12046-2

Dhariwal, A., Chong, J., Habib, S., King, I. L., Agellon, L. B., and Xia, J. 2017. MicrobiomeAnalyst: a web-based tool for comprehensive statistical, visual and meta-analysis of microbiome data. *Nucleic Acids Research* 45(W1):W180–W188. https://doi.org/10.1093/nar/gkx295

Edgar, R. C. 2010. Search and clustering orders of magnitude faster than BLAST. *Bioinformatics* 26(19):2460–2461. https://doi.org/10.1093/bioinformatics/btq461

Fadrosh, D. W., Ma, B., Gajer, P., Sengamalay, N., Ott, S., Brotman, R. M., and Ravel, J. 2014. An improved dual-indexing approach for multiplexed 16S rRNA gene sequencing on the Illumina MiSeq platform. *Microbiome* 2(6):1–7. https://doi.org/10.1186/2049-2618-2-6

Giuliani, S. E., Frank, A. M., Corgliano, D. M. Seifert, C., Hauser, L., and Collart, F. R. 2011. Environment sensing and response mediated by ABC transporters. *BMC Genomics* 12(S1):S8. https://doi.org/10.1186/1471-2164-12-S1-S8

Hammer, Ø., Harper, D. A. T., and Ryan, P. D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4(1):1–9.

Kaden, R., Spröer, C., Beyer, D., and Krolla-Sidenstein, P. 2014. *Rhodoferax saidenbachensis* sp. nov., a psychrotolerant, very slowly growing bacterium within the family *Comamonadaceae*, proposal of appropriate taxonomic position of *Albidiferax ferrireducens* strain T118T in the genus *Rhodoferax* and emended description of the genus *Rhodoferax*. *International Journal of Systematic and Evolutionary Microbiology* 64(4):1186–1193. https://doi.org/10.1099/ijs.0.054031-0

Kotsyurbenko, O. R., Simankova, M. V., Nozhevnikova, A. N., Zhilina T. N., Bolotina N. P., Lysenko, A. M., and Osipov, G. A. 1995. New species of psychrophilic acetogens: *Acetobacterium bakii* sp. nov., *A. paludosum* sp. nov., *A. fimetarium* sp. nov. *Archives of Microbiology* 163:29–34. https://doi.org/10.1007/BF00262200

Lee, D. J., Wong, B. T., and Adav, S. S. 2014. *Azoarcus taiwanensis* sp. nov., a denitrifying species isolated from a hot spring. *Applied Microbiology and Biotechnology* 98(3):1301–1307. https://doi.org/10.1007/s00253-013-4976-9

Lew, S., Koblížek, M., Lew, M., Medová, H., Glińska-Lewczuk, K., and Owsianny, P. M. 2015. Seasonal changes of microbial communities in two shallow peat bog lakes. *Folia Microbiologica* 60(2):165–175. https://doi.org/10.1007/s12223-014-0352-0

Liao, X., Lai, Q., Yang, J., Dong, C., Li, D., and Shao, Z. 2020. *Alcanivorax sediminis* sp. nov., isolated from deep-sea sediment of the Pacific Ocean. *International journal of systematic and evolutionary microbiology* 70(7):4280–4284. https://doi.org/10.1099/ijsem.0.004285

Liu, J. R., Tanner, R. S., Schumann, P., Weiss, N., McKenzie, C. A., Janssen, P. H., Seviour, E. M., Lawson, P. A., Allen, T. D., and Seviour, R. J. 2002. Emended description of the genus *Trichococcus*, description of *Trichococcus collinsii* sp. nov., and reclassification of *Lactosphaera pasteurii* as Trichococcus pasteurii comb. nov. and of *Ruminococcus palustris* as *Trichococcus palustris* comb. nov. in the low-G+C gram-positive bacteria. *International Journal of Systematic and Evolutionary Microbiology* 52(4):1113–1126. https://doi.org/10.1099/00207713-52-4-1113

Margesin, R., Spröer, C., Zhang, D. C., and Busse, H. J. 2012. *Polaromonas glacialis* sp. nov. and *Polaromonas cryoconiti* sp. nov., isolated from alpine glacier cryoconite. *International Journal of Systematic and Evolutionary Microbiology* 62(11):2662–2668. https://doi.org/10.1099/ijs.0.037556-0

Namsaraev, B. B., Zaitseva, S. V., Khakhinov, V. V., Imetkhenov, A. B., Rinchino, S. Kh., and Maksanova, L. B.-Zh. 2007. Mineral springs and lakes of the Barguzin Valley. 100 pp. Banzarov Buryat University Press. Ulan-Ude. (In Russian)

Nepomnyashchaya, Y. N., Slobodkina, G. B., Baslerov, R. V., Chernyh, N. A., Bonch-Osmolovskaya, E. A., Netrusov, A. I., and Slobodkin, A. I. 2012. *Moorella humiferrea* sp. nov., a thermophilic, anaerobic bacterium capable of growth via electron shuttling between humic acid and Fe(III). *International Journal of Systematic and Evolutionary Microbiology* 62(3):613–617. https://doi.org/10.1099/ijs.0.029009-0

Pierson, B. K. and Castenholz, R. W. 1974. A phototrophic gliding filamentous bacterium of hot springs, *Chloroflexus aurantiacus*, gen. and sp. nov. *Archives of Microbiology* 100(1):5–24. https://doi.org/10.1007/BF00446302

Plyusnin, A. M., Khazheeva, Z. I., Sanzhanova, S. S., and Angakhaeva, N. A. 2020a. Sulfate Mineral lakes of Western Transbaikalia: formation conditions, chemical composition of waters and bottom sediments. *Russian Geology and Geophysics* 61(8):858–873. https://doi.org/10.15372/RGG2019154

Plyusnin, A. M., Peryazeva, E. G., Chernyavskii, M. K., Zhambalova, D. I., Budaev, R. Ts., and Angakhaeva, N. A. 2020b. Genesis of water and dissolved matter in soda lakes of Nizhnii Kuitun of the Barguzin Depression. *Geography and Natural Resources* 41:258–265. https://doi.org/10.1134/S1875372841030075

Quast, C., Pruesse, E., Yilmaz, P., Gerken. J., Schweer, T., Yarza, P., Peplies, J., and Glöckner, F. O. 2013. The SILVA ribosomal RNA gene database project: improved data processing and web–based tools. *Nucleic Acids Research* 41(D1):D590–D596. https://doi.org/10.1093/nar/gks1219

Ren, Z., Wang, F., Qu, X., Elser, J. J., Liu, Y., and Chu, L. 2017. Taxonomic and Functional differences between microbial communities in Qinghai Lake and its input streams. *Frontiers in Microbiology* 8:2319. https://doi.org/10.3389/fmicb.2017.02319

Schloss, P. D. and Handelsman, J. 2006. Introducing SONS, a tool for operational taxonomic unit-based comparisons of microbial community memberships and structures. *Applied and Environmental Microbiology* 72(10):6773–6779. https://doi.org/10.1128/AEM. 00474-06

Sorokin, D. Y., Berben, T., Melton, E. D., Overmars, L., Vavourakis, C. D., and Muyzer, G. 2014. Microbial diversity and biogeochemical cycling in soda lakes. *Extremophiles* 18:791–809. https://doi.org/10.1007/s00792-014-0670-9

Sorokin, D. Y., Tourova, T. P., Kolganova, T. V., Detkova, E. N., Galinski, E. A. and Muyzer, G. 2011. Culturable diversity of lithotrophic haloalkaliphilic sulfate-reducing bacteria in soda lakes and the description of *Desulfonatronum thioautotrophicum* sp. nov., *Desulfonatronum thiosulfatophilum* sp. nov., *Desulfonatronovibrio thiodismutans* sp. nov., and *Desulfonatronovibrio magnus* sp. nov. *Extremophiles* 15(3):391–401. https://doi.org/10.1007/s00792-011-0370-7

Sorokin, D. Y., Tourova, T. P., Panteleeva, A. N., and Muyzer, G. 2012. *Desulfonatronobacter acidivorans* gen. nov., sp. nov. and *Desulfobulbus alkaliphilus* sp. nov., haloalkaliphilic heterotrophic sulfate-reducing bacteria from soda lakes. *International Journal of Systematic and Evolutionary Microbiology* 62(9):2107–2113. https://doi.org/10.1099/ijs.0.029777-0

Sorokin, D. Y., Trotsenko, Y. A., Doronina, N. V., Tourova, T. P., Galinski, E. A., Kolganova, T. V., and Muyzer, G. 2007. *Methylohalomonas lacus* gen. nov., sp. nov. and *Methylonatrum kenyense* gen. nov., sp. nov., methylotrophic gammaproteobacteria from hypersaline lakes. *International Journal of Systematic and Evolutionary Microbiology* 57(12):2762–2769. https://doi.org/10.1099/ijs.0.64955-0

Sorokin, D., Turova, T. P., Kuznetsov, B. B., Briantseva, I. A., and Gorlenko, V. M. 2000. *Roseinatronobacter thiooxidans* gen. nov., sp. nov., a new alkaliphilic aerobic bacteriochlorophyll-alpha-containing bacteria from a soda lake. *Microbiology* 69(1):75–82. https://doi.org/10.1007/BF02757261

Spring, S. 2003. Characterization of novel psychrophilic clostridia from an Antarctic microbial mat: description of *Clostridium frigoris* sp. nov., *Clostridium lacusfryxellense* sp. nov., *Clostridium bowmanii* sp. nov. and *Clostridium psychrophilum* sp. nov. and reclassification of *Clostridium laramiense* as *Clostridium estertheticum* subsp. laramiense subsp. nov. *International Journal of Systematic and Evolutionary Microbiology* 53:1019–1029. https://doi.org/10.1099/ijs.0.02554-0

Vigneron, A., Lovejoy, C., Cruaud, P., Kalenitchenko, D., Culley, A., and Vincent, W. F. 2019. Contrasting winter versus summer microbial communities and metabolic functions in a permafrost Thaw Lake. *Frontiers in Microbiology* 10:1656. https://doi.org/10.3389/fmicb.2019.01656

Wang, Y. and Bao, G. 2022. Diversity of prokaryotic microorganisms in alkaline saline soil of the Qarhan Salt Lake area in the Qinghai–Tibet Plateau. *Scientific Report* 12:3365. https://doi.org/10.1038/s41598-022-07311-3

Wang, Y. X., Liu, Y. P., Huo, Q. Q., Li, Y. P., Feng, F. Y., Xiao, W., Ding, Z. G., Lai, Y. H., and Cui, X. L. 2016. *Mongoliibacter ruber* gen. nov., sp. nov., a haloalkalitolerant bacterium of the family *Cyclobacteriaceae* isolated from a haloalkaline lake. *International Journal of Systematic and Evolutionary Microbiology* 66(2):1088–1094. https://doi.org/10.1099/ijsem.0.000836

Yamada, T., Sekiguchi, Y., Hanada, S., Imachi, H., Ohashi, A., Harada, H., and Kamagata, Y. 2006. *Anaerolinea thermolimosa* sp. nov., *Levilinea saccharolytica* gen. nov., sp. nov. and *Leptolinea tardivitalis* gen. nov., sp. nov., novel filamentous anaerobes, and description of the new classes *Anaerolineae* classis nov. and *Caldilineae* classis nov. in the bacterial phylum Chloroflexi. *International Journal of Systematic and Evolutionary Microbiology* 56(6):1331–1340. https://doi.org/10.1099/ijs.0.64169-0

Zhang, D. C., Liu, H. C., Xin, Y. H., Yu, Y., Zhou, P. J., and Zhou, Y. G. 2008. *Salinibacterium xinjiangense* sp. nov., a psychrophilic bacterium isolated from the China No. 1 glacier. *International Journal of Systematic and Evolutionary Microbiology* 58(12):2739–2742. https://doi.org/10.1099/ijs.0.65802-0

Zhao, C., Gao, Z., Qin, Q., and Ruan, L. 2012. *Mangroviflexus xiamenensis* gen. nov., sp. nov., a member of the family *Marinilabiliaceae* isolated from mangrove sediment. *International Journal of Systematic and Evolutionary Microbiology* 62(8):1819–1824. https://doi.org/10.1099/ijs.0.036137-0

Zhilina, T. N., Zavarzin, G. A., Rainey, F., Kevbrin, V. V., Kostrikina, N. A., and Lysenko, A. M. 1996. *Spirochaeta alkalica* sp. nov., *Spirochaeta africana* sp. nov., and *Spirochaeta asiatica* sp. nov., alkaliphilic anaerobes from the Continental Soda Lakes in Central Asia and the East African Rift. *International Journal of Systematic and Evolutionary Microbiology* 46(1):305-312. https://doi.org/10.1099/00207713-46-1-305