

Bacterial Communities during the Period of Massive under-Ice Dinoflagellate Development in Lake Baikal

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Abstract—Taxonomic diversity of Lake Baikal bacteria during the period of massive under-ice development of dinoflagellate *Gymnodinium baicalense* was studied. During the ice-covered period in 2013, both the abundance and biomass of *G. baicalense* were several orders of magnitude higher than the values for previous years, the maximum values were 8.9×10^6 cells/L and 405 g/m³, respectively. The taxonomic structure of bacterial communities was determined using the data obtained by 454 pyrosequencing (Roche) with Mothur 1.19.0. Predominance of three phyla was revealed: *Bacteroidetes*, *Proteobacteria*, and *Actinobacteria*. Massive dinoflagellate development resulted in a considerable decrease in the richness and diversity of bacterial communities compared to the results of the earlier long-term studies.

Keywords: Lake Baikal, dinoflagellates, under-ice bacterial communities, taxonomic composition, pyrosequencing

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In the under-ice water systems at the water–ice interface, a complex dynamic environment is formed, in which microbial communities containing bacteria, microalgae, and dinoflagellates develop due to low temperature, under-ice currents, changes in the nutrient concentrations, and decreased illumination depending on the snow depth.

Dinoflagellates are unicellular organisms belonging to the *Alveolata* supertype, which are second after diatomic algae in formation of primary products in water reservoirs (Belyakova et al., 2006). The ice-covered period is characterized by massive dinoflagellate bloom both in marine (Spilling, 2007) and freshwater reservoirs (Phillips and Fawley, 2002), including Lake Baikal (Votintsev et al., 1975; Bashenkhaeva et al., 2015). Endemic species *Gymnodinium baicalense* Antip. and *Peridinium baicalense* Kiss. et Zwetkoff (Pomazkina et al., 2010) in Lake Baikal can be responsible for up to 65% of the annual primary phytoplankton production (Votintsev et al., 1975). Bacteria were also found in the under-ice community with dinoflagellates (Bowman et al., 1997); their total number was several orders of magnitude higher than that in the water column in spite of low temperature (Smith et al., 1989) due to intense development of microalgae at the water–ice interface.

Recent studies carried out under laboratory conditions revealed that interrelations between marine dinoflagellates and bacteria can be both symbiotic (Tilney et al., 2014) and antagonistic (Zhang et al.,

2015). Bacteria are necessary for growth and development of *G. catenatum* during the period from cyst germination to intense bloom (Bolch et al., 2011); they can also stimulate toxin production by this dinoflagellate species (Albinsson et al., 2014). It is known that dinoflagellates *Gymnodinium* sp. are able to use cyanobacteria *Synechococcus* sp. as a nutrition source (Jeong, 1999). We have earlier studied the composition and structure of bacterial under-ice communities with domination of different species of microscopic eukaryotes (Bashenkhaeva et al., 2015). Taxonomic composition of bacteria in the under-ice communities was found to be independent of the diatom or dinoflagellate species, but the relative abundance of predominant bacterial forms varied depending on both the place of sampling and the period of community development.

In the present work, we studied biodiversity of bacterial communities during the period of intense under-ice development of dinoflagellates *G. baicalense* in the South Basin of Lake Baikal using massively parallel pyrosequencing of the V3–V4 region of the 16S rRNA gene. The following questions were put forward: (1) whether certain bacterial taxa prevailed through the whole period of the dinoflagellate bloom and (2) whether the taxonomic composition of bacteria was changed during development of dinoflagellates in the under-ice communities of Lake Baikal.

MATERIALS AND METHODS

Sampling. Fifteen water samples were collected from the lower ice surface at four stations of the Bol'shie Koty region (southern Lake Baikal) in the littoral zone (LZ), 80 m from the shore (the lake depth was 5–40 m); the slope zone (SZ), 200 m from the shore (the lake depth was 250 m); in the deep-water zone (DWZ), 1 km from the shore (the lake depth was 600 m); and in the pelagic zone (PZ), 6 km from the shore (the lake depth was 1000 m). The samples were collected at the end of February (26.02), in the middle and at the end of March (13.03 and 28.03, respectively), and in the beginning of April (10.04) in 2013 (Table 1). Samples were collected by divers using syringes and dispensed into sterile 2-L bottles. At each station, an integral sample was taken from the area of 70–100 m².

Species composition, abundance, and biomass of dinoflagellates and microalgae were analyzed under an AxiostarPlus light microscope (Zeiss, Germany); calculations were carried out according to the earlier described conventional methods (Bashenkhaeva et al., 2015).

Isolation of total DNA was performed with the use of lysozyme, 10% sodium dodecyl sulfate (SDS), and phenol-chloroform extraction, as described earlier (Bashenkhaeva et al., 2015).

Pyrosequencing. Amplification of fragments of the 16S rRNA gene encoding the V3–V4 regions was carried out using the universal primers U341F (CCTAC-GGGRSGCAGCAG) and U785R (GGACTAC-CVGGGTATCTAAKCC); the program parameters were as follows: 96°C, 3 min; 96°C, 30 s; 55°C, 30 s; 72°C, 40 s (30 cycles); and 72°C, 10 min. The amplified fragments obtained in four replicates were combined. Pyrosequencing was performed on a GS FLX 454 sequencer (Roche, United States) using the reagents of Titanium series according to GS FLX Titanium Sequencing Method Manual following the manufacturer's instructions.

Analysis of pyrosequencing data was performed using Mothur 1.35.1 program (<http://www.mothur.org>). The obtained sequences were analyzed using the Pyronoise algorithm; to avoid errors, only sequences of over 150 bp were selected and aligned with bacterial 16S rRNA gene sequences from the Silva database [http://www.mothur.org/wiki/Silva_reference_files]. Preclusterization was performed by grouping the sequences which differed by two nucleotides. The chimeric sequences were revealed using the UCHIME algorithm with the standard parameters. Taxonomic analysis was carried out according to the Ribosomal Database Project (RDP) (Cole et al., 2009) at the confidence threshold of 80%. The obtained sequences were grouped into the operational taxonomic units (OTUs) with genetic distance of 0.03. The biodiversity indices Chao1 (richness) and Shannon (diversity) were calculated on the basis of

revealed OTUs. Taxonomic identification of 27 the most abundant OTUs (the total number of sequences was not lower than 276) was performed by their comparing with the 16S rRNA nucleotide sequences from the GenBank database using the BLASTN program (<http://blast.ncbi.nlm.nih.gov>). A phylogenetic tree was constructed by the Maximum Likelihood method using the Kimura two-parameter model and MEGA (version 6) program. The obtained sequences were deposited to the GenBank (SRA section) under accession number SRR3999046.

RESULTS

Species composition, abundance, and biomass of dinoflagellates. In the ice-covered period of 2013, the snow-covered ice surface in the littoral and slope zones comprised 80% at the end of February and March and 100% at the beginning of April; in the deep-water and pelagic zones, it was about 30–50%. In the under-ice communities, dinoflagellates *Gymnodinium baicalense* Antip. prevailed. At the end of February, the under-ice fouling was brownish black and formed structured lines on the lower surface of ice. In March, foulings began to move away from the ice surface; by the beginning of April, water was brown-colored at the depth of over 1 m from the ice surface, and a clearly defined border with transparent water layer was formed in the upper under-ice horizon. At the end of February, in the littoral zone, the *G. baicalense* biomass was 98.05 g/m³ and increased gradually up to the maximum (388.33 g/m³) at the beginning of April (Fig. 1, Table 1). In the slope and deep-water zones, biomass at the beginning of vegetation was 125.08 and 141.22 g/m³, respectively, decreased in the middle of March, and increased again by April up to the maximum of 405.01 and 283.6 g/m³, respectively. In the pelagic zone, biomass was the lowest at the beginning of March with the minimum value (2.18 g/m³), peaked at the middle of March (283.6 g/m³), and then decreased by the beginning of April.

It should be noted that diatomic algae *Aulacoseira baicalensis* (K.I. Meyer) Simonsen, which typically bloom in Lake Baikal during this period (Bondarenko et al., 2006; Popovskaya et al., 2011), were found in the deep-water zone only in one station at the end of February (Fig. 1, Table 1). The under-ice communities contained the following algae species as minor components (no more than 3%) dinoflagellates *G. coeruleum* Dogiel, *Peridinium baicalense* Kiselev & Cvetkov, and *P. euryceps* K. Rengefors & B. Meyer; diatoms *Nitzschia graciliformis* Lange-Bertalot & Simonsen, *Synedra acus* subsp. *radians* (Kütz.) Skabitsch., *A. islandica* (O. Müller) Simonsen, and *Cyclotella minuta* (Skvortzov) Antipova; green algae *Monoraphidium arcuatum* (Korshikov) Hindák, *M. contortum* (Thuret) Komárková-Legnerová, *M. griffithii* (Berke-

Table 1. Cell number and biomass of dinoflagellates *G. baicalense* and the data of pyrosequencing of the V3–V4 region of the 16S rRNA gene.

Sampling zone	Sampling date	Cell numbers, ×10 ⁶ cells/L	Biomass, g/m ³	Number of sequences	Genetic distance, 0.03			
					OTU	Chao1	Shannon index	Good coverage, %
Littoral zone (50 m from the shore)	26/02/2013	2.2	98.05	2622	142	303.65 (248.14; 406.46)	2.74 (2.69; 2.78)	98.9
	13/03/2013	3.1	141.49	983	91	162.56 (137.76; 216.97)	3.32 (3.25; 3.39)	98.0
	28/03/2013	5.6	255.82	5134	122	242.81 (195.28; 340.22)	3.02 (2.98; 3.06)	99.2
	10/04/2013	8.6	388.33	6514	126	266.07 (208.11; 383.87)	2.98 (2.94; 3.01)	99.2
Slope zone (200 m from the shore)	26/02/2013	2.8	125.08	2307	73	180.46 (142.25; 265.39)	1.74 (1.7; 1.78)	99.6
	13/03/2013	3.2	146.4	884	72	137.75 (110.54; 202.84)	3.23 (3.16; 3.31)	97.5
	28/03/2013	1.5	67.55	353	52	104.83 (84.43; 156.23)	2.73 (2.62; 2.84)	96.7
	10/04/2013	8.9	405.01	77	22	–	–	94.3
Deep-water zone (1 km from the shore)	26/02/2013*	0.3	7.17	7657	136	293.06 (232.32; 413.98)	2.86 (2.83; 2.89)	99.4
	13/03/2013	3.1	141.22	964	66	154.11 (115.03; 249.72)	2.1 (2.03; 2.16)	98.9
	28/03/2013	1.01	45.96	870	84	148.00 (124.18; 203.05)	2.8 (2.71; 2.88)	98.2
	10/04/2013	6.3	283.6	34	9	–	–	76.5
Pelagic zone (6 km from the shore)	13/03/2013	0.05	2.18	1310	73	132.91 (110.56; 189.57)	3.06 (3.0; 3.12)	98.7
	28/03/2013	6.02	274.32	449	63	119.60 (94.89; 182.75)	2.94 (2.83; 3.06)	96.7
	10/04/2013	1.3	60.6	1244	91	180.53 (143.63; 255.64)	2.3 (2.18; 2.41)	96.1

An asterisk marks the station, where diatomic algae *Aulacoseira baicalensis* were developed.

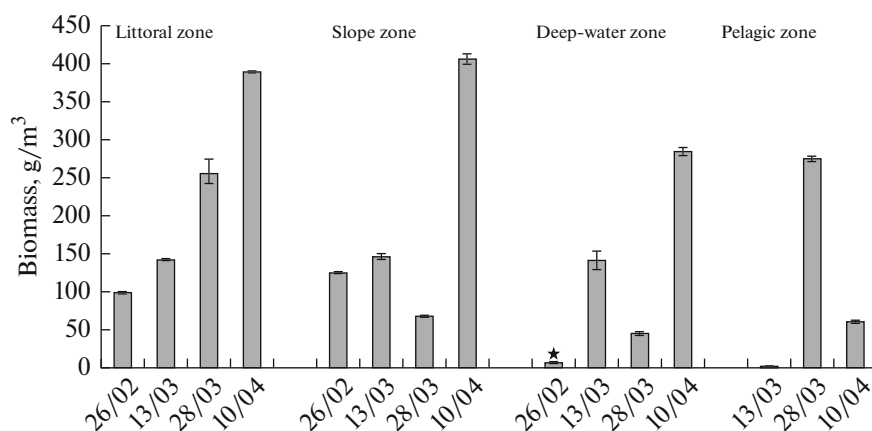


Fig. 1. Biomass of dinoflagellates in the under-ice communities in 2013. An asterisk marks the station, where diatomic algae *Aulacoseira baicalensis* developed.

ley) Komárková-Legnerová, and *Chlorella vulgaris* Beyerinck [Beijerinck]; and cryptophytes *Cryptomonas* sp.

Evaluation of bacterial diversity in the under-ice communities. Analysis of 15 under-ice samples (pyrosequencing of V3–V4 regions of the 16S rRNA gene with subsequent alignment, preclusterization, and removing of chimeric sequences) revealed 31409 sequences belonging to the domain *Bacteria* with the mean sequence length of 268 bp. In further studies, samples SZ10/04 and DWZ10/04 containing low numbers of sequences were discarded. The number of sequences varied from 353 to 7658 per sample. In total, 408 OTU_{0.03} were revealed; the number of OTUs per sample varied from 52 to 142. The values of Good's Coverage index were high (from 94.3 to 99.6%) in all samples, which indicated rather sufficient sequencing effort to capture the taxonomic diversity of samples (Table 1). The values of Chao1 (richness) and Shannon (diversity) indices varied from 104.83 to 303.65 and from 1.74 to 3.32, respectively (Table 1). According to the values of diversity indices, the most taxonomically complicated communities occurred in the littoral zone at the end of February and in the beginning of March. The richness of communities in the period of their development decreased, as was confirmed by a decrease in the Chao1 indices in all zones except for the pelagic zone, where the index value increased.

Composition of bacterial communities. Taxonomic composition of bacterial communities in the studied samples is shown on Fig. 2. The identified sequences were assigned to 14 phyla, 54 families, and 128 genera. The highest number of sequences in all samples belonged to the phyla *Bacteroidetes* (37.9%), *Proteobacteria* (31.7%), *Actinobacteria* (19.1%), *Verrucomicrobia* (4.3%), and *Deinococcus-Thermus* (3.9%). The members of phyla TM7, *Acidobacteria*, *Chloroflexi*, *Gemmatimonadetes*, *Nitrospira*, *Planctomycetes*, *Cya-*

nobacteria, *Firmicutes*, and SR1 constituted not more than 1% of the total number of sequences.

The members of *Bacteroidetes* were evenly distributed in various samples during the studied period; however, in the pelagic zone, the number of sequences was considerably lower than that in the samples from other stations. A percentage of *Bacteroidetes* in the samples from all studied stations was the highest in the initial period (end of February–early in March) and then decreased by the beginning of April (Fig. 2a). It can be assumed that a decrease in the *Bacteroidetes* number occurred when the biomass of dinoflagellates increased, which was clearly observed in the littoral zone. Representative OTU sequences from were taxonomically assigned on the basis of the full-size sequences of the 16S rRNA genes from the GenBank database. Out of 27 the most abundant OTUs, 11 were assigned to the phylum *Bacteroidetes*, among which 9 OTUs belonged to the family *Flavobacteriaceae* and by 1 OTU to each of the families *Cryomorphaceae* and *Chitinophagaceae*. The nearest homologues of OTU019 and OTU025 were *Flavobacterium psychrolimnae* from Lake Michigan (JX287711) and *Flavobacterium psychrolimnae* from an Antarctic lake (AJ585427) (Fig. 3). The OTU022 had 100% similarity with an Antarctic bacterium (AJ440977) and uncultivated *Flavobacterium* sp. from the high-altitude lake of Tibetan Highlands (EU703408); OTU009 and OTU013 showed high similarity (100%) with freshwater *Flavobacterium* sp. (KF499997) and uncultivated bacterium of the family *Flavobacteriaceae* from Lake Michigan (EU642364) (Fig. 3). The OTU023 had 100% similarity with uncultivated bacterium of the family *Cryomorphaceae* (FN668164) and uncultivated bacterium *Fluviicola* sp. from the high-altitude lake of Tibetan Highlands (EU703457).

In the under-ice communities of Lake Baikal, a percentage of *Proteobacteria* increased in the littoral and pelagic zones from the end of February to the

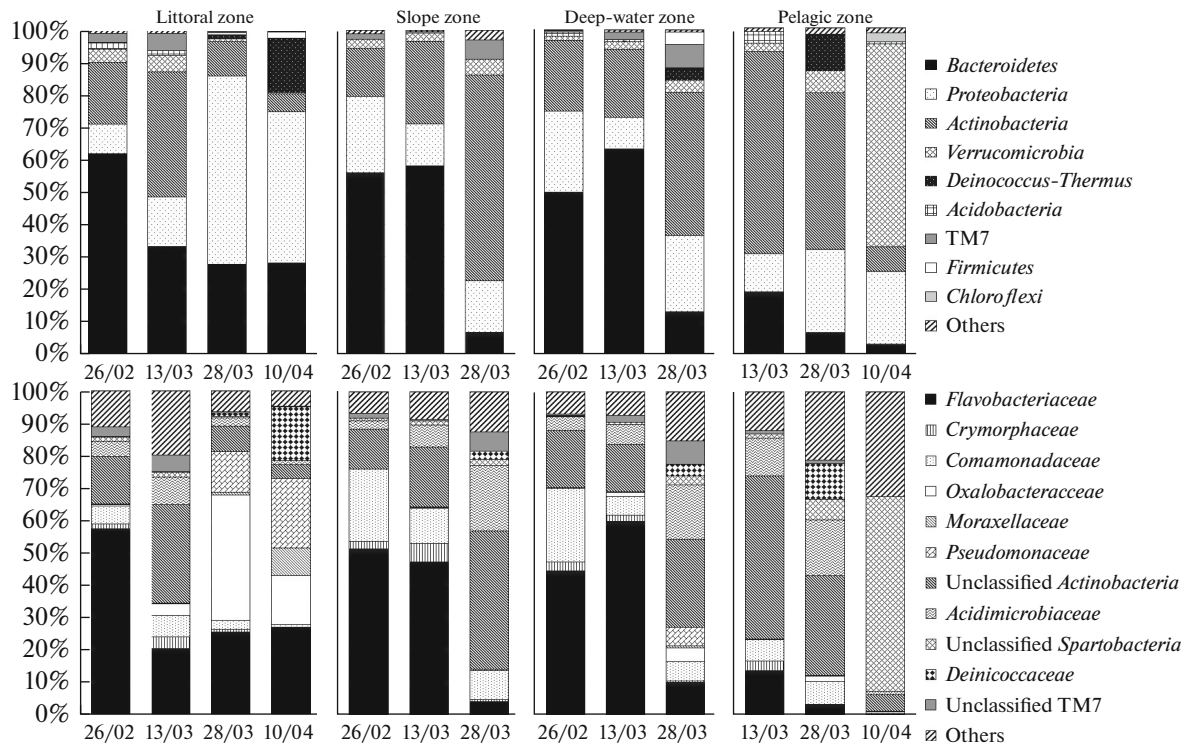


Fig. 2. Taxonomic composition of bacterial sequences from the under-ice communities at the level of phyla (a) and families (b).

beginning of April, whereas in the slope and deep-water zones, the percentage of this phylum changed insignificantly. The predominant sequences belonged to the class β -Proteobacteria (20.7%), families Oxalobacteraceae (9.8%) and Comamonadaceae (9.7%), and others (1.2%). A percentage of the class γ -Proteobacteria was lower almost by half (9.3%); it contained families Pseudomonadaceae (6.7%) and Moraxellaceae (1.9%). The class α -Proteobacteria comprised 1.4% and was represented mainly by families Caulobacteraceae, Sphingomonadaceae, and Rhodobacteraceae. Among abundant OTUs, five sequences belonged to the phylum Proteobacteria. In the phylogenetic tree, these OTUs formed clusters with *Massilia* sp. from the ice cores (KF295189)—OTU004; members of *Limnohabitans* sp. (KT175907) and *Limnohabitans curvus* (HE600681)—OTU024; Antarctic bacteria, uncultivated bacteria from an under-ice methane seep and high-altitude lakes, and *Rhodiferax antarcticus*—OTE005. The nearest homologues of bacteria belonging to the families Pseudomonadaceae and Moraxellaceae were *Pseudomonas psychrophila* (AB041885) and *Pseudomonas psychrotolerans* (AJ575816) for OTU006 as well as *Acinetobacter* sp. (KM979185) and uncultivated *Acinetobacter* sp. from the bottom sediments of Lake Dragon (China) (JF733705) for OTU021 (Fig. 3).

As seen from Fig. 2, during the studied period, a percentage of the phylum Actinobacteria decreased in the littoral and pelagic zones and increased in the

slope and deep-water zones. About 9.4% of bacteria belonged to unidentified Actinobacteria and 4.5%—to the family Acidimicrobiaceae. The most abundant OTU belonging to the phylum Actinobacteria had 97–100% similarity to the phylum Actinobacteria from Lake Ontario (KM031281), a member of the genus *Actinobacterium* from frozen ground (JN897005), uncultivated bacteria Actinomycetales from Lake Michigan (EU641194) and the high-altitude lakes of Tibetan plateau (EU703381), and with *Ilumatobacter fluminis* (JQ899217) (Fig. 4).

In the littoral zone, a percentage of the phylum Verrucomicrobia decreased with the community development as distinct from that in the pelagic zone, where the highest abundance of this phylum was observed at the end of April (57.5% of the community members). This phylum was represented mainly by unidentified sequences. Among the most abundant OTUs, two sequences were assigned to Verrucomicrobia, the nearest homologues of which (97–100% similarity) were Verrucomicrobia inhabiting freshwater reservoirs (HQ663543) and uncultivated forms of this phylum (KC24626, HM856577, and HQ663066) (Fig. 3).

A percentage of the phylum Deinococcus-Thermus at all the studied stations increased to the end of March; in the littoral zone, this phylum was the most abundant at the beginning of April. In the phylogenetic tree, the nearest relatives of OTU011 were *Deinococcus aquaticus* (JF276903), *Deinococcus* sp.

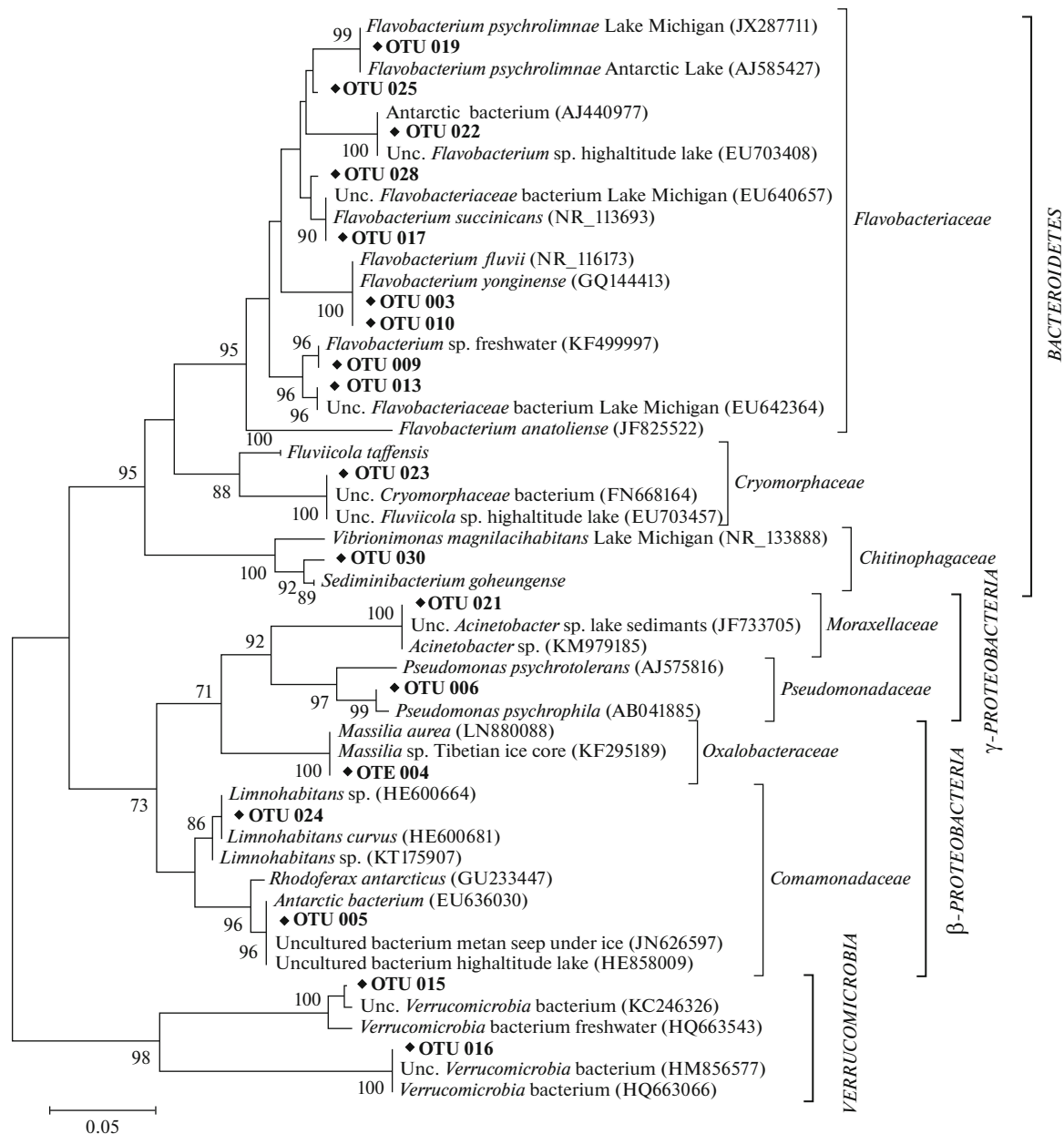


Fig. 3. Phylogenetic tree of nucleotide sequences of the most abundant OTUs belonging to the phyla *Bacteroidetes*, *Proteobacteria*, and *Verrucomicrobia* with genetic distance of 0.03 from the under-ice communities of Lake Baikal under massive development of dinoflagellates *G. baicalense*, which was constructed by the Maximum Likelihood method using the Kimura two-parameter algorithm. Numerals show the reliability of branching points determined by bootstrap analysis of 1000 alternative trees (values above 70 are considered significant).

(AB299741), *Deinococcus caeni* (DQ017709), and *Deinococcus* sp. from the Antarctic (DQ341427) (Fig. 4).

DISCUSSION

During the ice-covered period 2013, in the Bol'shie Koty (southern Baikal), communities with domination of dinoflagellates *Gymnodinium baicalense* Antip. were revealed. This species was described as a psychro-

philic endemic from Lake Baikal which is specific for the under-ice period (Obolkina et al., 2000). Massive under-ice development of dinoflagellates has been observed earlier; however, in previous years, biomass of *G. baicalense* was considerably lower (from 1 to 100 g/m³) (Votintsev et al., 1975; Annenkova et al., 2009; Pomazkina et al., 2010; Bashenkhayeva et al., 2015). Intense development of dinoflagellates in the littoral and slope zones can be associated with high snow cover in these regions, as was reported for the

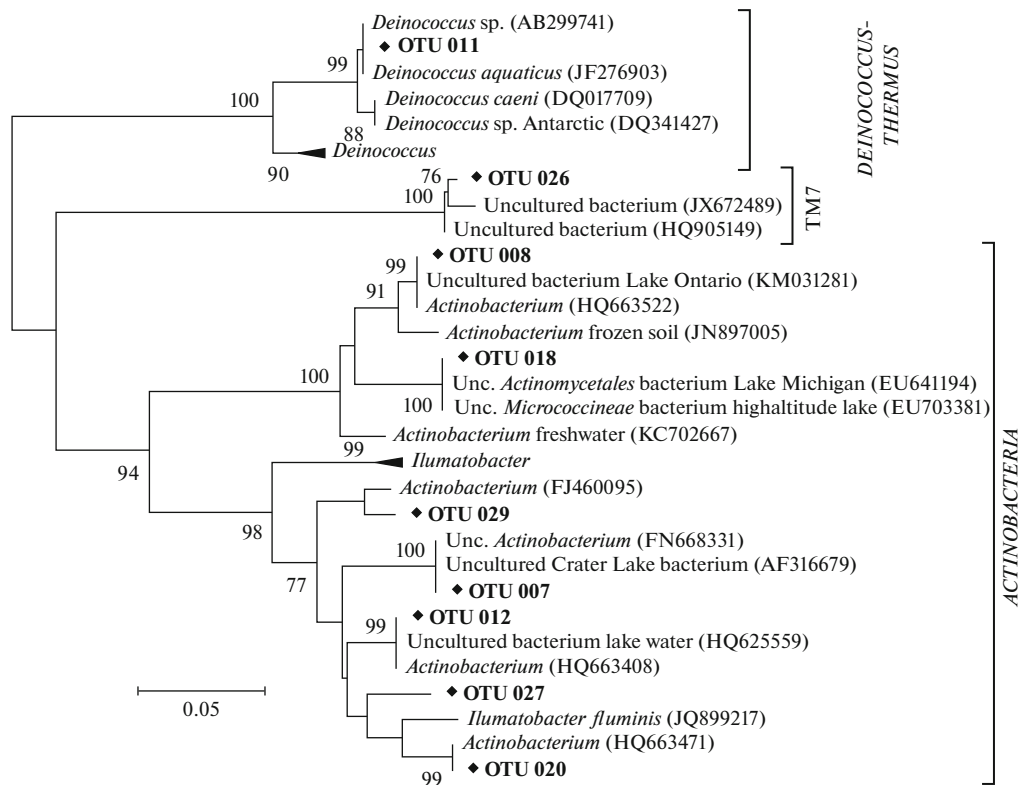


Fig. 4. Phylogenetic tree of nucleotide sequences of the most abundant OTUs belonging to the phyla *Deinococcus-Thermus*, TM7, and *Actinobacteria* with genetic distance of 0.03 from the under-ice communities of Lake Baikal under massive development of dinoflagellates *G. baicalense*, which was constructed by the Maximum Likelihood method using the Kimura two-parameter algorithm. Numerals show the reliability of branching points determined by bootstrap analysis of 1000 alternative trees (values above 70 are considered significant).

community from the lower ice surface in the Franklin Bay (Beaufort Sea, Canada), where dinoflagellates dominated in the case of the highest snow cover (Róžańska et al., 2009). Moreover, many dinoflagellates are capable of mixotrophic nutrition; under insufficient illumination because of high snow cover, they can use bacteria as a source of organic substances (Kirchner et al., 1996), thus adapting to environmental conditions.

Pyrosequencing of the V3–V4 regions of the 16S rRNA gene revealed that the under-ice communities with dinoflagellate domination were characterized by lower richness and diversity of bacteria than the previously studied communities, which contained various microalga species and had Chao1 index from 941 to 6477 (Bashenkhaeva et al., 2015). According to the Chao1 and Shannon indices, communities in the littoral zone at the end of February and in the beginning of March were characterized by the highest taxonomic diversity. In the coastal zone, the bottom effect and heterogeneity of snow covering of the ice may result in formation of under-ice currents (Zhdanov et al., 2002), which due to the water mixing can increase microbial diversity compared with that in the other zones.

In all the studied samples, bacteria of the phylum *Bacteroidetes* were revealed. Members of this phylum are among predominant taxa in communities from the cold-water seas (Zhang et al., 2014; Li et al., 2015), as well as from Lake Baikal in the freeze-up period (Ahn et al., 1999; Bashenkhaeva et al., 2015). Moreover, members of *Bacteroidetes* represent one of the widespread taxa associated with blooms of marine dinoflagellates (Garcés et al., 2007; Green et al., 2010). A percentage of *Bacteroidetes* in communities was the maximum in summer, period of intense bloom of *Alexandrium taylori*, and decreased with diminishing the dinoflagellate number (Garcés et al., 2007). In the studied communities, most *Bacteroidetes* belonged to family *Flavobacteriaceae* (34%) (Fig. 2b). Members of this family are widespread in various ecotopes (soils, freshwater reservoirs, and Arctic regions) (Li et al., 2015); they were also predominant in the plankton of Lake Baikal littoral zone (Parfenova et al., 2013). Moreover, a number of *Flavobacteriaceae* taxa are psychrophiles, which due to production of pigments and high content of fatty acids are able to survive in cold ecotopes (cited from *Bergey's Manual...*, 2005). The family *Cryomorphaceae*, which members are also found in our samples, is widespread in aquatic ecosys-

tems; moreover, most of the cultivated species have been isolated from cold ecotopes (Bowman et al., 2003).

Bacteria of the phylum *Proteobacteria* belonging mainly to the classes β - and γ -*Proteobacteria* were also revealed in all samples. Some members of the genus *Pseudomonas* (γ -*Proteobacteria*) are psychrophiles and possess mechanisms of surviving under extreme conditions (Muryoi et al., 2004); moreover, pure cultures of pseudomonads have been earlier isolated from the under-ice communities of Lake Baikal (Bashenkaeva et al., 2015). In the dinoflagellate-dominated communities, a high level of *Proteobacteria*, mainly members of the class α -*Proteobacteria*, as well as low content of γ -*Proteobacteria* have been also found (Green et al., 2004; Garcés et al., 2007).

The under-ice communities contained bacteria belonging to the phyla *Actinobacteria*, *Verrucomicrobia*, and *Deinococcus-Thermus*, which are widespread in diverse natural habitats, including communities of Arctic soils as well as of marine and freshwater reservoirs (Zhang et al., 2014); they are known as degraders of organic substances (cited from *Bergey's Manual...*, 2005). It was found that under massive development of marine toxic dinoflagellates, bacteria of the genus *Deinococcus* were able to excrete deinoxanthin, an algicidal component decreasing the number of dinoflagellates (Li et al., 2015). However, in the under-ice communities of Lake Baikal, a percentage of members of the family *Deinococcaceae* was the highest when the dinoflagellate biomass was the maximum.

Thus, in the ice-covered period 2013, in Lake Baikal (Southern Basin), unusually massive development of dinoflagellates *Gymnodinium baicalense* was observed; their biomass was several times higher than that in previous years. Massive development of dinoflagellates was accompanied by a considerable decrease in the richness and diversity of bacterial communities. During the period of dinoflagellate bloom, the phyla *Bacteroidetes*, *Proteobacteria*, and *Actinobacteria* prevailed in bacterial communities. The family *Flavobacteriaceae* was the most abundant (about 30% of the total number of sequences). In the littoral zone, unlike slope, deep-water-, and pelagic ones, a successive change in the composition of predominant bacterial taxa was observed during development of dinoflagellates: a decrease of percentages of the phyla *Bacteroidetes* and *Actinobacteria* was accompanied by an increase in the *Proteobacteria* level. Of interest is that the same phyla prevailed in the communities during bloom of marine dinoflagellates (Garcés et al., 2007; Green et al., 2010).

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REFERENCES

- Ahn, T., Hong, S., Kim, D., Suck, J., and Drucker, V.V., The bacterial community of Southern lake Baikal in winter, *J. Microbiol.*, 1999, vol. 37, pp. 10–13.
- Albinsson, M.E., Negri, A.P., Blackburn, S.I., and Bolch, C.J.S., Bacterial community affects toxin production by *Gymnodinium catenatum*, *PLoS One*, 2014, vol. 9, no. 8. e104623. doi 10.1371/journal.pone.0104623
- Annenkova, N.V., Belykh, O.I., Denikina, N.N., and Belikov, S.I., Identification of dinoflagellates from the Lake Baikal on the basis of molecular genetic data, *Dokl. Biol. Sci.* 2009, vol. 426, pp. 253–257.
- Bashenkaeva, M.V., Zakharova, Y.R., and Khanaev I.V., Psychrophilic bacteria in sub-ice communities of Lake Baikal, *Goldschmidt2015 Abstracts*, 2015, p. 221.
- Bashenkaeva, M.V., Zakharova, Y.R., Petrova, D.P., Khanaev, I.V., Galachyants, Y.P., and Likhoshway, Y.V., Sub-ice microalgal and bacterial communities in freshwater Lake Baikal, Russia, *Microb. Ecol.*, 2015, vol. 70, pp. 751–765.
- Belyakova, G.A., D'yakov, Yu.T., and Tarasova, K.L., *Botanika. T. 1: Vogorosli i griby* (Botany. Vol. 1. Algae and Fungi), Moscow: Akademiya, 2006.
- Bergey's Manual of Systematic Bacteriology I–II*, Garrity, G.M., Ed., New York: Springer, 2005.
- Bolch, C.J.S., Subramanian, T.A., and Green, D.H. The toxic dinoflagellate *Gymnodinium catenatum* (Dinophyceae) requires marine bacteria for growth, *J. Phycol.*, 2011, vol. 47, pp. 1009–1022.
- Bondarenko, N.A., Timoshkin, O.A., Röpstorf, P., and Melnik, N.G., The under-ice and bottom periods in the life of *Aulacoseira baicalensis* (K. Meyer) Simonsen, a principal Lake Baikal alga, *Hydrobiologia* 2006, vol. 568, pp. 107–109. doi 10.1007/s10750-006-0325-7
- Bowman, J.P., Mancuso, C., Nichols, C.M., and Gibson, J.A.E., *Algoriphagus ratkowskyi* gen. nov., sp. nov., *Brumimicrobium glaciale* gen. nov., sp. nov., *Cryomorpha ignava* gen. nov., sp. nov. and *Crocinitomix catalasitica* gen. nov., sp. nov., novel flavobacteria isolated from various polar habitats, *Int. J. Syst. Evol. Microbiol.*, 2003, vol. 53, pp. 1343–1355.
- Bowman, J.P., McCammon, S.A., Brown, M.V., Nichols, D.S., and McMeekin, T.A., Diversity and association of psychrophilic bacteria in Antarctic sea ice, *Appl. Environ. Microbiol.*, 1997, vol. 63, pp. 3068–3078.
- Cole, J.R., Wang, Q., Cardenas, E., Fish, J., and Chai, B., The ribosomal database project: improved alignments and new tools for rRNA analysis, *Nucleic Acids Res.*, 2009, vol. 37, pp. 141–145.
- Garcés, E., Vila, M., Reñé, A., Alonso-Sáez, L., Anglès, S., Lugliè, A., Masó, M., and Gasol, J.M., Natural bacterioplankton assemblage composition during blooms of *Alexandrium* spp. (Dinophyceae) in NW Mediterranean coastal waters, *Aquat. Microb. Ecol.*, 2007, vol. 46, pp. 55–70.
- Green, D.H., Hart, M.C., Blackburn, S.I., and Bolch, C.J.S., Bacterial diversity of *Gymnodinium catenatum* and its relationship to dinoflagellate toxicity, *Aquat. Microb. Ecol.*, 2010, vol. 61, pp. 73–87.

- Green, D.H., Llewellyn, L.E., Negri, A.P., Blackburn, S.I., and Bolch, C.J.S., Phylogenetic and functional diversity of the cultivable bacterial community associated with the paralytic shellfish poisoning dinoflagellate *Gymnodinium catenatum*, *FEMS Microbiol. Ecol.* 2004, vol. 47, pp. 345–357.
- Jeong H.J., The ecological roles of heterotrophic dinoflagellates in marine planktonic community, *J. Eukaryot. Microbiol.*, 1999, vol. 46, no. 4, pp. 190–396.
- Kirchner, M., Sahling, G., Uhlig, G., Gunkel, W., and Klings, K.-W., Does the red tide-forming dinoflagellate *Noctiluca scintillans* feed on bacteria?, *Sarsia*, 1996, vol. 81, pp. 45–55. doi 10.1080/00364827.1996.10413610
- Li, Y., Liu, Q., Li, C., Dong, Y., Zhang, W., Zhang, W., and Xiao, T., Bacterial and archaeal community structures in the Arctic deep-sea sediment, *Acta Oceanol. Sinica*, 2015, vol. 34, pp. 93–113.
- Li, Y., Zhu, H., Lei, X., Zhang, H., Guan, C., Chen, Z., Zheng, W., Xu, H., Tian, Y., Yu, Z., and Zheng, T., The first evidence of deinoxanthin from *Deinococcus* sp. Y35 with strong algicidal effect on the toxic dinoflagellate *Alexandrium tamarense*, *J. Hazardous Mater.*, 2015, vol. 290, pp. 87–95.
- Muryoi, N., Sato, M., Kaneko, S., Kawahara, H., Obata, H., Yaish, M.W.F., Griffith, M., and Glick, B.R., Cloning and expression of *afpA*, a gene encoding an anti-freeze protein from the Arctic plant growth-promoting rhizobacterium *Pseudomonas putida* GR12-2, *J. Bacteriol.*, 2004, vol. 186, pp. 5661–5671.
- Obolkina, L.A., Bondarenko, N.A., Doroshenko, L.F., Grobunova, L.A., and Molozhavaya, O.A., The find of a cryophilic association in Lake Baikal, *Dokl. Earth Sci.*, 2000, vol. 371, no. 3, pp. 592–594.
- Phillips, K.A. and Fawley, M.W., Winter phytoplankton blooms under ice associated with elevated oxygen levels, *J. Phycol.*, 2002, vol. 38, pp. 1068–1073.
- Pomazkina, G.V., Belykh, O.I., Domysheva, V.M., Sakirko, M.V., and Gnatovsky, R.Yu., Structure and dynamics of phytoplankton of Southern Baikal (Russia), *Al'gologiya*, 2010, vol. 20, no. 1, pp. 56–72.
- Popovskaya, G.I., Genkal, S.I., and Likhoshvai, E.V., *Diatomovye vodorosli planktona ozera Baikal* (Planktonic Diatoms of Lake Baikal), Novosibirsk: Nauka, 2011.
- Rózańska, M., Gosselin, M., Poulin, M., Wiktor, J.M., and Michel, C., Influence of environmental factors on the development of bottom ice protist communities during the winter–spring transition, *Mar. Ecol. Prog. Ser.*, 2009, vol. 386, pp. 43–59. doi 10.3354/meps08092
- Smith, R.E.H., Clement, P., and Cota, G.F., Population dynamics of bacteria in Arctic Sea ice, *Microb. Ecol.*, 1989, vol. 17, pp. 63–76.
- Spilling, K., Dense sub-ice bloom of dinoflagellates in the Baltic Sea, potentially limited by high pH, *J. Plankton Res.*, 2007, vol. 29, pp. 895–901. doi 10.1093/plankt/fbm067
- Tilney, C.L., Pokrzywinski, K.L., Coyne, K.J., and Warner, M.E., Growth, death, and photobiology of dinoflagellates (*Dinophyceae*) under bacterial-algicide control, *J. Appl. Phycol.*, 2014, vol. 26, pp. 2117–2127.
- Votintsev, K.K., Meshcheryakova, A.I., and Popovskaya, G.I., *Krugovorot organicheskogo veshchestva v ozere Baikal* (Organic Matter Turnover in Lake Baikal), Novosibirsk: Nauka, 1975.
- Zhang, J., Zhang, X., Liu, Y., Xie, S., and Liu, Y., Bacterioplankton communities in a high-altitude freshwater wetland, *Ann. Microbiol.*, 2014, vol. 64, pp. 1405–1411.
- Zhdanov, A.A., Granin, N.G., and Shimaraev, M.N., Subglacial currents in Lake Baikal (based on new experimental data), *Geogr. Nat. Resour.*, 2002, no. 1, pp. 79–83.

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