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SHORT COMMUNICATIONS

Planktonic Microbial Communities of Thermokarst Lakes of Central Yakutia Demonstrate a High Diversity of Uncultivated Prokaryotes with Uncharacterized Functions

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Abstract—Although thermokarst alas lakes of Central Yakutia are of great climatic and economic importance, there is currently virtually no information on microbial communities and microbial processes in these lakes. This paper characterizes the hydrochemical features and presents a primary analysis of the diversity of planktonic microbial communities in three alas lakes of Central Yakutia—Tyungulyu, Taby, and Kharyyalakh. It was shown that in terms of the water physicochemical composition, the studied lakes were quite typical for this region; they had increased alkalinity and trophicity, but differed from each other in microbiological indicators. Chemoheterotrophic prokaryotes predominated in the studied planktonic communities, but a significant proportion of the 16S rRNA gene sequences were most similar to uncultured microorganisms whose functional potential is still unknown.

Keywords: thermokarst lakes, alases, microbial diversity, 16S rRNA gene, Central Yakutia, climate

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According to recent estimates, the cryolithozone of the Northern Hemisphere occupies 14 to 22% of the dry land area (Obu et al., 2019). Permafrost is especially common in Russia (Siberia), United States (Alaska), and Canada. Comparative investigation of permafrost dynamics in the Holocene and during the last decades revealed that the regions with predominance of ice-rich permafrost are highly sensitive to variations in temperature and other climatic factors (Ulrich et al., 2019). Under conditions of the global warming, activation of thermokarst processes, resulting in emergence of subsidence reliefs and formation of thermokarst lakes, is one of the manifestations of permafrost degradation. These processes occur widely in Russia in the regions of continuous permafrost, including Central Yakutia.

The thermokarst depressions of Central Yakutia are termed alases. These are depressions with mild slopes and flat bottom, up to several km in diameter (sometimes, up to tens km). Approximately 16000 such depressions with the total area of ~4400 km^2 were revealed on the Central Yakutia Lowland (Bosikov, 1991; Suzuki et al., 2001). The slopes of alases are usually covered with meadow vegetation, and a lake is located at the center. This relief historically determined the economic importance of alases to the indigenous population and, therefore, high anthropogenic impact (Bosikov, 1991). The alas lakes of Central Yakutia are relatively diverse in their morphometric and hydrochemical characteristics, although they are mostly small, shallow basins with elevated salinity and pH (Kopyrina et al., 2020; Ushnitskaya et al., 2021).

In the course of permafrost thawing and formation of alas systems, buried organic matter (OM) is released into the basins and becomes available for microbial transformation (Kallistova et al., 2019). Human activity, including animal husbandry, results in additional release of significant amounts of modern OM into alas lakes. Thus, varying climatic and anthropogenic factors, as well as diversity of the hydrochemical composition of alas lakes water, affect the structure of microbial communities and the patterns of OM transformation.

High rates of methane emission from alas systems determine their climatic role; and the basins are characterized by the highest emission of this greenhouse gas (Desyatkin et al., 2016). Methane is released both from the thawing gas-saturated permafrost and due to imbalance between microbial methanogenesis and methane oxidation in the course of degradation of buried and modern OM (Kallistova et al., 2019).

In spite of the great climatic and economic significance of the alas lakes of Central Yakutia, there are practically no works dealing with microbial communities and microbial processes in these lakes. The goal of the present work was therefore primary analysis of diversity of planktonic microbial communities in three alas (thermokarst) lakes of Central Yakutia.

The studied area was located in Central Yakutia at 62° N, in the middle reaches of the Lena River, in the zone of continuous occurrence of permafrost. Climatic conditions of the region are significantly affected by the Siberian anticyclone forming in Central Asia during winter; its large branch occupies all Eastern Siberia. The climate is affected by frequent incursions of the air from the Arctic Ocean, which in summer contains very little water vapor. The climate is sharply continental, with a long cold winter and a short, hot summer. According to the data from www.worldclim.org, the average annual temperature at the sampling area varies from –12.4 to –8.7°C, while the highest monthly average temperature in summer is 22.2 to 25.0°C. For the lakes, the ice-free period is 120–125 days (Arzhakova et al., 2007).

Our work was carried out in mid-July 2023 at three alas lakes: Tyungulyu, Taby, and Kharyyalakh (Table 1); these depressions resulted from thawing of buried ice in the permafrost. Lake Tyungulyu was chosen for research as a known object for investigation of emission of greenhouse gases, CO_2 and CH_4 (Desyatkin et al., 2016, 2018) and was often studied in other respects (Kopyrina et al., 2020; Ushnitskaya et al., 2021). Two other lakes were chosen randomly.

Chemical analysis was carried out using the methods described in the manual on chemical analysis of terrestrial surface waters (Semenov, 1977). The measurements were performed using an PE-5300VI spectrophotometer (GK EKROS, Russia), a Fluorat-02-2M fluorimeter (LLC Lumex-Marketing, Russia), and an AAnalyst400 atomic absorption spectrometer (PerkinElmer Inc., United States). Water temperature was measured with a Checktemp electronic thermometer (HANNA Instruments, United States) and pH, with a Multitest IPL-101 ion meter (LLC NPP SEMIKO, Russia). Methane was determined by phase equilibrium degassing method (McAuliffe, 1971).

To characterize the microbial communities, water samples (0.5 L) were collected and filtered through a membrane with 0.22-μm pore diameter. The biomass-bearing filter was homogenized with liquid nitrogen. DNA isolation, amplification, sequencing, analysis of the 16S rRNA gene fragments, clustering of the sequences into operational taxonomic units (OTUs), removal of chimeric sequences, and OTU taxonomic identification were carried out as described by Gruzdev et al. (2023). Nucleotide sequences of the 16S rRNA genes were deposited to the Sequence Read Archive NCBI database, BioProject PRJNA1027611.

The surface water layer, from which the samples were collected, was relatively well heated (Table 1). While deficiency of dissolved oxygen was found in the Lakes Kharyyalakh and Taby, in Lake Tyungulyu this parameter was within the normal range. According to pH, the Lakes Taby and Tyungulyu were moderately alkaline, while Lake Kharyyalakh was slightly alkaline. Characteristically, water salinity usually increases in the course of development of endorheic thermokarst Lakes. Thus, the Lakes Taby and Tyungulyu were mesohaline, according to the classification of Kitaev (2007). In Lake Kharyyalakh the water was moderately fresh. According to major ion composition, the water in the Lakes Tyungulyu and Taby was of the sodium chloride type, while that of Lake Kharyyalakh was of the calcium hydrocarbonate type. Water hardness in the Lakes Kharyyalakh, Taby, and Tyungulyu was medium hard, hard, and very hard, respectively. Lake Kharyyalakh had more intense water color; together with Lake Taby, it was mesopolyhumose. Lake Tyungulyu had the less intense water color and was a mesohumose one. The studied lakes had elevated content of easy-to-oxidize organic matter (EOOM) and high content of hard-to-oxidize organic matter (HOOM). In all cases, high concentrations of ammonium nitrogen were found, with the highest value in Lake Tyungulyu and the lowest, in Lake Kharyyalakh. Nitrite concentration was also high, with the maximum in Lake Taby. Nitrate ions concentrations varied widely, with the highest values in the Lakes Tyungulyu and Taby. The highest concentrations of mineral and total phosphorus occurred in the Lakes Tyungulyu and Taby. Total iron content was high in all three lakes. Methane concentrations in the water varied significantly, from 0.9 μmol/dm^3 (Lake Tyungulyu) to 39 μmol/dm^3 (Lake Kharyyalakh) (Table 1).

High concentrations of nitrogen and phosphorus compound, high intensity of water color, EOOM, and HOOM were caused by anthropogenic load (animal husbandry, municipal waste, etc.), which all studied lakes experienced to a certain degree and which resulted in arrival of organic matter and nutrients from the catchment area. As a result, the trophic level of the lakes increased. By the classification by Wetzel (2001), according to the concentrations of mineral nitrogen, the Lakes Tyungulyu and Taby were hypertrophic, while Lake Kharyyalakh was β-eutrophic. According to phosphorus concentrations, all the lakes were hypertrophic. Thus, the three studied lakes located relatively close to each other differed considerably in their hydrochemical characteristics. Elevated pH and trophic level may be considered the common features of the studied lakes. These results are in agreement with those of a more large-scale work by Ushnitskaya et al. (2021) on the hydrochemical characterization of

Table 1. Analysis results for three studied thermokarst lakes in Central Yakutia (average values ± standard deviation, if applicable)

Parameter	Lake		
	Tyungulyu	Taby	Kharyyalakh
Geographic parameters of the lakes			
Coordinates, degrees (N; E)	62.202739; 130.655056	62.132187; 130.268169	62.10725; 128.37102
Elevation above sea level, m	140	147	283
Length, m	600	803	1690
Width, m	600	551	800
Water plane area, 10^3 m^2	237.6	305.1	922.4
Shoreline length, km	1.93	2.22	4.52
Physicochemical parameters of the water			
Temperature at the time of sampling, °C	17.70	27.40	20.30
pH	9.68 ± 0.02	9.07 ± 0.02	8.63 ± 0.01
Oxygen (O_2), mg/dm^3	6.70 ± 0.08	4.88 ± 0.07	5.14 ± 0.11
Methane, μmol/dm^3	0.86	4.48	39.31
Salinity, mg/dm^3	3148.29 ± 10.36	1723.70 ± 10.85	375.61 ± 1.84
Hardness, mmol/dm^3	14.44 ± 0.06	7.70 ± 0.03	3.88 ± 0.00
Calcium, mg/dm^3	14.43 ± 0.00	18.44 ± 0.00	42.28 ± 0.00
Magnesium, mg/dm^3	166.70 ± 0.69	82.38 ± 0.34	21.51 ± 0.00
Sodium, mg/dm^3	724.00 ± 7.07	548.00 ± 7.07	40.80 ± 0.71
Potassium, mg/dm^3	54.00 ± 0.10	94.40 ± 0.10	17.10 ± 0.10
Hydrocarbonates, mg/dm^3	778.62 ± 0.00	415.55 ± 2.59	210.15 ± 1.04
Chlorides, mg/dm^3	700.14 ± 2.51	382.33 ± 0.75	21.27 ± 0.00
Sulfates, mg/dm^3	710.40 ± 0.00	182.60 ± 0.00	22.50 ± 0.00
Ammonium nitrogen (N-NH_4), mg/dm^3	1.51 ± 0.00	1.00 ± 0.02	0.48 ± 0.01
Nitrite nitrogen (N-NO_2), mg/dm^3	0.03 ± 0.00	0.17 ± 0.00	0.05 ± 0.00
Nitrate nitrogen (N-NO_3), mg/dm^3	0.46 ± 0.00	0.52 ± 0.00	0.10 ± 0.00
Mineral phosphorus (P-PO_4), mg/dm^3	0.013 ± 0.00	0.106 ± 0.00	0.007 ± 0.00
Total phosphorus (P_{tot}), mg/dm^3	1.00 ± 0.00	2.00 ± 0.00	0.13 ± 0.01
Total iron (Fe_{tot}), mg/dm^3	1.85 ± 0.03	2.00 ± 0.01	1.66 ± 0.01
Silica (Si-SiO_2), mg/dm^3	1.44 ± 0.01	2.05 ± 0.01	1.34 ± 0.03
Water color, Pt/Co grad.	64 ± 0.01	89 ± 0.00	129 ± 1.02
EOOM (by BOD), mg/dm^3	2.31 ± 0.08	4.88 ± 0.06	3.64 ± 0.06
HOOM (by COD), mg/dm^3	76.00 ± 0.00	66.50 ± 0.14	107.00 ± 0.28
Alpha-diversity indices for microbial communities			
Berger-Parker	0.05	0.53	0.17
Chao1	392.10	402.10	302.20
Simpson	0.02	0.31	0.07
Shannon_e	4.74	2.30	3.55

* BOD_5, biochemical oxygen demand in 5 days; EOOM, easy-to-oxidize organic matter, determined by BOD; HOOM, hard-to-oxidize organic matter, determined by COD; COD, chemical oxygen demand.

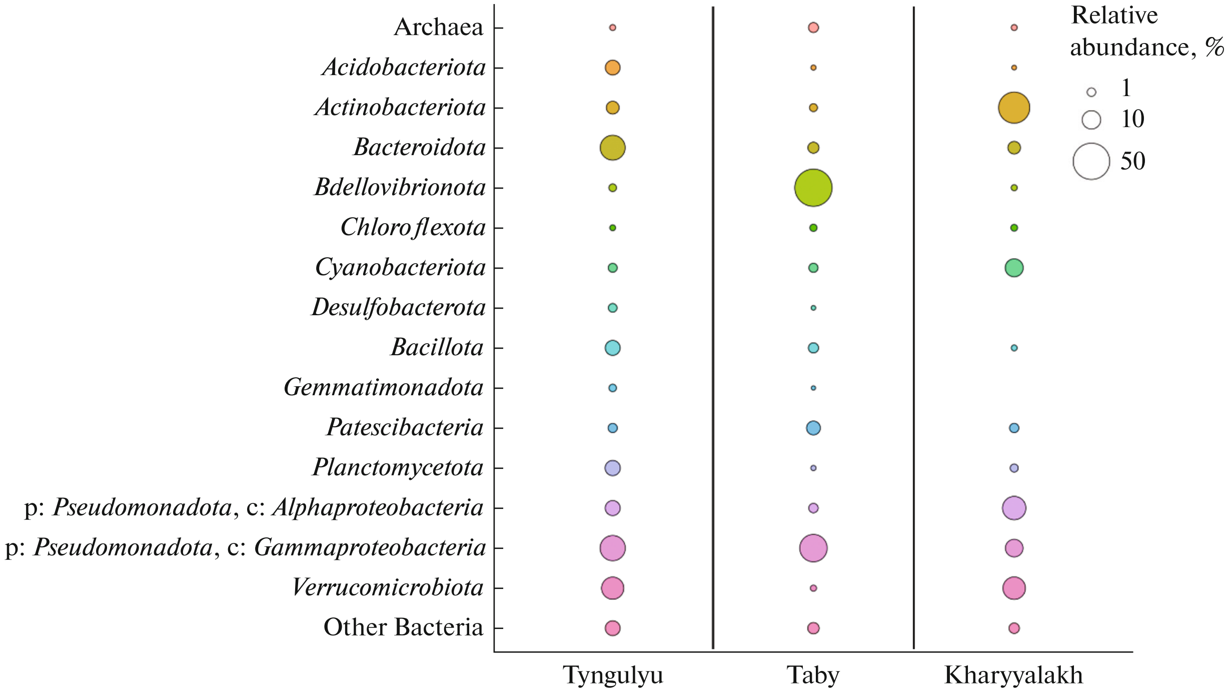

Fig. 1. Diversity of planktonic microbial communities in three alas lakes of Central Yakutia at the level of phylogenetic groups.

diverse lakes in the Ust'-Aldan region of Central Yakutia. The lakes studied in the present work were therefore hydrochemically typical for this region.

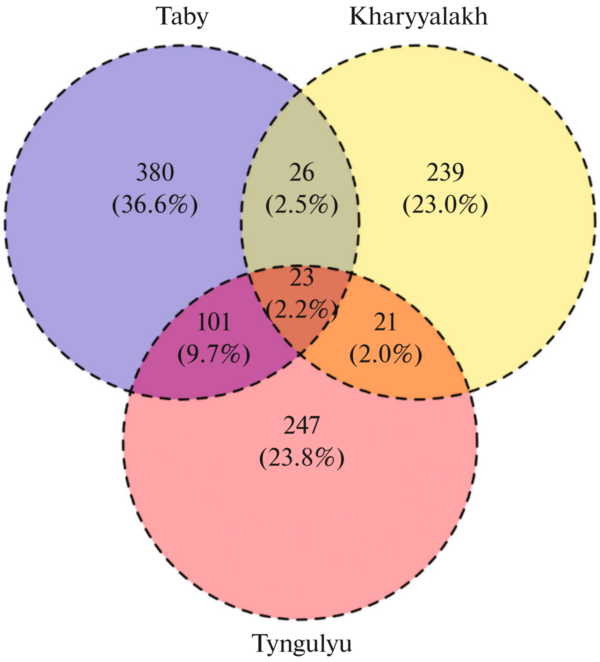

Fig. 2. Numbers of common and unique OTUs in planktonic communities in three alas lakes of Central Yakutia (Venn diagram).

Analysis of diversity of the 16S rRNA gene fragments revealed predominance of *Bacteria* in all planktonic communities, while *Archaea* constituted a minor part (Fig. 1). The Venn diagram showed large differences between the communities in their microbial composition. All three lakes shared only 2.2% of the OTUs (Fig. 2). The alpha-diversity indices revealed that prokaryotic communities of the Lakes Tyungulyu and Taby were more diverse than that of Lake Kharyyalakh (Table 1).

Heterotrophic bacteria of the class *Gammaproteobacteria* (22.2%) and the phyla *Verrucomicrobiota* (16.4%) and *Bacteroidota* (21.5%) (Fig. 1) were predominant in Lake Tyungulyu planktonic communities. No evidently dominant OTUs were revealed: only 25 out of 392 OTUs had relative abundance from 1 to 5%. Interestingly, however, most of the revealed OTU sequences could not be reliably identified, since their closest relatives were uncultured members of families or higher taxa.

In Lake Taby, members of the phylum *Bdellovibrionota* constituted half of the OTUs (54%); they were related to an uncultured *Daphnia* pathogen, "*Spirobacillus cienkowskii*" (Rodrigues et al., 2008). Association of this microorganism with *Daphnia* was not established in the present work, while the result itself is surprising and requires further investigation. The second most abundant group were members of the class *Gammaproteobacteria*, family *Comamonadaceae* (26.2%), related to members of the genus *Limnohabitans* and to two closely related genera, *Hydrogenophaga* and *Malikia*. Heterotrophic members of the genus *Limnohabitans* are widespread worldwide in freshwater lakes, preferably with near-neutral or alkaline pH; they have several phylogenetic lineages and are considered an important component of the trophic network in the plankton community (EOOM utilizers), although most representatives remain uncultured or difficult to cultivate (Kasalický et al., 2013). Members of the genus *Hydrogenophaga* are chemoorganotrophs or chemolithoautotrophs using H_2 as an energy source (Willems et al., 1989). The genus *Malikia* is characterized by its ability to accumulate intracellular polyhydroxyalkanoates and polyphosphates (Spring et al., 2005).

Lake Kharyyalakh differed in microbial composition from the Lakes Tyungulyu and Taby (Fig. 1). Predominant in its plankton were members of the phyla *Actinobacteriota* (36.1%) and *Verrucomicrobiota* (16.8%) and of the class *Alphaproteobacteria* (18.5%). Sequences of the phylum *Cyanobacteriota* were also abundant in the water (9.8%). The sequences identified as the CL500-29_marine_group (family *Ilumatobacteraceae*, *Actinobacteriota*) had the greatest representation in the community (16.4%). These are uncultured microorganisms, and little is known concerning their ecology and functional significance. They are known to be widespread in both marine and lake habitats and are considered universal heterotrophs, capable of utilizing various dissolved organic substances under oxic conditions (Zhou et al., 2020). The sequences belonging to the hgcI clade (family *Sporichthyaceae*, *Actinobacteriota*) comprised 10.8% of the total OTU number. Members of this clade are uncultured, widespread in freshwater habitats, and have genetic prerequisites for ability to assimilate carbohydrates and nitrogen-rich organic compounds (Ghylin et al., 2014). Moreover, the hgcI clade has genetic potential for light assimilation using actinorhodopsin, which may promote anaplerotic carbon assimilation and may indicate the possibilities for both heterotrophic and autotrophic metabolism (Ghylin et al., 2014).

Among *Verrucomicrobiota*, predominant OTUs were identified only at the level of the family *Chthoniobacteraceae* (11.4%), which is insufficient for assessment of their role in the community.

Predominant among *Alphaproteobacteria* were aerobic chemoorganotrophic freshwater bacteria '*Candidatus* Fonsibacter ubiquis' (13.5%), formerly known as SAR11 clade IIIb or LD12 (Henson et al., 2018). Only one cultured member of this clade is presently known (Henson et al., 2018); another species, '*Candidatus* Fonsibacter lacus,' was described based on metagenomic data (Tsmentzi et al., 2019). The genome of *Ca.* "Fonsibacter ubiquis" was found to contain the tentative homologs of the genes for methyl phosphonates synthesis, transport, and degradation (rpsblast homology from 25 to 46%), which may indicate involvement of this organism in aerobic methanogenesis (Kallistova et al., 2023). '*Candidatus* Fonsibacter ubiquis' is thought to be adapted to oligotrophic environments with simple carbon compounds (Henson et al., 2018), and its detection in the β-eutrophic Lake Kharyyalakh is an interesting finding requiring further investigation.

Lake Kharyyalakh was the only one among the studied lakes where high representation of cyanobacteria (phylum *Cyanobacteriota*) was found, with predominance of unicellular ones (unidentified members of the family *Prochlorococcaceae* and members of the genus *Microcystis*). Predominance of unicellular cyanobacteria was noted in a recent work on diversity and ecological characterization of cyanobacteria and algae of Yakutia thermokarst lakes, which summarized morphological observations of many years (Kopyrina et al., 2020). Unfortunately, direct comparison is not possible.

Thus, most of both dominant and minor OTUs revealed in the studied planktonic communities of three alas lakes in Central Yakutia represented uncultured microorganisms with unclear functions, although predominance of chemoheterotrophic prokaryotes in the studied communities may be stated. In the water of thermokarst lakes of other regions, e.g., Canada (Negandhi et al., 2014, 2016) and Yamal Peninsula in Russia (Savvichev et al., 2021), predominance and high diversity of organotrophic bacteria of the phyla *Bacteroidetes*, *Pseudomonadota*, *Actinobacteria*, and *Verrucomicrobia* was also shown. The surface horizons of the water column had a high relative abundance of unicellular cyanobacteria of the family *Prochlorococcaceae* (automatically identified as *Cyanobiaceae*) and of heterocystous cyanobacteria identified as members of the family *Nostocaceae* (Savvichev et al., 2021), which was also comparable to our results.

We have previously carried out comprehensive investigation of microbial processes of the methane cycle in thermokarst and polygenetic lakes of the Yamal Peninsula and revealed diverse pathways of methanogenesis and intense aerobic and anaerobic methane oxidation both in the sediments (Kallistova et al., 2021) and in the water column (Savvichev et al., 2021). Methane concentrations in the water of Yamal lakes were comparable to those revealed in the three studied lakes in Central Yakutia. Similar to the water of Yamal lakes, methanotrophic microorganisms were not numerous; they were detected only in the water of Lake Kharyyalakh (0.26% of all OTUs) and belonged to the order *Methylococcales* and the families *Methylomonadaceae* (the genus was not identified) and *Methylococcaceae* (genus *Methyloparacoccus*). Methanogenic archaea were revealed mainly in Lake Taby with the lowest concentration of dissolved oxygen. Their relative abundance was also low (0.33% of all OTUs), and their diversity was represented by the families *Methanobacteriaceae*, *Methanomicrobiaceae*, and *Methanosaetaceae*.

Thus, our data indicate that planktonic microbial communities of alas lakes in Central Yakutia are diverse and abound with uncultured prokaryotes with the presently unknown functional potential. The basic and applied significance of microbiological investigation of such lakes in Yakutia is determined by necessity of the understanding of dynamics of the functioning of microbial communities under conditions of sharply continental climate with predominance of low temperatures and by the potential possibility to control microbial processes of the carbon cycle (greenhouse gas emission) under conditions of global climatic changes. Moreover, our data indicate that the alas lakes of Central Yakutia may act as sources for the search of new industrially significant strains (e.g., phosphate-accumulating organisms of the genus *Malikia*), adapted to the low-temperature conditions common in various regions of Russia.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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