

Article

Differences in Bacterial Communities of Deep and Shallow Subarctic Ice-Covered Lakes in the Northern Pole of Cold

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Abstract

The cold conditions of these habitats, as well as the morphometric features and origins of long-term ice-covered freshwater lakes, influence the structure and diversity of bacterial communities, which remain poorly understood. This study focused on long-term ice-covered lakes of contrasting origins (tectonic–glacial, glacial, and thermokarst), located in the highland subarctic region of Eastern Yakutia—an area that includes the Northern Hemisphere’s Pole of Cold, characterized by extremely low temperatures. The differences in bacterial community diversity between deep lakes of tectonic–glacial origin and shallow lakes of glacial and thermokarst origin are shown by metabarcoding of the 16S rRNA gene. According to ANOVA, the water quality parameters were homogeneous between samples from the deep and shallow, and their effect on the bacterial community structure was insignificant. The deep lake communities were dominated by groups indicative of oligotrophic, stratified, and cold environments: *Cyanobium_PCC*–6307 (low-light picocyanobacteria), *Methyloacidiphilaceae* (methanotrophs in oxygenated conditions), and the heterotrophic psychrotolerant genera *Acinetobacter* and *Paenisporosarcina*. Shallow lakes, by contrast, were enriched in taxa associated with high-light, well-mixed, and sediment-influenced conditions: SAR11 (Clade_III) (photoheterotrophic oligotrophs), *Methylobacter* (methanotrophs at neutral-pH), and taxa dominant in sediments (*Gemmataceae* и *Terrimicrobium*). The broadly distributed genera *Candidatus_Planktophila*, *Ilumatobacter*, and *Polynucleobacter* represent cosmopolitan freshwater generalists with diverse metabolic capabilities, explaining their consistent presence across both lake types. The novelty of this study lies in identifying a link between the structure of bacterial communities and the morphometric characteristics of lakes under conditions of homogeneous environmental parameters. Despite similar chemical compositions, opposite patterns were observed in deep and shallow lakes: in deep lakes, autochthonous taxa associated with stratification (low-light-tolerant cyanobacteria, aerobic methanotrophs) predominated, whereas sediment-associated and photoheterotrophic taxa dominated in shallow lakes, indicating a stronger connection between the benthos and the pelagic zone and a dependence on allochthonous carbon. Our results demonstrate that morphometry appears to be an important factor of the stability of microbial composition and carbon flux in permafrost regions. We revealed the heterogeneity of bacterial communities in subarctic lakes and identified dominant groups and key taxa, contributing to a better understanding of the ecological structure and functioning of lake ecosystems in cold regions and providing a basis for their monitoring.



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1. Introduction

The study of microbial ecology in ice-covered lakes is attracting increasing attention, as new species of microbes, element cycles and metabolic mechanisms are continually being discovered in these habitats [1,2]. Under-ice communities are characterized by their rich diversity of extremophilic prokaryotes that are adapted to low temperatures [3–5]. The richness and viability of under-ice microbial communities depend on physical and chemical processes. Winter shifts in these gradients can result in simultaneous changes to the communities and their trophic pathways [1,6,7]. For example, some ice- and snow-covered lakes have been shown to contain bacterial communities characterized by a predominance of reductive metabolic pathways, such as fermentation and methanogenesis [8]. Similarly, the close correlation between nitrification rates and ammonium concentrations under ice [9,10] suggests that the accumulation of reduced nitrogen species fuels winter blooms of nitrifying bacteria [11].

According to metabarcoding data, polar and high-altitude environments are typically dominated by the phyla *Pseudomonadota* (*Proteobacteria*) and *Actinomycetota* (*Actinobacteria*) [2,7,12–14]. Recently, there has been a significant expansion in access to 16S rRNA metabarcoding data and to metagenomic and metatranscriptomic data from freshwater prokaryotes under ice. For example, diversity and metabolic potential have been studied in freshwater lakes in Kangerlussuaq, Greenland [15], Lake Erie [4], boreal lakes near Quebec in Canada [16,17], Lake Vostok in Antarctica [18], Lake Baikal in Eastern Siberia [19–21], and Wuliangsu Lake in the temperate continental monsoon zone of China [22]. Only a few studies have reported on the composition of under-ice microbial communities in high arctic subarctic regions, as the harsh environment makes sampling difficult.

The subarctic lakes of Yakutia (Eastern Siberia, Russia) that we study are located in the mountainous Oymyakon Highlands region, which is known as the ‘Pole of Cold’ and is the coldest place in the Northern Hemisphere. The region has a sharply continental climate and the highest temperature range, with an annual range of more than 60 °C [5]. The cold season lasts from late October to mid-June, when the lakes are covered in ice and snow. Previously, we used metabarcoding for the first time to assess the composition and distribution of microbial communities during the glacial period in two subarctic lakes, Labyntyr and Vorota [5,23]. Significant differences in bacterial diversity and composition were observed at the bottom surface of the ice and in the water column during the ice cover period in spring (April, May, and June). Therefore, more research is needed on the lakes in this region to improve our understanding of the diversity and richness of bacterial communities beneath the ice. Although the lakes are located in similar geographical and ecological conditions, they differ in terms of their morphometric characteristics and origin. Importantly, these lakes are located in remote, hard-to-reach areas unaffected by anthropogenic activity. Understanding microbial diversity and community dynamics in these cold habitats provides information on the stability and adaptation of bacterial communities to extreme environmental conditions without the influence of anthropogenic factors.

This study characterized deep and shallow freshwater lakes of various origins located in the highland subarctic region and in the extreme cold zone of the Pole of Cold of the Northern Hemisphere. Using 16S rRNA gene metabarcoding, we aimed to identify differences in the diversity and structure of bacterial communities in poorly studied, long-

term ice-covered ecosystems and to determine their relationship with habitat conditions. We hypothesized that, because the geographic and environmental conditions are similar, the morphometry and origin of the lakes would influence differences in the structure of their bacterial communities during the under-ice period.

2. Materials and Methods

2.1. Study Region

The subarctic freshwater deep lakes Vodorazdelnoye and Labyinky, the shallow lakes Myamichi, Ulu, and Dead, as well as the source and mouth of the Labyinky River (located on the Oymyakon Upland in Eastern Yakutia Figure 1A) were explored in April 2021 and 2022. Lake Vodorazdelnoye (LVR) is located on the Suntar-Khayata Ridge, is of glacial–tectonic origin, and has a water depth of 66 m. The Labyinky River (LR) originates from Lake Vodorazdelnoye, is 107 km long, streams through mountainous terrain, flows into the southern part of the lake of the same name Labyinky and flows out into its northern part. Lake Labyinky (LL), which is of tectonic–glacial origin and has a maximum depth of 75 m and an average depth of 52 m [24], is located at the junction of the Suntar-Khayata Ridge and the Oymyakon plateau. Lake Myamichi (LM), a thermokarst formation 3 m deep, is part of the Small Labyinky Lakes system, located 20 km from the lower shore of Lake Labyinky. Lake Ulu (LU) is of glacial origin, with an average depth of 15 m [25]. Lake Dead (LD) is a glacial cirque lake, 6 m deep, round in shape, with no noticeable inflow or outflow. LU and LD are located 172 km northwest of Lake Vodorazdelnoye and 100 km from the nearest settlement of Tomtor (Figure 1B).

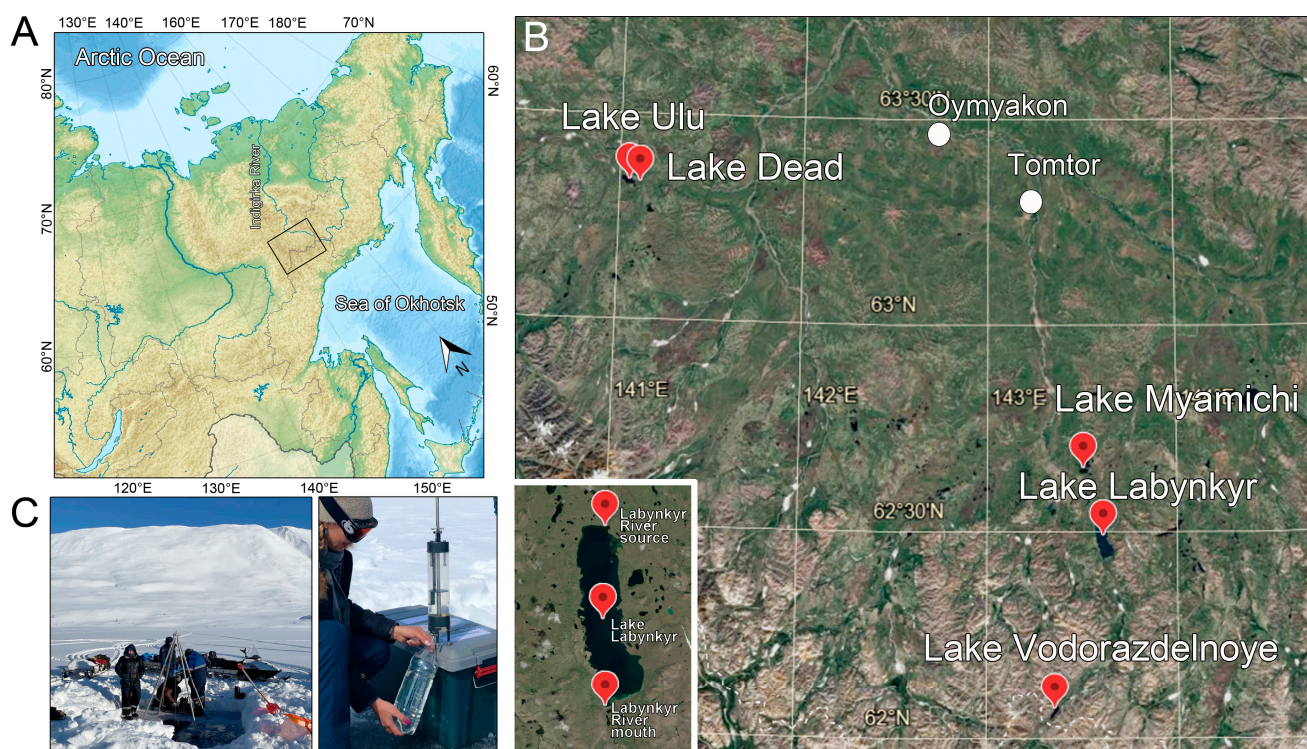


Figure 1. Geographical location of the Suntar Khayata Range and the Oymyakon Highland (A), lake sampling sites (B) and water sampling from under the ice (C).

2.2. Sampling and Environmental Characteristics

A total of 13 water samples (Table S1) were collected: one in Lake Vodorazdelnoye (LVR22); two in the northern part (LLn21 and LLn22), one in the middle part (LLm22) and one in the southern part (LLs21) of Lake Labyinky; two at the source (LRs21 and LRs22)

and one at the mouth (LRm21) of Labyntyk River; two in Lake Myamichi (LM21, LM22); two in Lake Ulu (LU21, LU22); and one in Lake Dead (LD). Methods for assessing total bacterial abundance (TBA), total microalgae abundance (TMA), total microalgae biomass (TMB), and species composition of phytoplankton, as well as methods for determining the physicochemical parameters of the environment, such as ice and snow cover thickness, water temperature (T), pH, water electrical conductivity (EC_{25}), dissolved oxygen concentrations (DO), silicon (Si), phosphate (PO_4^{3-}), total phosphorus (TP), nitrite (NO_2^-), nitrate (NO_3^-), ammonium (NH_4^+), total nitrogen (TN) and total organic carbon (TOC) were presented by us earlier [5]. Water samples were collected using a Niskin bottle ($V = 2$ L) from under the ice at a depth of 2 m in each lake and the mouth of the Labyntyk River. Samples were collected using sterile plastic bottles from the surface of open water at the source of the Labyntyk River. Two liters of water were collected for phytoplankton composition analysis, one liter for physicochemical analysis, and three liters for total DNA extraction.

2.3. DNA Extraction and PCR Amplification

Water samples of 3 L were first pre-filtered using a 100 μm sieve, and then filtered through 0.2 μm analytical track membranes (ATM) (“REATREK-Filter”, Obninsk, Russia) immediately after sampling. Biomass was washed from the filters into sterile flasks filled with 5 mL of TE buffer (10 mM Tris-HCl, 1 mM EDTA; pH 7.5), frozen, and transported at -20 °C to the laboratory, where the samples were stored at -80 °C until further analysis. Total DNA was extracted using lysozyme (1 mg mL^{-1}), proteinase K, 10% SDS, and phenol:chloroform:isoamyl alcohol mixture (25:24:1) according to the protocol based on Rusch et al. [26]. The concentration and purity of the extracted DNA were assessed using an Eppendorf BioSpectrometer-basic spectrophotometer (Eppendorf, Germany). DNA concentration varied from 6 to 44 ng/ μL , A260/280 ratio from 1.82 to 2 (Table S2). The V3-V4 region of the 16S rRNA gene was amplified using primers U341F (5'-CCTACGGGGRSGCAGCAG-3') [27] and U785R (5'-GGACTACCVGGGTATCTAAKCC-3') [28]. High-throughput sequencing (HTS) was performed by the Core Centrum “Genomic Technologies, Proteomics and Cell Biology” of ARRIAM (Saint-Petersburg, Russia), using the MiSeq Illumina Genome Sequencer system with the Reagent Kit v3 to obtain 300 bp paired-end reads.

The sequence data were submitted to the Sequence Read Archive database (<https://www.ncbi.nlm.nih.gov/sra/>) (accessed on 31 December 2025) of the National Center for Biotechnology Information under accession number PRJNA1234357.

2.4. HTS Data Analysis and Statistical Analyses

Analysis of sequencing data was performed using Usearch v.10 [29], Vsearch v.2.9.1 [30], and Mothur v.1.43.10 [31]. Raw reads were merged, primer sequences were truncated, and reads were filtered by an expected error threshold of 1.0 using Usearch (option -fastq_maxee 1.0). Next, sequences were denoised using the Vsearch command “-cluster_unoise.” zOTUs were subjected to chimera filtering by UCHIME-denovo, followed by UCHIME-reference in Vsearch. Finally, a community composition matrix was generated by remapping of merged and quality-filtered reads to the chimera-free set of zOTUs. Community composition data analysis was performed using vegan v.2.5-6 [32] and phyloseq [33]. For the analysis, zOTUs with read counts greater than 50 were selected to construct a count matrix. The taxonomy of each zOTU representative sequence was analyzed against the SILVA 16S rRNA database (version 138) in mothur v.1.43.0, with a probability cutoff set to 80%. To identify the taxonomic affiliation of bacterial zOTU to the genus level, nucleotide sequence analysis was performed using BLASTN (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>, accessed on 31 December 2025) and the GenBank database. Names of phyla were according

to the descriptions by Oren and Garrity [34]. Statistical analyses were performed in R. The rarefaction curves, ACE index (non-parametric species richness estimators), and the Shannon and Simpson indices were calculated to measure the alpha diversity. To minimize the influence of extremely low-abundance sequence variants, ASVs represented by fewer than 50 reads across the entire dataset were excluded prior to downstream analyses. Sensitivity analyses using both more stringent and more relaxed filtering thresholds produced nearly identical ordination patterns, indicating that the principal ecological conclusions were robust to the selected cutoff. For principal component analysis (PCA) and correspondence analysis (CA), zOTUs with relative abundance above 0.1% were plotted. Differences in bacterial community composition between lake groups were tested using PERMANOVA (adonis2, 999 permutations) based on Bray–Curtis dissimilarities. Homogeneity of multivariate dispersion was assessed using betadisper and a permutation test (PERMDISP). The Venn diagram was generated with R and the VennDiagram package. The top 60 abundant zOTUs were visualized using the R package pheatmap [35]. The zOTU counts were $\log_2(x + 1)$ transformed. The pairwise distance matrix computed using the Bray–Curtis dissimilarity index was used to cluster the zOTU profiles using UPGMA. The pairwise distance matrix was computed using the Bray–Curtis dissimilarity, and clusters were generated using affinity propagation followed by sample-based agglomerative clustering. One-way ANOVA (including ANOVA for unbalanced datasets) was used to assess differences in continuous environmental variables, alpha diversity metrics, and the abundances of individual microeukaryotic taxa between deep and shallow lakes. Prior to ANOVA, the assumptions of normality and homogeneity of variances were evaluated using the Shapiro–Wilk test on model residuals and Levene’s test, respectively. Variables that violated one or both assumptions were analyzed using the Kruskal–Wallis test. *p*-values were adjusted for multiple comparisons using the false discovery rate (FDR) procedure, and both raw and adjusted *p*-values were reported.

3. Results

3.1. Comparison of Environmental Characteristics

The analysis of physicochemical parameters was carried out at each sampling point during the period when the lakes were completely covered with snow, the thickness of which varied from 30 to 51 cm, while the ice thickness ranged from 80 to 120 cm (Table S3). When comparing the environmental parameters, all samples were divided into two groups according to the heterogeneity of the origin and morphometric parameters of the lakes. The first group (Deep) included samples from deep-water lakes of tectonic–glacial origin Labyntyr (LL) and Vodorazdelnoye (LVR), as well as from the connected Labyntyr River (LR). The second group (Shallow) included the remaining samples from shallow lakes: thermokarst Myamichi (LM), glacial Ulu (LU), and cirque Dead (LD). ANOVA analysis and Kruskal–Wallis test (Table S4) revealed no differences in the values of physical (ANOVA *p*-value: 0.42–0.74; Kruskal–Wallis *p*-value: 0.57–0.91), chemical (ANOVA *p*-value: 0.42–0.83; Kruskal–Wallis *p*-value: 0.19–1) and biological (ANOVA *p*-value: 0.08 to 0.93; Kruskal–Wallis *p*-value: 0.24–0.67) parameters between the Deep and Shallow group samples and showed their ecological homogeneity (Figure 2).

The measured parameters showed considerable variation across all samples, with the full range of values presented in Figure S1. In particular, these were the concentrations of phosphate (0.168 mg L^{-1}), total nitrogen (2.847 mg L^{-1}) and phosphorus (0.072 mg L^{-1}) in sample LVR22; nitrate (1.243 mg L^{-1}) and organic matter ($30.788 \text{ mgC L}^{-1}$) concentrations in sample LD21; and ammonium ion (0.264 mg L^{-1}) content in sample LM21. The minimum silicon (0.11 mg L^{-1}) concentration was also found in sample LVR22. In the phytoplankton of all the studied lakes, representatives of Bacillariophyta dominated, subdominants were

Chrysophyta, Chlorophyta, Cryptophyta, and in smaller quantities Cyanobacteria, Dinophyta, Charophyta, Haptophyta and Euglenophyta were detected. The total abundance and biomass of phytoplankton were highest in samples LD21 (360×10^3 cells L^{-1} and 174 mg m^{-3}) and LU22 (526×10^3 cells L^{-1} and 316 mg m^{-3}). Total bacterial abundance (TBA) was low in most samples and ranged from 0.1×10^6 to 1.0×10^6 cells mL^{-1} , with the highest values 3.0×10^6 cells mL^{-1} determined in sample LD21 (Table S3).

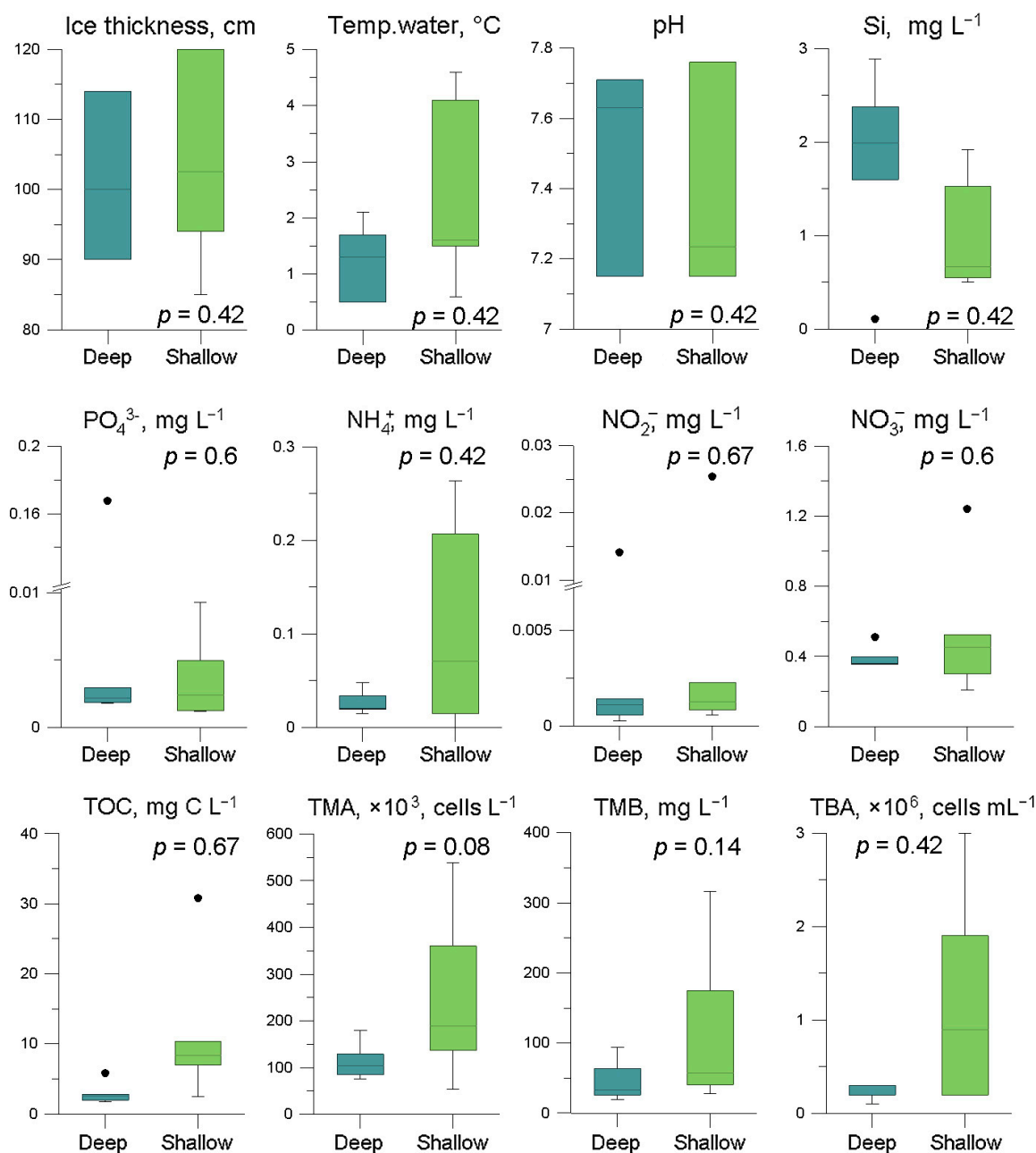


Figure 2. Comparison of physicochemical parameters, quantitative indicators of microalgae and bacteria from Shallow and Deep lakes. The values on the Y axis for the PO_4^{3-} and NO_2^- parameters have a gap (two stripes on the axis) due to the large difference in values between the groups.

3.2. Bacterial Diversity

Metabarcoding of the V3-V4 region of the 16S rRNA gene for 13 samples yielded 225,020 reads, with an average of 18,955 per sample (sequencing depth varied from 10,165 to 35,500). They were grouped into 829 zOTUs (146 to 248 zOTUs in each sample), of which 88% were identified at the phylum level and 25% at the genus level. Rar-

efaction curves calculated for all samples reached saturation (Figure S2), indicating that the number of reads was sufficient to estimate bacterial richness. ANOVA of the taxonomic richness indices (ACE) ($F = 1.06$; p -value = 0.37) and diversity (Shannon ($F = 2.64$; p -value = 0.33), Simpson ($F = 3.96$; p -value = 0.33)) of bacterial communities revealed no significant differences between samples from the Deep and Shallow groups (Table S4, Figure 3A).

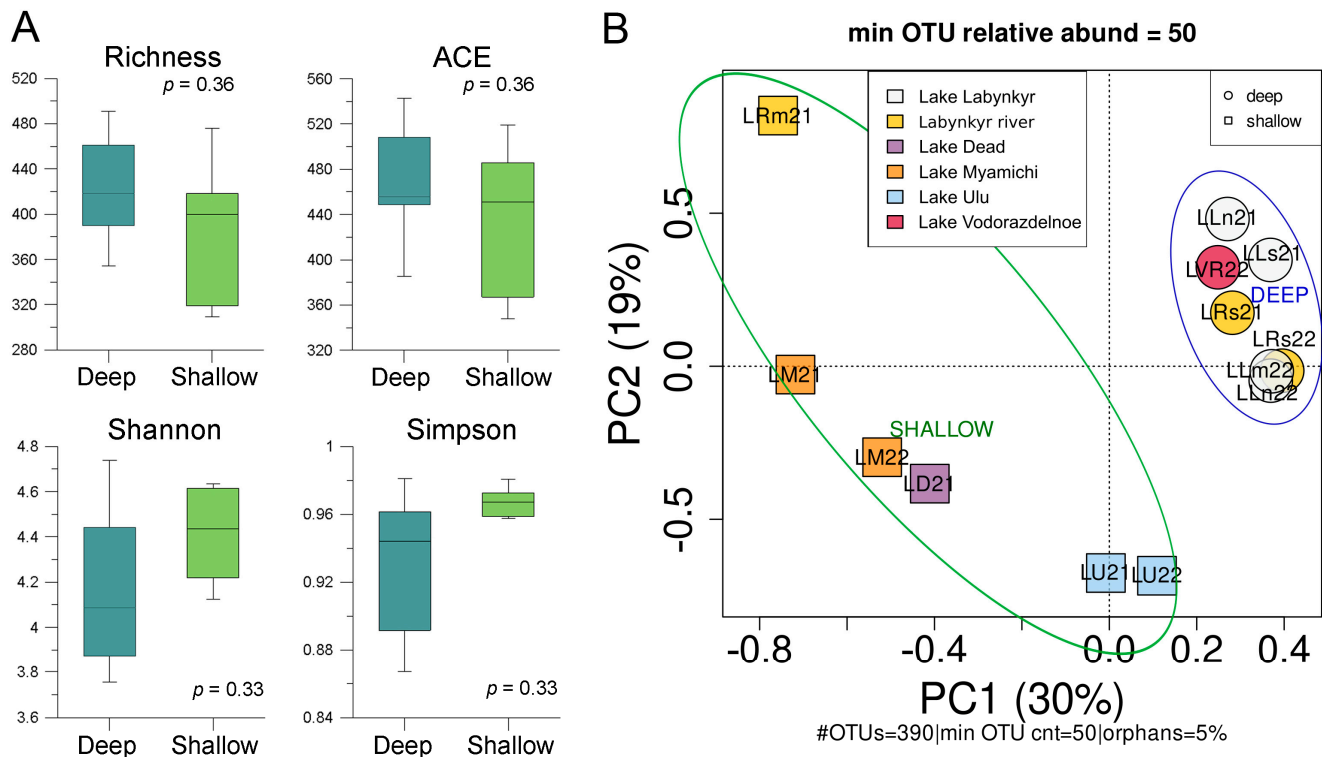


Figure 3. Comparison of bacterial diversity in Deep and Shallow lakes. (A) Diversity and richness indices; (B) principal component analysis (PCA) ordination of log-transformed zOTU abundance values ($\log_2(x + 1)$); PCA shows tight clustering of Deep group samples (Bray–Curtis distance < 0.2).

Exploratory analysis revealed high intragroup similarity of the Deep group, as well as the aggregation of Shallow group communities into a more diffuse cluster (Figure 3B). Bacterial community composition differed significantly between deep and small lakes (PERMANOVA based on Bray–Curtis dissimilarities, pseudo- $F = 3.29$, $R^2 = 0.230$, $p = 0.007$). The multivariate dispersion did not differ between lake groups (PERMDISP, $F = 0.19$, $p = 0.74$), indicating that the observed differences reflected shifts in community composition rather than differences in within-group variability. One shallow lake sample (LRm21) showed a distinct community composition characterized by increased abundances of methanotrophic taxa (*Methylobacter* and *Methylobacter*), resulting in its separation from the remaining deep lake samples in unconstrained ordinations (Figure 3B) and hierarchical clustering (Figure S3). Because LRm21 showed an unusual community composition, we repeated the PERMANOVA after excluding this sample. The results remained significant and even showed a stronger separation between lake types (R^2 and pseudo- F increased from 0.23 to 0.33 and from 3.2 to 4.91, respectively, $p = 0.004$), indicating that the observed differences were not driven by a single outlying sample.

According to the Venn diagrams, the proportions of shared 15% (125 zOTUs) and unique zOTUs 14.6% (121 zOTUs) for all lakes were approximately the same, with the highest number of unique zOTUs found in LU (Figure 4A). Samples from the Deep group contained 288 common zOTUs and 38 unique zOTUs, while samples from the Shallow

group contained 225 zOTUs and 21 zOTUs, respectively. When comparing deep and shallow lakes, the number of shared zOTUs was shown to be higher between Shallow LM, LU, LD and Deep LL communities than with Deep LVR. Also, the highest number of common zOTUs from samples from both groups was detected in LU samples, and the lowest number in the LVR sample (Figure 4A). Comparison of samples collected from different parts of the LL, as well as from the mouth and source of the LR, revealed 127 zOTUs shared and 27 zOTUs unique to all samples (Figure 4B). However, greater similarity was found between LL and LR_s (209 zOTUs common), less similarity between LL and LR_m, and, accordingly, the maximum number of unique zOTUs (24) was shown in LR_m.

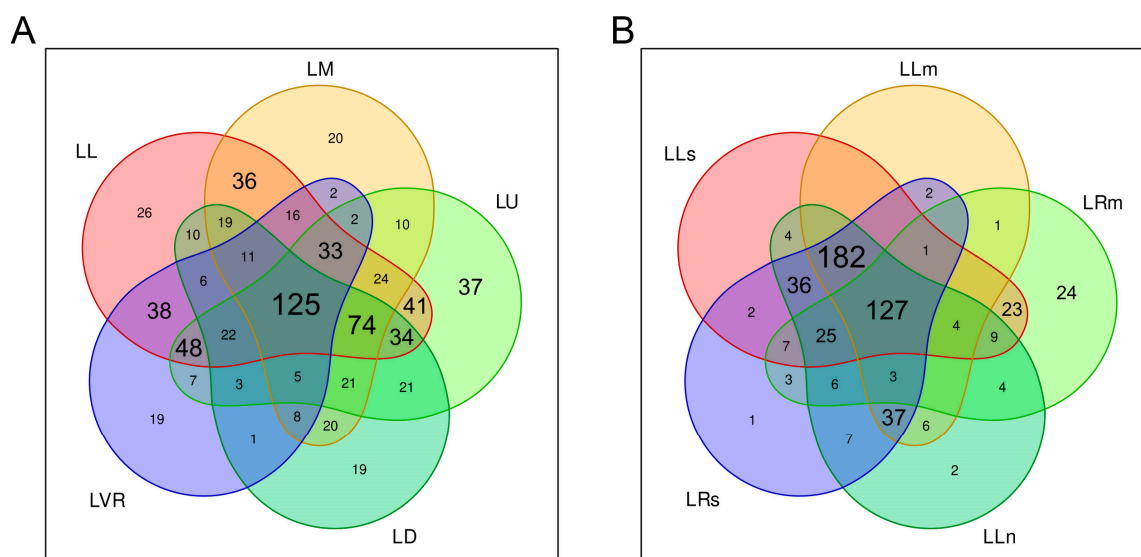


Figure 4. Venn diagrams showing the numbers of shared and unique zOTUs in under-ice communities: (A) samples taken from the lakes Labyntyr (LL), Vodorazdelnoe (LVR), Myamichi (LM), Ulu (LU), Dead (LD); (B) samples taken from the lake LL, mouth (LR_m) and source (LR_s) of the Labyntyr River.

3.3. Structure of Bacterial Communities

A total of 31 phyla were classified in the Bacteria domain, of which *Pseudomonadota* (20–56%), *Actinomycetota* (17–44%), and *Cyanobacteria* (0.1–35%) dominated in all samples, with *Verrucomicrobiota* (1–21%), *Bacteroidota* (2–13%), and *Planctomycetota* (0–9%) being subdominants. The relative abundance of the minor phyla *Bacillota*, *Chloroflexota*, *Acidobacteriota*, *Patescibacteria* was no more than 0.8–2%; phyla with a threshold below 0.8% were classified as “other” (Figure 5A). The dominant *Pseudomonadota* and *Actinomycetota* were distributed relatively evenly across all the samples studied. *Pseudomonadota* was most abundant in LL_m22, LR_s22, and LR_m21 (Figure 5B), while *Actinomycetota* was found in smaller proportions in these samples (Figure 5C). The highest relative abundance of dominant *Cyanobacteria* was observed in samples from the Deep group (LL_n21, LL_s21, LR_s21), in a smaller proportion in samples from the Shallow group (LM21, LU21, LU22, LD21) and in minimal quantities were found in the LM22 sample (Figure 5D). A uniform distribution of relative abundance was found for the subdominant phyla, with the highest proportion of *Verrucomicrobiota* in LVR22 (Figure 5E), *Bacteroidota* in LL_n22 (Figure 6A), and *Planctomycetota* in LD21 (Figure 6B). In contrast, the highest proportion of minor phyla was observed only for individual samples or groups of samples, namely, *Bacillota* were abundant in two samples (LR_s22 and LVR22), *Chloroflexota* were mainly distributed in Shallow group samples (LM21, LM22, LU21, LU22, LD21) (Figure 6C), *Patescibacteria* were most abundant in LVR22, and *Acidobacteriota* in LM22 (Figure 5A).

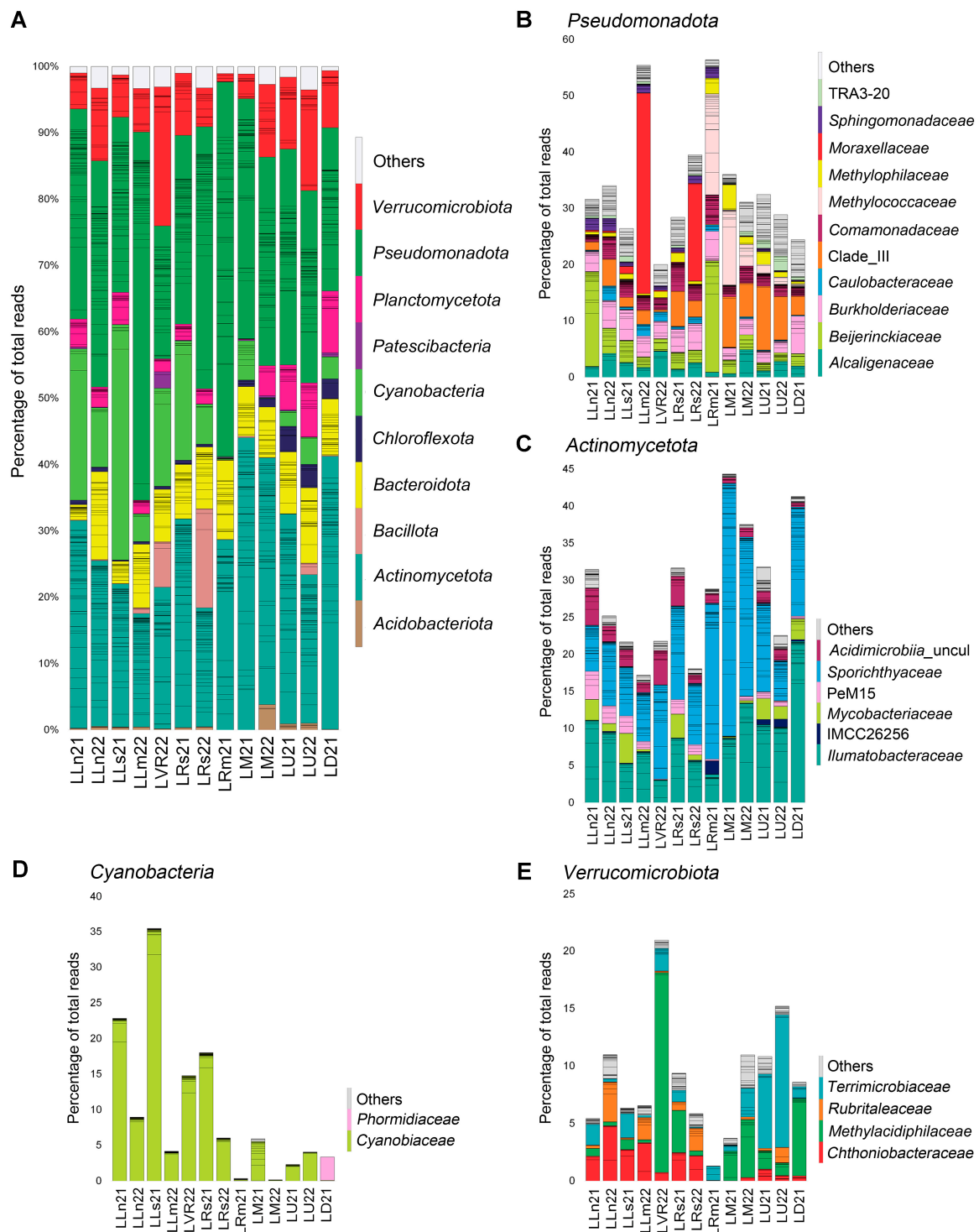


Figure 5. Structure of bacterial communities in ice-covered lakes showing zOTUs relative abundances at (A) phylum and family level for *Pseudomonadota* (B), *Actinomycetota* (C), *Cyanobacteria* (D), and *Verrucomicrobiota* (E), individual zOTUs are separated by black lines.

The highest richness of zOTUs of the dominant phyla *Pseudomonadota* (Figure 5B) and *Actinomycetota* (Figure 5C) was shown in the Deep group and differed in composition from the Shallow group. Even greater differences in community composition were found at the family level. However, some families were abundant and had a relatively homogeneous distribution in all samples, such as *Burkholderiaceae*, *Alcaligenaceae*, *Comamonadaceae*, *Sporichthyaceae*, *Ilumatobacteraceae* and *Acidimicrobia_uncultured*. The relative abundance of *Beijerinckiaceae* representatives was higher in the Deep group, while the proportion of

Clade_III and *Methylophilaceae* representatives was higher in the Shallow group samples. *Moraxellaceae* representatives dominated in two similar zOTUs samples (LLm22 and LRs22), *Methylococcaceae* zOTUs were predominantly represented in samples LR21 and LM21, and *Mycobacteriaceae* zOTUs were not detected in samples LRm21 and LVR22. The dominant phylum *Cyanobacteria* (Figure 5D) was represented by *Cyanobiaceae* everywhere and in a higher proportion in the samples of the Deep group, and *Phormidiaceae* were detected only in the sample LD21 from the Shallow group. The highest zOTU diversity among the subdominant phyla was found in *Bacteroidota* (Figure 6A). Within this phylum, the four most abundant *Chitinophagaceae*, *Crocinitomicaceae*, *Aurantibacillaceae* and *Spirosomaceae* were present in varying proportions in each sample. A division into groups based on the abundance of families from the phylum *Verrucomicrobiota* (Figure 5E) and *Planctomycetota* (Figure 6B) was also revealed. Namely, representatives of *Chthoniobacteraceae*, *Rubritaleaceae* and *Pirellulaceae* dominated in the samples of the Deep group, and *Terrimicrobiaceae* and *Gemmataceae* in the samples of the Shallow group. At the same time, representatives of *Methylacidiphilaceae* were the most abundant in two samples from Shallow LD21 and Deep LVR22.

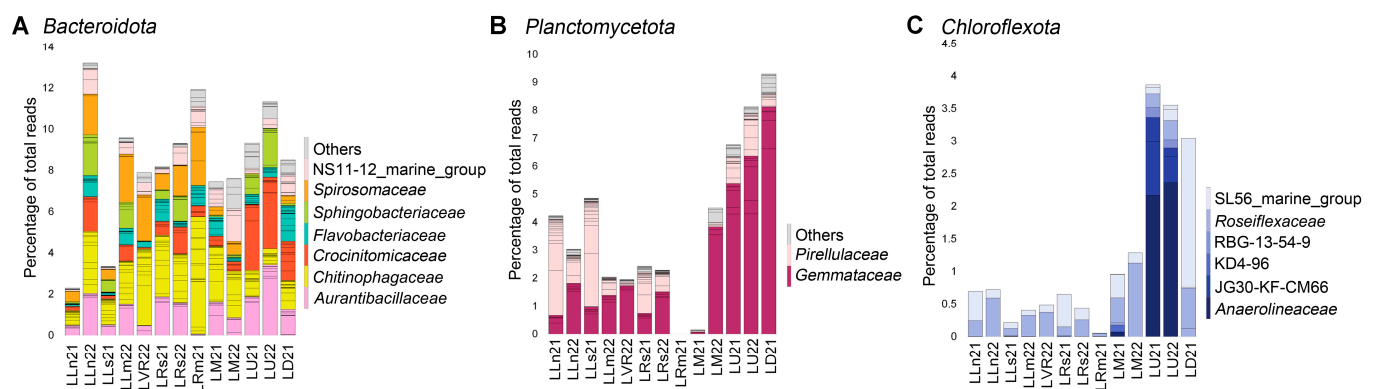


Figure 6. Structure of bacterial communities in ice-covered lakes showing zOTUs relative abundances at family level for *Bacteroidota* (A), *Planctomycetota* (B), and *Chloroflexota* (C); individual zOTUs are separated by black lines.

3.4. Relationships of Communities of Deep and Shallow Lakes

The beta diversity of bacterial communities based on identified zOTUs is represented by PCA (Figure 3B) and CA (Figure 7) plots.

As can be seen, the seven samples from the Deep group are quite closely clustered together despite being collected in different years. The other group consists of samples from shallow lakes that are widely spaced. It should be noted that the LU samples are relatively equidistant from the Deep and Shallow groups, and rather occupy an intermediate position between them. Finally, the LR mouth sample is located separately from both groups. The heat map clustering results confirm the division of the communities into two groups and the isolated position of the LRm21 sample (Figure S3).

The community composition differed markedly between deep and shallow lakes (Figure 7). At the phylum level, *Cyanobacteria*, *Actinomycetota*, and *Pseudomonadota* dominated across all samples, but their relative abundances shifted consistently with lake depth. Notably, shallow lakes were enriched in taxa associated with high-light, benthic, and methane-rich conditions (e.g., SAR11 Clade III, *Methylobacter*, *Gemmataceae*), whereas deep lakes harbored higher proportions of cyanobacteria (*Cyanobium_PCC-6307*) and methanotrophs (*Methylacidiphilaceae*). The full taxonomic composition, including percentages for all major zOTUs, is presented in Table 1. Some abundant zOTUs in subdominant and minor phyla were not detected in all samples or were represented by less than 0.01%, which

[illegible]

Table 1. Relative abundance (%) of the 50 most abundant phylotypes of identified in under-ice bacterial communities of subarctic lakes. The color shading of cells indicates the relative abundance of each taxon. Color intensity is calculated relative to the maximum value in the entire table (not for each column separately).

LL	LVR	LRs	LRm	LM	LU	LD	Phylum	Phylotype
4.8	10.8	7.0	16.3	20.0	7.6	11.1	<i>Actinomycetota</i>	<i>Candidatus_Planktophila</i>
8.2	3.1	6.9	3.9	10.0	10.4	21.8	<i>Actinomycetota</i>	<i>Ilumatobacter</i>
23.1	14.7	10.6	0.2	3.6	2.9	0.1	<i>Cyanobacteria</i>	<i>Cyanobium_PCC–6307</i>
0.7	17.3	1.7	0.0	3.4	1.4	6.7	<i>Verrucomicrobiota</i>	<i>Methylacidiphilaceae</i>
6.3	0.2	0.7	19.7	1.2	0.1	0.0	<i>Pseudomonadota</i>	<i>Methylobacterium-Methylorubrum</i>

Table 1. Cont.

LL	LVR	LRs	LRm	LM	LU	LD	Phylum	Phylotype
4.5	3.1	4.5	5.2	2.4	2.0	6.6	<i>Pseudomonadota</i>	<i>Polynucleobacter</i>
2.1	0.3	4.2	0.1	7.9	9.9	3.4	<i>Pseudomonadota</i>	Clade_III
0.1	0.0	0.0	16.8	9.6	1.1	0.2	<i>Pseudomonadota</i>	<i>Methylobacter</i>
1.9	1.8	3.0	4.5	8.9	2.0	2.4	<i>Actinomycetota</i>	<i>Sporichthyaceae</i>
1.0	1.7	1.2	0.0	1.4	5.7	8.1	<i>Planctomycetota</i>	<i>Gemmataceae</i>
5.2	0.2	10.6	0.0	0.0	0.0	0.0	<i>Pseudomonadota</i>	<i>Acinetobacter</i>
2.5	4.6	2.1	0.9	1.4	1.8	1.5	<i>Pseudomonadota</i>	GKS98_freshwater_group
0.1	5.8	7.3	0.0	0.0	0.5	0.0	<i>Bacillota</i>	<i>Paenisporosarcina</i>
1.5	0.0	0.4	0.2	0.9	8.4	0.8	<i>Verrucomicrobiota</i>	<i>Terrimicrobium</i>
1.0	3.0	2.1	1.6	1.9	0.7	1.1	<i>Bacteroidota</i>	<i>Sediminibacterium</i>
2.7	0.0	1.7	0.0	0.2	2.4	2.8	<i>Actinomycetota</i>	<i>Mycobacterium</i>
1.9	4.3	1.6	0.5	0.5	0.3	0.2	<i>Actinomycetota</i>	<i>Acidimicrobiia</i>
0.7	1.1	1.0	0.2	3.3	1.8	0.5	<i>Pseudomonadota</i>	<i>Candidatus_Methylopumilus</i>
1.9	0.3	1.5	0.0	1.2	1.3	2.2	<i>Pseudomonadota</i>	<i>Beijerinckiaceae</i>
0.8	0.5	1.7	0.1	1.4	2.5	1.3	<i>Bacteroidota</i>	<i>Aurantibacillaceae</i>
0.9	2.1	1.2	2.8	0.5	0.0	0.4	<i>Bacteroidota</i>	<i>Pseudarcicella</i>
0.5	0.1	0.9	0.5	0.5	3.6	1.9	<i>Bacteroidota</i>	<i>Fluviicola</i>
2.9	0.7	2.3	0.0	0.1	0.8	0.3	<i>Verrucomicrobiota</i>	<i>Chthoniobacter</i>
0.9	0.6	1.3	1.9	0.8	0.8	0.4	<i>Pseudomonadota</i>	<i>Limnohabitans</i>
0.9	0.7	1.6	0.9	0.8	0.9	0.7	<i>Pseudomonadota</i>	<i>Comamonadaceae</i>
2.7	0.1	1.6	0.2	0.3	0.9	0.4	<i>Actinomycetota</i>	PeM15
0.3	0.5	0.4	3.6	0.4	0.3	0.3	<i>Bacteroidota</i>	<i>Ferruginibacter</i>
2.9	0.2	1.0	0.0	0.1	1.2	0.5	<i>Planctomycetota</i>	<i>Pirellulaceae</i>
0.3	0.3	0.6	2.1	0.7	0.4	0.7	<i>Pseudomonadota</i>	<i>Rhodoferrax</i>
0.2	2.7	1.1	0.0	0.0	1.1	0.0	<i>Deinococcota</i>	<i>Deinococcus</i>
0.3	0.3	0.6	1.0	0.7	0.5	1.7	<i>Bacteroidota</i>	<i>Flavobacterium</i>
0.3	0.6	0.6	1.0	1.1	0.3	1.0	<i>Bacteroidota</i>	<i>Sphingobacteriales</i>
0.8	0.2	1.3	0.1	0.6	0.3	0.7	<i>Verrucomicrobiota</i>	<i>Luteolibacter</i>
0.6	0.0	0.4	0.1	0.4	1.6	0.6	<i>Pseudomonadota</i>	<i>Burkholderiales</i>
0.0	2.0	0.0	1.0	0.3	0.0	0.3	<i>Verrucomicrobiota</i>	FukuN18_freshwater_group
0.1	2.5	0.1	0.0	0.1	0.2	0.6	<i>Patescibacteria</i>	<i>Saccharimonadales</i>
0.2	0.1	0.3	0.0	0.3	0.2	2.3	<i>Chloroflexota</i>	SL56_marine_group
0.0	0.0	0.0	0.0	0.0	0.0	3.3	<i>Cyanobacteria</i>	uncultured
0.7	0.0	0.9	0.0	0.1	1.2	0.1	<i>Bacteroidota</i>	<i>Pedobacter</i>
0.1	0.0	0.1	1.8	0.0	0.9	0.2	<i>Actinomycetota</i>	IMCC26256
0.8	0.2	0.3	0.1	0.2	1.1	0.2	<i>Actinomycetota</i>	<i>Gaiellales</i>
0.1	0.7	1.6	0.0	0.0	0.5	0.0	<i>Bacillota</i>	<i>Bacillus</i>
0.8	0.2	0.2	1.1	0.1	0.3	0.1	<i>Pseudomonadota</i>	<i>Sphingomonas</i>
0.0	0.0	0.0	2.6	0.0	0.0	0.0	<i>Pseudomonadota</i>	<i>Methylothera</i>
0.3	0.7	0.1	0.0	0.0	0.9	0.5	<i>Pseudomonadota</i>	<i>Legionella</i>
0.3	0.4	0.2	0.0	0.7	0.2	0.7	<i>Chloroflexota</i>	uncultured
0.5	1.2	0.3	0.4	0.0	0.0	0.0	<i>Pseudomonadota</i>	<i>Brevundimonas</i>
0.7	0.0	0.7	0.0	0.9	0.0	0.0	<i>Armatimonadota</i>	<i>Armatimonas</i>
0.3	0.5	0.3	0.0	0.4	0.2	0.7	<i>Pseudomonadota</i>	<i>Rhizobiales</i>
0.3	1.7	0.3	0.0	0.0	0.0	0.0	<i>Pseudomonadota</i>	FukuN57

4. Discussion

4.1. Heterogeneity of Lake Basins and Homogeneity of the Environment

The subarctic and arctic regions are experiencing rapid changes due to global warming, accompanied by thawing and erosion of permafrost. All the lakes under study are located on the Oymyakon Upland, which has been subject to glacial activity from the southern Suntar-Khayata Mountains [36]. The lakes we studied were divided into two groups according to their types of origin and average depths. It is known that in deep and shallow lakes, vertical and horizontal mixing processes responsible for the transport and distribution of dissolved substances and organisms differ [37]. Such processes are controlled by differential heating of water, which is caused by heat from bottom sediments and by penetration of solar radiation associated with variability of ice and snow cover [1].

Samples from deep lakes of tectonic–glacial origin (LL, LVR) and the associated LR were assigned to the Deep group. In large and deep lakes, heat retention from sediments is less important for lake-wide circulation, while solar radiation-driven circulation dominates throughout the ice-covered period [38]. The Shallow group included samples from shallow lakes of thermokarst and glacial origin. It is known that LU and LD were initiated by glacier retreat during MIS 3 (Marine Isotope Stage 3). Glacial (moraine) deposits are present throughout the catchment, indicating that the area was influenced by historical glacial activity [25]. Global warming has been shown to increase both the rate and extent of glacier melt in high-latitude and high-altitude regions. These processes can influence microbial communities, affecting the abiotic and biotic characteristics of lakes. For example, increased turbidity due to mineral particles brought in with meltwater causes limited light penetration into the water, changing conditions for primary producers and further indirectly affecting microbial communities [39]. In addition, the microbial diversity of glacier-fed lakes may be altered by species introduced from glacial water [40,41], soil [42] and meltwater from permafrost [43]. LM is the largest in the group of the Small Labyntyr Lakes, which were formed as a result of the permafrost melting, with the resulting basins filled with meltwater and sediment. Numerous thermokarst lakes represent an important aquatic environment type in arctic and subarctic regions [44,45] and are considered as biogeochemical hotspots in the permafrost landscape. It has been shown that rapid thawing of permafrost beneath thermokarst lakes could more than double the rate of carbon release from these numerous northern lakes by the end of the century [46]. Microbial communities in them are similar to communities in other freshwater lakes, but are enriched with microorganisms from the methane cycle [47,48].

This study showed that the physical and chemical parameters of water samples collected from five long-term ice-covered subarctic lakes in April of different years (2021 and 2022) were relatively similar. This observation can be explained by the influence of the seasonality factor of the ice cover period on the ecology of lakes in the studied region and by extremely low winter temperatures. The gradient of environmental factors is observed in different lakes during the open water period, as it depends on atmospheric exchange, meteorological conditions and exposure to sunlight. By contrast, the influence of these factors is either absent or greatly reduced when lakes freeze during the cold season [1], which lasts eight or more months of the year in the north.

These conditions determine the homogeneity of environmental parameters at the end of the long ice cover period of lakes that differ in morphotype and are geographically distant from each other. This stability of environmental factors is similar to trends observed by Butler et al. [11] in a freshwater reservoir during a sustained ice-covered period. Despite the similarity of environmental conditions, the studied lakes have significant differences in morphometric characteristics and the genesis of lake basins, which play an important role in the formation of the structure of microbial communities [49].

4.2. Comparison of Bacterial Structure of Subarctic Lakes

We showed that cold-tolerant or resistant *Pseudomonadota*, *Actinomycetota*, *Cyanobacteria*, *Verrucomicrobiota*, *Bacteroidota* in lakes of Eastern Yakutia covered by ice for a long time were the majority. According to previous studies of under-ice bacterial communities in lakes located in the subarctic region of Canada [7,17], arctic lakes in West Greenland [15], the Himalayan Tsomgo lake [13], Lake Baikal in Eastern Siberia [19,20], lakes in the Hoh Xil region of northern Qing–Tibetan Plateau [2], many of the bacterial phylotypes identified there were also found in the lakes we studied. It is generally recognized that microbial communities are unbalanced: a small number of species are extremely abundant and are called the “abundant biosphere”, while a large number of species are low in abundance and are called the “rare biosphere” [50]. Abundant microorganisms make up the majority of the microbial biomass, whereas rare microorganisms exist to maintain microbial diversity. We showed that common abundant taxa have different relative abundances in subglacial bacterial communities of different types of subarctic lakes.

In our work, the genus *Candidatus_Planktophila* turned out to be the most abundant and common for all the under-ice communities. These bacteria from *Actinomycetota* (acl) are widespread in freshwater ecosystems and have very small cells with very small genome sizes (1.2–1.4 Mbp). Genomic analysis of acl actinobacterial cultures from Lake Zurich revealed a surprising diversity of their metabolic pathways, especially carbohydrate transport and metabolism [51]. The authors showed that the process of genome optimization resulted in a high degree of auxotrophy for various vitamins, amino acids and reduced sulfur. Such microdiversification of the acl actinobacterial genotype may explain their global success in the oligotrophic freshwater environments we studied. *Ilumatobacter* zOTUs and *Polynucleobacter* zOTUs were also common and abundant in all samples. These phylotypes are abundant representatives of bacterioplankton in freshwater lakes, and their composition can be regulated by dissolved organic matter produced by phytoplankton [20,52]. We showed that the under-ice phytoplankton in all studied lakes was characterized by the dominance of centric diatoms of the genera *Pantocsekiella* and *Lindavia*. It is known that winter phytoplankton can reach high abundance [53], and centric diatoms are one of the main producers of dissolved organic matter in ice-covered water bodies [4,19,54,55]. Thus, the dissolved organic matter of diatoms supports the growth of these groups of heterotrophic bacteria, which may explain their abundance in the lakes we studied.

PCA and CA based on bacterial community composition showed a close grouping of LL, LVR, and LRs samples from the Deep group from the rest of the samples. This group shared zOTUs with the picocyanobacterium *Cyanobium_PCC*–6307, which dominated in abundance in all samples, with a maximum of 23% in LL. *Cyanobium* has been described as the dominant genus in various studies, including in the North Patagonian Andean lakes (between 900 and 1950 m a.s.l.) [56]. *Cyanobacteria* have been shown to be metabolically active in cold habitats [57] and also provide nitrogen and organic matter to heterotrophic microorganisms, thereby influencing their diversity. We have also previously identified *Cyanobium_PCC*–6307 in under-ice communities both in LL and in the nearby deep-water Lake Vorota, the abundance of which increased from April and reached its maximum values in early June [5]. Considering that the abundance of this taxon was shown over several cold seasons (2016, 2017, 2021, 2022) in deep-water lakes of the study region, it can be assumed that picocyanobacteria *Cyanobium_PCC*–6307 is well adapted to low temperatures and higher light intensity, which allows their active development under ice. For example, Møller et al. [58] found high abundance of cold-adapted GpI *Cyanobacteria* in snow and freshwater samples at Station Nord in north-eastern Greenland.

However, despite the general similarity of the Deep group communities, each of them contains zOTUs that are present in significant numbers in only one or two samples, while

in the remaining samples their proportion was no more than 3% or they were completely absent. Thus, representatives of *Verrucomicrobiota* from the *Methyloacidiphilaceae* were found in the largest proportion (17.3%) in LVR, while the smallest amount was in LRm (0.03%). High abundances of *Verrucomicrobiota* have been found in many freshwater ecosystems, including systems in the Arctic and in lakes under ice [15,16,20,59]. Their presence is due to their resistance to UV light and their ability to dissolve organic matter. Some studies suggest that *Verrucomicrobiota* abundance is facilitated by high nutrient availability, particularly in ecosystems with high phosphorus content [60]. Among the Deep group samples, the most abundant were representatives of *Acinetobacter* (*Pseudomonadota*) in LL (5.2%) and LRs (10.6%), and the main proportion of zOTU *Paenisporosarcina* (*Bacillota*) belonged only to LVR (5.9%) and LRs (7.3%) among all the studied samples. Interestingly, abundant zOTU *Acinetobacter* was found, bacteria of this genus are inhabitants of freshwater ecosystems, wastewater and activated sludge, and have also been isolated from various animal sources and humans [61]. *Acinetobacter* has attracted increasing attention in recent years due to their rapid transformation rate, development of resistance to a wide range of antibiotics and disinfectants, survival during desiccation, and persistence in the environment for long periods of time. Some members of the genus play an important role in improving the biological removal of phosphorus in wastewater and demonstrate hydrocarbon decomposition capacity. However, despite the remarkable capabilities of these bacteria [62], their properties and adaptation to cold environmental conditions have not been examined in detail. Representatives of the zOTU *Paenisporosarcina* identified here have been isolated from cold habitats, including soil near the Pindari glacier of the Himalayan mountain ranges [63] and King George Island, West Antarctica [64]. Such data confirm the important contribution of these taxa to Deep group communities due to the peculiarities of their metabolism under conditions of constantly low temperatures.

Samples from the Shallow group were widely spaced in the PCA plot, indicating less similarity between the communities of these samples. This is supported by the lower number of shared zOTUs in the Venn diagram and cluster analysis. Moreover, the similarity of communities from Shallow group samples was determined by less abundant taxa from dominant and subdominant phyla. Commonly abundant among all Shallow group samples was zOTU Clade_III, which is part of the SAR11 clade of Alphaproteobacteria. The SAR11 clade is a group of highly successful marine pelagic bacteria, among the most abundant in aquatic environments, comprising approximately 25% of planktonic cells in the upper regions of the photic zone [65]. It contains a recently diverged freshwater clade (subtype III), which, due to its close relationship to the saltwater SAR11 lineages, allows comparative studies of the population dynamics of bacteria that have shifted their ecological niche from the open oceans to physically restricted lake ecosystems [66]. Freshwater bacteria LD12 from the SAR11 group, identified for the first time in an Arctic lake, make up 1% to 21% of freshwater bacterioplankton [66]. Ultramicrobacteria LD12 not only have similar phenotypic and metabolic features to their sister group, the marine genus *Pelagibacter*, but also appear to thrive in a similar spatiotemporal niche in freshwaters, as shown in prealpine lakes [67]. These processes of transition to freshwater ecological niches and changes in metabolic characteristics of SAR11 representatives explain their abundance in the communities we observed.

Planctomycetota included common zOTUs of the family *Gemmataceae* and were more abundant in the two geographically close lakes LU and LD. The ecological functions of *Gemmataceae* are poorly understood to date, but these planctomycetes are ubiquitous and are less abundant bacteria in freshwater ecosystems. *Gemmataceae*, among others, have been found in large numbers under ice [11,68] and include cold-adapted psychrotolerant taxa [69]. Similarly to more abundant bacterial groups in aquatic systems, planctomycetes

representatives consist of a small number of abundant and common zOTUs and a large number of low-abundance zOTUs [70]. Among the dominant phyla, abundant zOTUs of *Methylobacter* (*Pseudomonadota*) and *Sporichthyaceae* (*Actinomycetota*) were associated with LM samples, while zOTUs of *Terrimicrobium* (*Verucomicrobiota*) were found in the highest proportion (8.4%) in LU samples. The abundance of methanotrophic *Methylobacter* is not surprising, as they are common in stratified lakes and generally contribute significantly to bacterial production, even more so in winter [68]. *Sporichthyaceae*, like many actinomycetes, have a substrate-dependent plastic strategy for using organic matter with a preference for low-molecular-weight carbon sources obtained from microalgae [71]. The abundance of phytoplankton shown in our study may well be a source of nutrition for these bacteria. Actinomycetes from this family have been described as facultative anaerobes and are predominantly representatives of the soil biosphere [72,73], which explains their abundance in shallow LM due to the possible influx of microorganisms from bottom sediments.

Among all the communities, LRm occupies a special position; the sample was collected at the mouth of the Labyntyr River, which connects two lakes, flowing out of LVR and into LL. We hypothesized that these three interconnected water bodies could have similar community structure due to the introduction, from the lake into the river, and then from the river into the lake, of some bacterial taxa that had similar abundance during the period of under-ice development. However, the LRm community contained the highest number of unique zOTUs, and exploratory and cluster analyses showed no similarity to either Deep or Shallow group samples. The structure and diversity in LRm compared to other communities were characterized by the presence of abundant taxa, with the highest abundance of zOTUs *Methylobacterium-Methylorubrum* (19.7%), *Methylobacter* (16.8%) and lower abundance of zOTUs *Ferruginibacter*, *Rhodoferrax*, *Methylotenera*, as well as the absence of several common abundant taxa such as *Methylococcoides*, *Gemmataceae*, *Acinetobacter*, and *Paenibacillus*. The maximum abundance of *Methylobacterium-Methylorubrum* zOTUs, as well as *Methylobacter*, in LRm is explained by the differences in their habitats and potential interactions with the environment, most notably in the phycosphere. Sample LRm21 was collected from the river mouth at a depth of 2 m from the bottom, with aquatic vegetation present. *Methylobacter*, a widespread, abundant, and ecologically important genus of methanotrophs, is known to frequently inhabit areas near the soil surface [74], and methylobacterial members of the genus *Methylobacterium* are widespread in nature and are ubiquitous on plant surfaces, potentially dominating the phycosphere population [75]. Subglacial sediments are among the biggest contributors to global methane (CH₄) emissions. Seasonal and long-term climate change, as well as thermal acclimatization of methanotrophs, can have a significant impact on the global methane cycle. It has been shown that the effect of temperature on methane consumption is directly related to how different strains adapt their physiology during thermal acclimatization [74]. CH₄, which has a greenhouse warming potential (GWP) of approximately 28–30, is consumed by microbial methanotrophs. In winter, lake water is often supersaturated with methane, which can lead to massive methane release into the atmosphere after ice melt. However, for some lakes, prolonged ice cover can also reduce overall methane emissions by significantly increasing the time it takes for methane to reach the atmosphere, thus promoting more efficient microbial oxidation. As methane accumulates under ice, if a suitable electron acceptor, such as O₂, is available, the CH₄ will undergo oxidation. Microbial processes beneath the ice largely determine what will be emitted into the atmosphere after ice melt [1].

5. Conclusions

This study characterized bacterial communities in various subarctic lakes during the ice cover period. Environmental conditions were similar in lakes separated from each other

by location, and stability of environmental factors under ice cover was maintained over the same period (April) in two consecutive years. Extending a previous study of under-ice bacterial communities in the Northern Cold Pole region from Labyntyr and Vorota Lakes, the results of this work clearly show a closer similarity of composition in deep lake samples and less similarity among shallow lake samples. Common abundant taxa and rare taxa were identified for all samples, which obviously have an impact on the separation of Deep and Shallow community groups. It was also shown that the abundance of many taxa differed between samples in both community groups. This variation in the abundance of dominant taxa between the Deep and Shallow community groups during the ice cover period is likely attributable to the morphometric characteristics and origin of the lakes. These are the first results on the relationship between morphometry and the composition of microbial communities in different lakes of Yakutia (Pole of Cold region), and future studies with a larger sample and repeated sampling are needed to confirm the relative importance of morphometry as a factor.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/w18151890/s1>, Figure S1: Physicochemical parameters and quantitative values of microalgae and bacteria from ice-covered lakes, Figure S2: Bacterial diversity in water samples from ice-covered lakes, as characterized by rarefaction curves of zOTUs, Figure S3: Hierarchical clustering of $\log_2(x + 1)$ -transformed zOTUs counts. Rows, zOTUs; columns, samples. Clustering was performed on a matrix of Bray–Curtis dissimilarity, Table S1: Characteristics of the sampling site, Table S2: Characteristics of the DNA sampling, Table S3: Physical, chemical and biological characteristics of samples, Table S4: ANOVA and Kruskal–Wallis test between the parameters of Deep and Shallow groups of subarctic lakes.

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