

## Stratified Distribution of Nutrients and Extremophile Biota within Freshwater Ice Covering the Surface of Lake Baikal

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Biological entities and gradients of selected chemicals within the seemingly barren ice layers covering Lake Baikal were investigated. Ice cores 40–68 cm long were obtained from inshore and offshore sites of Southern Lake Baikal during the cold period of a year (March–April) in 2007 and 2008. In microscopic observations of the melted ice, both algae and bacteria were found in considerable numbers ( $>10^3$  cells/L and  $>10^4$  cells/ml, respectively). Among all organisms found, diatom was generally the most predominant taxon in the ice. Interestingly, both planktonic and benthic algae were present in considerable numbers ( $2\text{--}4 \times 10^4$  cells/L). Dominant phototrophic picoplankton were comprised of small green algae of various taxa and cyanobacteria of *Synechococcus* and *Cyanobium*. The bacterial community consisted mostly of short rod and cocci cells, either free-living or aggregated. Large numbers of yeast-like cells and actinomycete mycelium were also observed. Concentrations of silica, phosphorus, and nitrate were low by an order of magnitude where biota was abundant. The profile of the ice could be interpreted as vertical stratification of nutrients and biomass due to biological activities. Therefore, the organisms in the ice were regarded to maintain high activity while thriving under freezing conditions. Based on the results, it was concluded that the freshwater ice covering the surface of Lake Baikal is considerably populated by extremophilic microorganisms that actively metabolize and form a detritus food chain in the unique large freshwater ecosystem of Lake Baikal.

**Keywords:** freshwater ice, chemical composition, ice organisms, picoplankton, actinomycetes, diatoms

### Introduction

While ice layers covering the surfaces of large bodies of water look barren for living organisms, there have been reports of finding microbial communities within ice (e.g. Horner, 1976; Mel'nikov, 1980; Miteva *et al.*, 2004; Mosier *et al.*, 2007). While research on organisms living in freshwater ice is relatively rare (Salonen *et al.*, 2009), the richness of living organisms in marine ice is well-established, based on the results of more frequent studies (McRoy *et al.*, 1972; Horner, 1976; Dunbar, 1979; Mel'nikov, 1980; Falk-Petersen *et al.*, 2000; Thomas and Dieckman, 2002). The structure of sea ice is usually more complex, and it can be classified into two distinctive forms: solid versus granulated ice. The latter has water-filled interstitial spaces where salinity increases as a result of freezing. The layers of nonfreezing highly-saline interstitial water can act as lenses that enhance the transmission of incident radiation, accelerating the melting of ice (Falk-Petersen *et al.*, 2000). The colonization of sea ice starts with rapid proliferation of algae, with diatoms being one of the most significant microalgal constituents of ice-embedded communities. They form filaments and other morphological patterns that hang from the underside of the ice. These bundles are colonized by epiphytic algae, bacteria, and protists, building a dynamic community.

For freshwater ice, several studies reported the presence of ice-dwelling microorganisms. A community comprised of bacteria, algae, flagellates, and ciliates was discovered in freshwater ice of Alpine and Pyrenean lakes, along with a large amount of liquid-phase water in the ice (Felip *et al.*, 1995). This study showed that ice communities appeared as an essential element of the lake ecosystem since they were rich with a number of species, despite freezing temperatures and the seasonality of the habitat. Besides assemblages of species living trapped between ice crystals, the undersides of ice layers of freshwater ice were also shown to be heavily populated by microorganisms (e.g. Yur'ev and Lebedev, 1988). During a period of intensive consolidation and melting of freshwater ice in the Amur River, a large amount of algae was found on the underside of ice layers in the river (Yur'ev and Lebedev, 1988). Observations of freshwater ice algae have been made in several other river systems, including the Belaya River-Lake Kandry-Kul system (Shkundina, 1988), and the St. Lawrence River system (Frenette *et al.*, 2008). Distribution of chlorophyll and photosynthetic activity were demonstrated in the Kantatsky Water Reservoir and Lake Baikal (Zavoruev, 2000). Votintsev and Meshcher-yakova (1961) pioneered research on the chemical composition of Baikalian ice. Their studies showed that the ice was poorly mineralized, its chemical composition being al-

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**Table 1.** Designation and descriptions of ice cores

Core name	Date	Site	Distance (m)	Depth (m)	Length (cm)	No. of segments	Water temp. (°C)
A73	Mar. 28, 2007	A	50	1.5	61	5	0.1
A74	Apr. 18, 2007	A	50	1.5	40	5	0.3
B73	Mar. 28, 2007	B	290	3.4	63	5	0.1
C73	Mar. 28, 2007	C	4,000	1,400	68	5	0.1
C83	Mar. 18, 2008	C	4,000	1,400	67	5	0.1

most similar to the atmospheric precipitation in the surrounding area of Pribaikalye. The finding of cryophilic communities in the ultrapure Baikalian ice (Bondarenko *et al.*, 2000, 2006; Obolkina *et al.*, 2000) was unexpected, but subsequent studies showed that they were an important part of the food web of the Lake Baikal ecosystem in late winter (Timoshkin, 2001; Bordonosky *et al.*, 2003).

In this study, we aimed to characterize extremophile microorganisms in the ice cover of Lake Baikal in late winter. Photo- and heterotrophic constituents of ice-dwelling assemblages were analyzed in both littoral and pelagic zones. The influence of ice microorganisms on the chemical composition of the ice was analyzed by comparing vertical profiles of chemical elements with those of microorganisms. Based on the results, the spatio-temporal dynamics of the extremophiles were also assessed.

## Materials and Methods

### Ice cores

Five ice cores were obtained during surveys of the Southern Baikal in March-April, 2007 and in March, 2008 (Table 1 and Fig. 1). The three sampling sites A, B, and C were located 50 m, 290 m, and 4 km off the shoreline of Cape Berezovy (51°50'41.6" N, 104°54'10.5" E), respectively. Ice cores were obtained by drilling out a block of ice with an area of ~0.25 m<sup>2</sup>. Under sterile laboratory conditions, the cores were split into 5 segments, 2–17 cm long (see column heading of Table 2), for chemical and biological analyses.

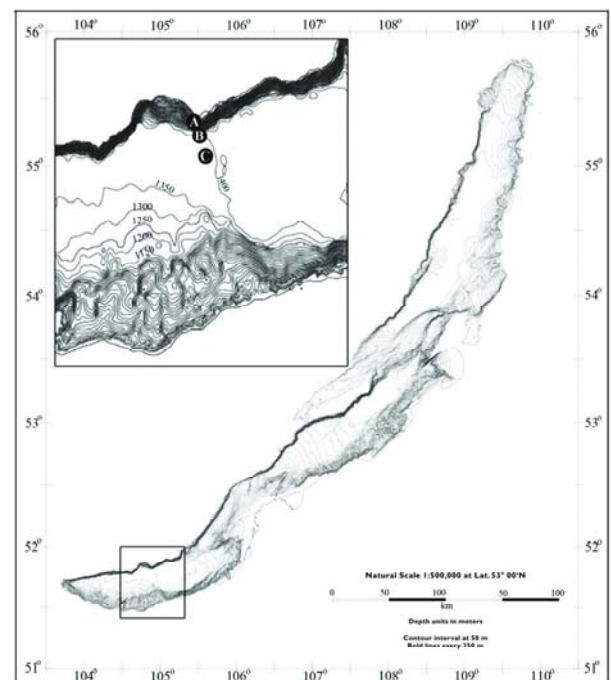
### Chemical analyses

Ice segments were melted in polypropylene containers at room temperature. Measurements of pH were conducted directly with the melted water at 25°C. The melted water was filtered through a 0.45-µm cellulose acetate filter to measure total dissolved solids (TDS) and concentrations of dissolved ions. Concentrations of cations (Ca<sup>2+</sup>, Mg<sup>2+</sup>, Na<sup>+</sup>, and K<sup>+</sup>) were determined by an AAS-30 atomic absorption spectrometer (Zeiss, Germany), according to published methods (Allan, 2004). Concentrations of anions (HCO<sub>3</sub><sup>-</sup>, Cl<sup>-</sup>, NO<sub>3</sub><sup>-</sup>, and SO<sub>4</sub><sup>2-</sup>) were measured using a Millichrom A-02 chromatograph (Econova, Russia). Contents of major nutrients were determined using the following appropriate colorimetric methods (Wetzel and Likens, 2000): the indophenol blue method for NH<sub>4</sub><sup>+</sup>, Griss's method for NO<sub>2</sub><sup>-</sup>, Deniges's method for PO<sub>4</sub><sup>3-</sup>, and the ammonium molybdate method for Si.

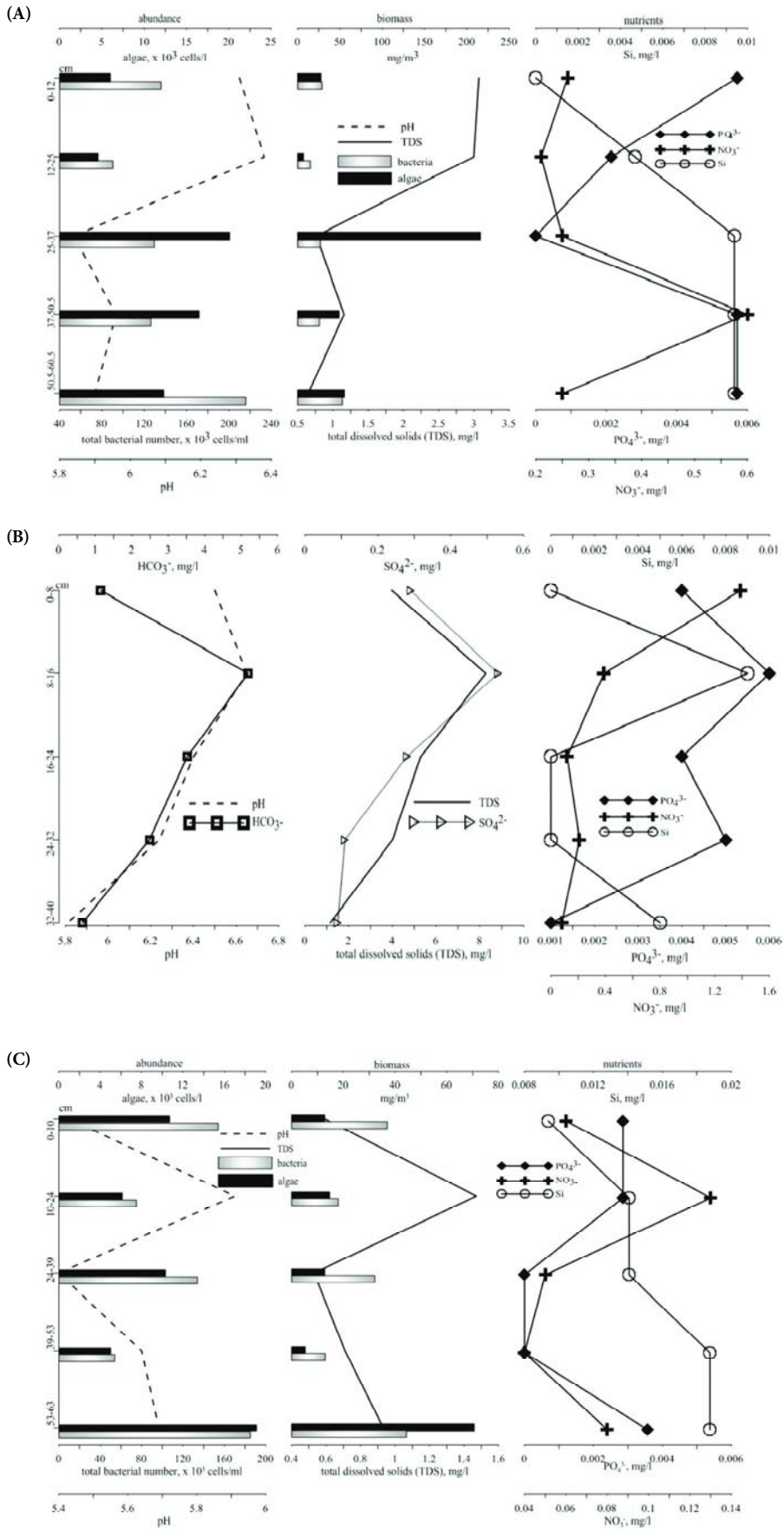
### Biological analyses

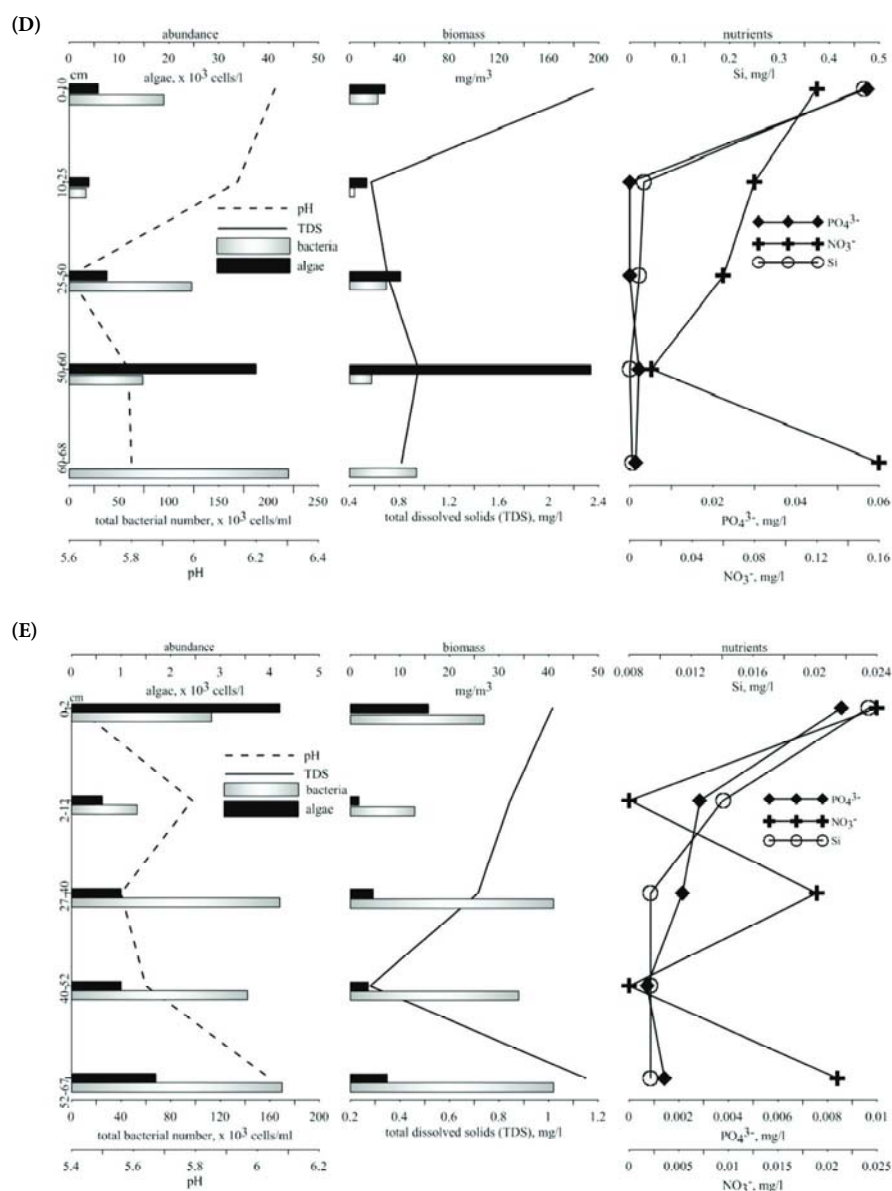
For quantification and identification of microorganisms embedded in the ice cores, segmented ice cores were melted in dark vessels at room temperature. The melted water samples were immediately fixed by either glutaraldehyde (2% final concentration) or Utermöhl solution. For enumeration of total bacterial number (TBN) comprising autotrophic picoplankton and bacteria, 10–200 ml of glutaraldehyde-fixed samples were stained with 4',6-diamidino-2-phenylindole (DAPI) and filtered through 0.22-µm porosity black polycarbonate filters according to a standard protocol (Wetzel and Likens, 2000).

The filters were air dried, placed on a drop of immersion oil under a cover slip, and examined at the magnification of ×1,250 using an Axiovert 200 (Zeiss, Germany) microscope with a HBO 100-W mercury lamp. To obtain the quantity of autotrophic picoplankton, which consisted mostly of cyanobacteria, the same procedures were performed by phycobilin autofluorescence instead of DAPI-staining. To observe and count flagellates, primuline-staining and pre-



**Fig. 1.** Bathymetric map showing locations of sampling sites, A-C, off Cape Berezovy of Lake Baikal. Values in the map indicate water depth in meters.





**Fig. 2.** Vertical distribution of water chemistry and biological variables. (A) core A73, (B) core A74, (C) core B73, (D) core C73, and (E) core C83.

stained filters of 1- $\mu\text{m}$  porosity were used. The cell sizes and shapes of bacteria, picocyanobacteria, and flagellates were measured from microphotographs (Drozdov *et al.*, 2006) taken with a Penguin 600CL camera (Pixera Corp., USA) using the VideoTest-Razmer 5.0 software package (VideoTest, Russia). Biomass was estimated from the average cell volume and abundance.

For species identification and quantitative estimations of the microalgae, the water samples fixed with Utermöhl solution were settled for 10 days and concentrated by sedimentation (Kiselev, 1956). The concentrate, usually 0.1 ml, was applied onto a Nageotte chamber and examined using a Peraval light microscope (Zeiss) at  $\times 720$  or lower magnifications. The algal species were identified based on taxonomic keys described by Starmach (1985) and Gleser *et al.*

(1992).

To analyze the detailed structures of the microorganisms, scanning electron microscopy (SEM) was employed. The materials for observation were placed onto a 0.45- $\mu\text{m}$  porosity filter and dehydrated in ethyl alcohol solution by gradually increasing the alcohol concentration. Subsequently, the samples were dried at 40°C, gold coated in a Balzers SCD 004 sputter-coater (Bal-Tec AG, Liechtenstein), and examined using SEM 525 M (Philips, Netherland). The biomass of algal cells was estimated by measuring the geometrical dimensions of cells under a microscope (Makarova and Pichkily, 1970; Wetzel and Likens, 2000).

## Results

### Water chemistry

Reflecting the thickness of the ice cover over the lake, the ice cores were 40 to 68 cm long. The vertical distributions of pH and TDS showed obvious patterns of chemical stratification in the ice cores (Fig. 2). Except in the core C83, levels of pH and TDS tended to be high in the upper layers (0–25 cm), with >2 mg/L values of TDS and >6.1 pH values, while TDS remained at <1 mg/L and pH at <6.1 in the lower layers (>25 cm).

Among the anions measured in this study,  $\text{HCO}_3^-$  showed a correlation with pH ( $r=0.71$ ,  $P<0.05$ , permutation test), and  $\text{SO}_4^{2-}$  with TDS ( $r=0.91$ ,  $P<0.05$ ) (Fig. 2B). While the correlation between  $\text{SO}_4^{2-}$  and TDS revealed that  $\text{SO}_4^{2-}$  was the primary dissolved inorganic component in the ice, the former correlation indicates that the pH in the ice was largely determined by a carbonate-bicarbonate buffer system, which is typical in lake water-atmosphere contact (Wetzel and Likens, 2000). It is known that the fresh water of Lake Baikal has a calcium-bicarbonate buffer system. Therefore,

$\text{HCO}_3^-$  and  $\text{Ca}^{2+}$  were also dominant ions in the ice cores.

### Algal biomass

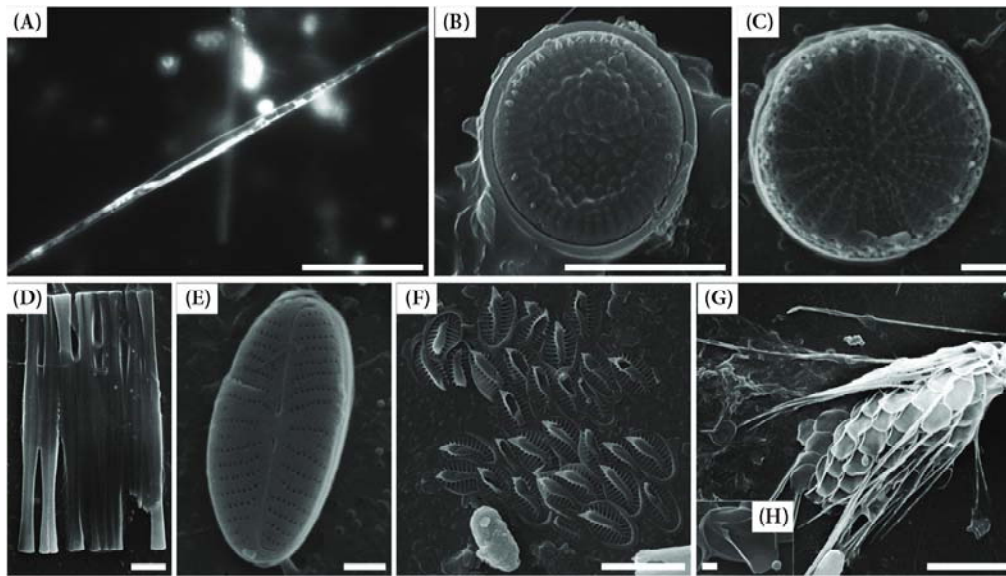
The abundance and biomass of microalgae varied considerably within the ice core. The vertical profiles showed a high algal concentration in the 25–37 cm segments of ice core A73, while C73 showed a peak of algal abundance (>200 mg/m<sup>3</sup>) within the 50–60 cm zone. Except for those peaks, algal biomass generally remained below 60 mg/m<sup>3</sup>. In C83, the maximal algal biomass was about 5–17 times lower than in other cores. This was reflected in the quantitative characteristics of the spring phytoplankton. In 2007, spring productivity was 4 to 5 times higher ( $820\pm 20$  mg/m<sup>3</sup>) than in 2008 ( $185\pm 15$  mg/m<sup>3</sup>).

When the integrity and taxonomic identity of algal cells were subjected to detailed microscopic examination, planktonic and benthic algae were determined to be intact and possibly viable, as judged from their shape (Table 2). The autofluorescence of photosynthetic pigments suggested that some cells were viable (Fig. 3A). In cores A73, B73, and C73, the planktonic diatoms *Aulacoseira baicalensis*, *A. islandica*,

**Table 2.** Incidences (+) of algal species in ice cores by segments<sup>a</sup>

Phylum	A73					B73					C73					A74					C83					
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	
Species	12	25	37	51	61	10	24	39	53	63	10	25	50	60	68	8	16	24	32	40	2	12	40	52	67	
Chrysophyta																										
<i>Dinobryon cylindricum</i>		+		+	+			+				+	+										+			+
<i>Mallomonas vannigera</i>					+					+															+	
<i>Synura petersenii</i>					+					+															+	
Cryptophyta																										
<i>Cryptomonas gracilis</i>		+	+		+	+									+										+	
<i>Rhodomonas pusilla</i>								+							+		+	+	+	+		+	+	+	+	
Dinophyta																										
<i>Gymnodinium baicalense</i>																			+	+		+	+	+	+	
<i>Peridinium baicalense</i>														+			+	+	+	+		+	+	+	+	
Bacillariophyta																										
<i>Aulacoseira baicalensis</i>		+	+	+	+					+		+	+	+	+		+	+	+	+						
<i>A. islandica</i>			+	+			+	+		+		+	+	+	+		+	+	+	+						
<i>Cyclotella minuta</i>	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+
<i>Fragilaria crotonensis</i>				+	+										+											
<i>Stephanodiscus</i> sp.																			+	+	+					
<i>Stephanodiscus meyeri</i>																			+	+	+					
<i>Synedra acus</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+					
<i>Achnanthes pusilla</i>					+					+															+	+
<i>Gomphonema ventricosum</i>	+	+	+	+	+			+		+		+		+			+								+	+
<i>Gomphonema</i> sp.								+																	+	
<i>Cocconeis placentula</i>		+	+	+																					+	
<i>Cymbella</i> sp. <sub>1</sub>	+	+								+					+											
<i>Cymbella</i> sp. <sub>2</sub>	+	+					+	+	+																+	
<i>Hannaea baicalensis</i>																									+	
<i>Navicula</i> sp.	+	+						+		+															+	
<i>Nitzschia</i> sp. <sub>1</sub>		+													+					+		+		+		
<i>Nitzschia</i> sp. <sub>2</sub>			+																						+	
Chlorophyta																										
<i>Koliella longiseta</i>					+					+					+											
<i>Monoraphidium</i>					+					+																

<sup>a</sup> column headings: the first row=core name, the second row=segment designation, numbered from top to bottom, the third row=depth (cm) of the bottom of a segment.



**Fig. 3. Diatoms and chrysophytes in ice cores.** (A–E) diatoms, (F–H) chrysophytes; (A) fluorescence microscopy, (B–H) scanning electron microscopy; (A) *Synedra acus* subsp. *radians*. Cell with chloroplasts; (B) *Cyclotella minuta*; (C) *Stephanodiscus* sp.; (D) *Fragilaria crotonensis*; (E) *Achnanthes pusilla*; (F) scales of *Synura petersenii*; (G) scales and spines of *M. vannigera*; (H) scales of *M. vannigera*. Scale bars: A=25  $\mu\text{m}$ ; B, D, and G=10  $\mu\text{m}$ ; C, E, and H=1  $\mu\text{m}$ ; F=5  $\mu\text{m}$ .

and *Synedra acus* dominated among the Baikal ice dwellers. The following species were detected in lower amounts: *Cyclotella minuta*, *Stephanodiscus* sp., and *Fragilaria crotonensis* (Figs. 3B–D). *Gomphonema ventricosum* dominated among benthic organisms. Trace amounts of *Cocconeis*, *Cymbella*, *Navicula*, *Nitzschia*, and *Achnanthes* (Fig. 3E) were also present. Green algae were represented by *Monoraphidium* and *Koliella longiseta*.

All the samples contained disrupted cells of algae, diatom valves, and thecae of dinoflagellates, as well as scales and spines of chrysophytes, *Mallomonas* and *Synura* (Figs. 3F–H). While collecting the ice cores, we observed extensive proliferation of *Mallomonas* under the ice of littoral zones, with *M. vannigera* as the predominant species (Fig. 3G). We found that the proportion of destroyed cells was greater in the upper ice layers (up to 90%) and gradually decreased downward to 10–30%.

#### Abundance of autotrophic picoplankton

Autotrophic picoplankton prevailed with cyanobacteria from the genera *Synechococcus* and *Cyanobium*, as well as with green algae (chlorococci) of picoplankton size. The cyanobacteria included rod-shaped, ellipsoid, and coccoid morphotypes (1.0–1.5  $\mu\text{m}$  in size). The eukaryotic picoplankton were spherical and  $\sim 2$   $\mu\text{m}$  in diameter. Most samples were dominated by colonies of cyanobacteria (Fig. 4A) and cyanobacteria from crustacean faecal pellets (Figs. 4E–F) frozen into the ice from the water below the ice. The coccoid morphotypes were phycoerythrin-rich, while rod-shaped ones consisted of phycocyanin-rich cyanobacteria. In the ice, cyanobacteria were less diverse than in the plankton of Lake Baikal. The endemic plankton species *Synechocystis limnetica* was not found in the cores. Single cells of the large planktonic colonial cyanobacteria from

the genera *Anabaena* and *Oscillatoria* were present only in the coastal samples. The picocyanobacterial cells in the cores were found to be viable as shown by fluorescence of their photosynthetic pigments and subsequent cultivation (data not shown). In the upper core layers, mostly disrupted cells were present.

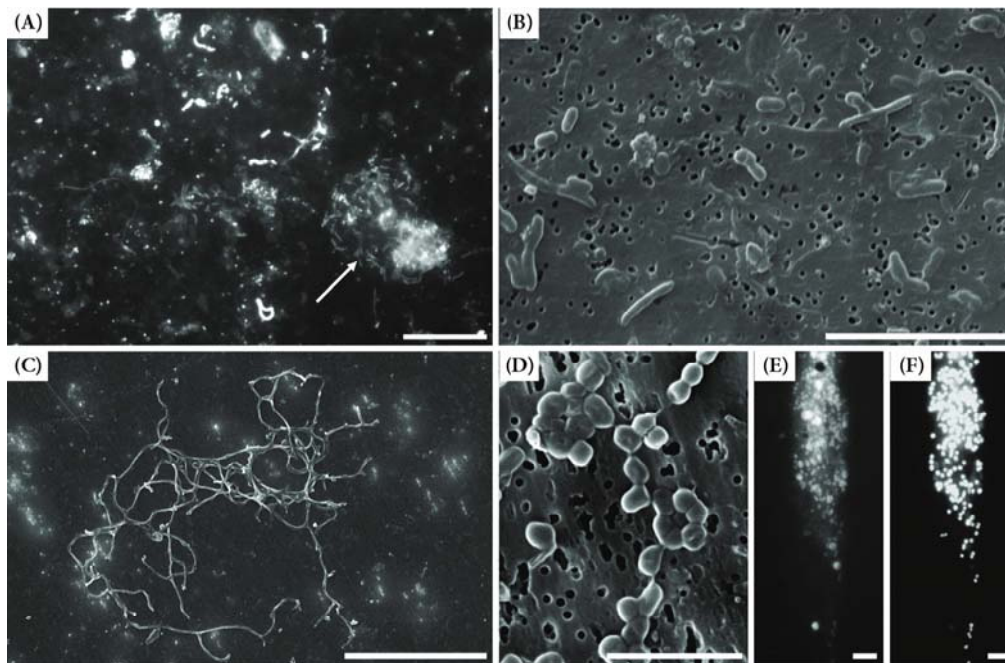
In 2007, picocyanobacterial abundance varied from 0.7 to  $43 \times 10^3$  cells/ml, and the maximum value was found in the middle layers of the cores A73 and B73 (25–37 and 24–39 cm, respectively). The concentration measured in the cores from the offshore site in the same year was an order of magnitude lower (0.9 to  $4.9 \times 10^3$  cells/ml). Maximal numbers of cyanobacteria were detected in the lower layers (cores C73 and C83). In core C83, cyanobacteria and picoalgae numbers were lower than those in the ice cores sampled at the coastal and offshore sites in 2007.

#### Biomass of heterotrophic bacteria

TBN ranged from 0.1 to  $2.2 \times 10^5$  cells/ml. Bacterial biomass did not show vertical stratification and was lower than algal biomass (Fig. 2). In C83, bacterial biomass was higher than algal biomass. Most bacteria were short rods and cocci (0.3 to 1.5  $\mu\text{m}$  in diameter), as either free-living or aggregated into long strands and shapeless colonies (Figs. 4A, B, and D). Crustacean pellets were also a major source of bacteria (Figs. 4E and F). In March 2007, large amounts of yeast-like cells and actinomycete mycelium were found in the middle ice layers of core A73 (Fig. 4C).

#### Inorganic nutrients

Vertical profiles of nitrate, phosphate, and silica were markedly different among the ice cores (Fig. 2). In the case of phosphate, the top layers of ice cores generally showed



**Fig. 4.** Morphological variations of bacteria and cyanobacteria from ice cores. (A) morphotypes of single and aggregated (arrow) bacteria; (B) coccoid, ellipsoid and rod-like cells of bacteria and cyanobacteria; (C) actinomycetes; (D) aggregations of coccoid bacteria; (E and F) crustacean pellet comprising mainly picoplanktonic cyanobacteria; (E) DAPI staining, ultraviolet filter; (F) autofluorescence of picocyanobacteria, green filter; (A, E, and F) fluorescence microscopy; (B, C, and D) scanning electron microscopy. Scale bars: A and B=10  $\mu\text{m}$ ; C=50  $\mu\text{m}$ ; D-F=5  $\mu\text{m}$ .

high values in the vertical profiles although the depth of the minimum concentration differed. In the A73 and C73 cores, the depths for the minimum of nitrate concentration coincided with the maximum for algal biomass, implying the utilization of essential inorganic nutrients by the algae. In shore samples, silica was low in the top layers while it was maximal at the offshore site. Typically, a low concentration of silica in water is indicative of growth of coastal siliceous scale-bearing chrysophytes and diatoms. Therefore, the difference in vertical profiles could be related to the growth of diatoms. In core C83, algal growth was low throughout the core, and the concentrations of phosphate and silica were highest on the top. The profile appears to indicate atmospheric origin of the two nutrients. In this ice core, nitrate concentration was exceptionally low when compared to the other cores (Fig. 2).

The ammonium and nitrite-nitrogen concentrations varied from 0.01 to 0.06 and from 0.001 to 0.005 mg/L, respectively. Destruction of ice organisms contributed to high ammonium and nitrite concentrations. When these observations were considered together with covariation of vertical profiles of nitrate or silica with algal biomass, it was concluded that the chemical composition of ice layers in Lake Baikal was related to the growth and demise of extremophile microorganisms within the ice.

## Discussion

### Viability of algae

The data in this study and observations from previous re-

search (Bondarenko *et al.*, 2000, 2006; Obolkina *et al.*, 2000; Bordonsky *et al.*, 2003) show considerable temporal and spatial variations in the abundance and composition of organisms in the ice covering Lake Baikal. The presence of microorganisms in ice depended on the location of the ice, e.g., littoral or pelagic locations. Monthly and annual differences in the composition and abundance of various species of algae and bacterial biomass were demonstrated in this study. This observation strongly indicates that the microbial extremophiles in the Baikal ice cover are highly dynamic and viable. The results of many studies testify to the viability of organisms inhabiting the solid ice (Bondarenko *et al.*, 2000, 2006; Zavoruev, 2000; Mosier *et al.*, 2007; Frenette *et al.*, 2008), and the data obtained in the Greenland Ice Sheet Project showed that Greenland ice cores contained a diversity of microorganisms, maintaining their survival for at least 120,000 years (Miteva *et al.*, 2004).

A low concentration of nitrate in core C83 accounted for low algal biomass. The correspondence of the depth of the minimal nitrate concentration, and the maximum algal biomass in cores A73 and C73 also indicates utilization of nitrate by the algal community. The autofluorescence of photosynthetic pigments also suggested the viability of algal cells (Fig. 3A). We were actually able to cultivate some cyanobacteria from the ice. The dynamics of the vertical profiles of silica and phosphorus also corroborated the utilization of inorganic nutrients via microbial metabolism. On the other hand, increases in ammonium concentration and the appearance of nitrites could be explained as death and/or decomposition of the ice microbes.

### Origins of biota in ice

Since planktonic and benthic algae were found in the ice cores, several possibilities can be raised. The presence of benthic organisms in pelagic locations of the lake, particularly in the upper part of the ice, could be the result of autumn storm activity. Another explanation is that the ice attached to the coast drifted into the pelagic regions via offshore currents during the initial period of ice formation. Other evidence supporting this are the presence of terrigenous particles of various size and shape and the remains of diatom valves as well as cysts of chrysophytes in all samples collected in 2008.

### Intersystem comparison

The results of this study suggest that the ice communities of Lake Baikal resemble marine and freshwater ice studied in other areas. Ice algae contributed to the primary production of Lake Baikal in a similar way to Polar oceans (Horner, 1985). Due to a short ice-cover period on Lake Baikal, only two of the three structural components observed during primary production within sea ice can occur, i.e. algae overgrowing on the bottom of the ice cover and specialized microalgal communities inhabiting the seasonal ice. The difference is that an algal community thriving in multi-year ice does not exist in Lake Baikal (Hegseth, 1998). The ice communities of Lake Baikal are dominated by diatoms like those of marine environments (McRoy *et al.*, 1972; McRoy and Goering, 1974; Horner, 1976; Dunbar, 1979; Satoh *et al.*, 1989) and river environments (Yur'ev and Lebedev, 1988; Frenette *et al.*, 2008). Also found in Baikal ice were dinoflagellates (e.g. *Gymnodinium* and *Peridinium*), as well as cryptomonads, which are common dwellers of sea ice and snow-ice cover of Alpine lakes (Felip *et al.*, 1995). Bacteria and colorless flagellates abundant in Baikalian ice have also been found in sea ice (David *et al.*, 1986).

### Material cycle

Heterotrophic organisms remineralize organic matter produced by algae, so the products of mineralization can be utilized for further photosynthetic activity of the producers. Ice bacteria may be involved in amino acid release (David *et al.*, 1986). An analysis of dissolved free amino acids produced by algae in Antarctic lake ice showed that amino acids were typically present in the middle layers of ice cores (Yang, 1995). The dissolved amino acids stored in the ice were considered an essential part of the organic matter and a nutrient reservoir for algae and microorganisms. Therefore, the association of hetero- and phototrophic organisms in ice communities provides benefits of enhancing their survival under extreme conditions by building a short, but highly viable, food chain. In the course of earlier investigations (Timoshkin, 2001; Bordonsky *et al.*, 2003; Bondarenko *et al.*, 2006), it became evident that freeze-resistant organisms of Lake Baikal serve as a plentiful and valuable food resource for planktonic and benthic animals, because they include high concentrations of unsaturated fatty acids (over 75%), including linoleic, eicosapentaenoic (EPA), and docosahexaenoic (DHA) acids (Osipova *et al.*, 2009). These

compounds, providing freeze-resistance, might be transferred through the food chain involving ice algae.

### Conclusion

This study describes the ice-dwelling communities of Lake Baikal and their impact on the ice chemistry. It has been shown that stratified distribution of microalgae and their activity strongly affects the chemistry of ice layers. Therefore, the abundance of microalgae within ice will have evident effects on the quantitative characteristics of the spring bloom of phytoplankton in Lake Baikal. Prolific growth of organisms in extreme conditions suggests that there are certain benefits of ice dwelling in contrast to life in the under-ice waters, although there is still much to be examined to support this conclusion. Significant changes in the chemical composition of the ice also testified to the high metabolic activity of extremophiles in the ice of Lake Baikal.

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