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Photosynthetic potential of phytoplankton in the deep water of Lake Baikal, Russia

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Abstract We examined the photosynthetic activity of the phytoplankton community collected from the surface to a depth of 1000 m in the south basin of Lake Baikal. Experiments were conducted in June (mixing period) and August (stratified period). The carbon fixation rate was measured by the use of a ^{13}C tracer after the incubation of samples under light conditions in the upper water column. Photosynthetic fixation of ^{13}C was detected for samples collected from a depth of 500 m, indicating the viability of phytoplankton in deep water. The community composition was dominated by Bacillariophyceae in deep water. The finding of lower activity at a depth of 200 m than that at a depth of 500 m in August suggests that the spring diatom bloom could be a significant source of viable populations at a depth of 500 m. Photosynthetic activity was not detected in samples collected at a depth of 1000 m.

Key words Deep water · Light · Photosynthesis · Phytoplankton · Water mixing

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Introduction

Lake Baikal is the deepest lake (1620 m) in the world and contains the world's largest volume of freshwater (23000 km^3), corresponding to about 20% of total lake water volume on Earth (Kozhova and Izmest'eva 1998). Despite its depth, Weiss et al. (1991) have suggested that the time scale of deep water renewal is relatively short (about 8 years). The mixing mechanism has been the subject of intensive research during the past decade (e.g., Shimaraev et al. 1993).

Vertical mixing can enhance the transport of phytoplankton from the euphotic to the aphotic zone, although other mechanisms such as diffusion and sinking (sedimentation) could also contribute to downward transport. The fates of phytoplankton cells in the aphotic zone may include consumption by grazers, lysis, and burial in the sediment. Beside these processes, one could hypothesize that some phytoplankton cells survive in the aphotic zone for a certain period of time and reenter the euphotic zone as a result of upward transport driven by vertical mixing. In Lake Tahoe, a deep (450 m) oligotrophic lake, Kiefer et al. (1972) have reported that aphotic phytoplankton are viable throughout the water column. Tilzer et al. (1977) have suggested that viable cells in the aphotic zone could reenter the euphotic zone by upwelling, and these cells could play an important role as seed populations for the vernal bloom. Given the large extension of the aphotic zone and the active renewal of deep water (Weiss et al. 1991), the role of viable phytoplankton in the aphotic zone could be significant in the pelagic ecosystem of Lake Baikal. However, little is known about the viability of phytoplankton in the deep water of Lake Baikal. The purpose of the present study was to examine the photosynthetic activity of phytoplankton cells collected from the deep waters of Lake Baikal.

Methods

Surveys were conducted during a mixing period (24–25 June 2001) and during a thermally stratified period (16–17 August 2001) aboard the RV *Vereshchagin*. June and August correspond to the months of highest and lowest water transparency, respectively (Shostakovich 1924). Water samples were collected at a station in the south basin (sampling station, 5 km off Listvyanka: 51°48′N, 104°57′E, 1430 m deep), using 10-l Niskin water samplers. Sampling depths were 0, 5, 20, 50, 100, 200, 500, and 1000 m. Water samples for determination of chlorophyll *a* concentrations were divided into three fractions according to the cell size using a 20-μm-mesh net and a 2-μm-mesh Nuclepore membrane filter. Thus we had fractions of less than 2 μm (picophytoplankton) and less than 20 μm (pico- and nanophytoplankton), and a fraction including all phytoplankton (pico-, nano- and microphytoplankton). After the fractionation, phytoplankton were collected on Whatman GF/F glass-fiber filters. Chlorophyll *a* concentrations were measured by a modified method of Marker et al. (1980). Concentrations of NO_3-N and PO_4-P were determined by the hydrazine reduction method (Mullin and Riley 1955) and the molybdate method (Murphy and Riley 1962), respectively. At the same time as samples were collected, water temperature was measured vertically with a conductivity, temperature and depth (CTD) probe (3.0-inch Micro CTD, Falmouth Scientific, Cataumet, MA, USA). Micro- and nanophytoplankton were identified and counted using a Karl Zeiss Jena Amplival microscope with magnifications of ×400 and ×800. Cell counts were converted to algal biomass taking account of measurements of individual cells according to Makarova and Pichkily (1970).

The carbon uptake rate of phytoplankton was measured using ^{13}C. Water samples for measurement of primary production were collected from depths of 5, 100, 200, 500, and 1000 m (a depth of 50 m was added in August) at the sampling station. Immediately after sampling, 300-ml polycarbonate bottles were filled with lake water. Then, we added $NaH^{13}CO_3$ (5%–10% of the total inorganic C of the lake) to the bottles. The bottles were incubated for 6 h between 1100 and 1700 (the meridian time is 1400) local time at another station (incubation station; 200 m off the Limnological Institute at Listvyanka: 51°52′N, 104°50′E, 50 m deep). Taking the differences in transparency into consideration, the incubation depths in June (1.6, 2.6, 4.3, 8.2, 14.6, and 23.6 m) were different from those in August (0.1, 1.3, 3, 5.9, 9.8, and 12.6 m). Thus we incubated one bottle with water collected from each depth at each incubation depth. After incubation, the water in the bottles was filtered onto precombusted (450°C) Whatman GF/F glass-fiber filters. The filters were treated with HCl fumes to remove carbonate and then dried in a desiccator. The concentrations of organic C and the isotope ratios of ^{13}C and ^{12}C in the samples were determined with a $^{13}CO_2$ analyzer (EX-130S, Jasco, Tokyo, Japan). The concentrations of inorganic C in the water samples were determined with a total organic C analyzer (TOC-500, Shimadzu, Kyoto, Japan). The carbon uptake rate was calculated according to Hama et al. (1983). Water temperature was also examined with the CTD probe. Using a quantameter (LI-1000, LiCor, Lincoln, NB, USA), the light conditions during the incubation were calculated by the relationship between light attenuation and light intensity in the air. The air light intensity was measured every 30 min on the deck of the vessel anchored near the incubation station.

Results

The vertical distributions of temperature (Fig. 1), chlorophyll *a* (Fig. 2A), and nutrient concentrations (Fig. 2B) were relatively uniform in the upper 200 m in June, whereas a clear thermal stratification was observed in August (Fig. 1), with high concentrations of chlorophyll *a* and depletion of nutrients in the upper 50-m layer (Fig. 2). The different size fractions of phytoplankton (<2 μm, 2–20 μm, and >20 μm) contributed almost equally to the total chlorophyll *a* concentrations in June, whereas pico- (<2 μm) and nanophytoplankton (2–20 μm) were dominant in August (Fig. 2A). The total amounts of chlorophyll *a* integrated over the upper water column (200 m for June, 50 m for August) were greater in June (106 mg m^{-2}) than in August (77 mg m^{-2}), with a noticeable decline of microphytoplankton (>20 μm fraction) over the season (Table 1).

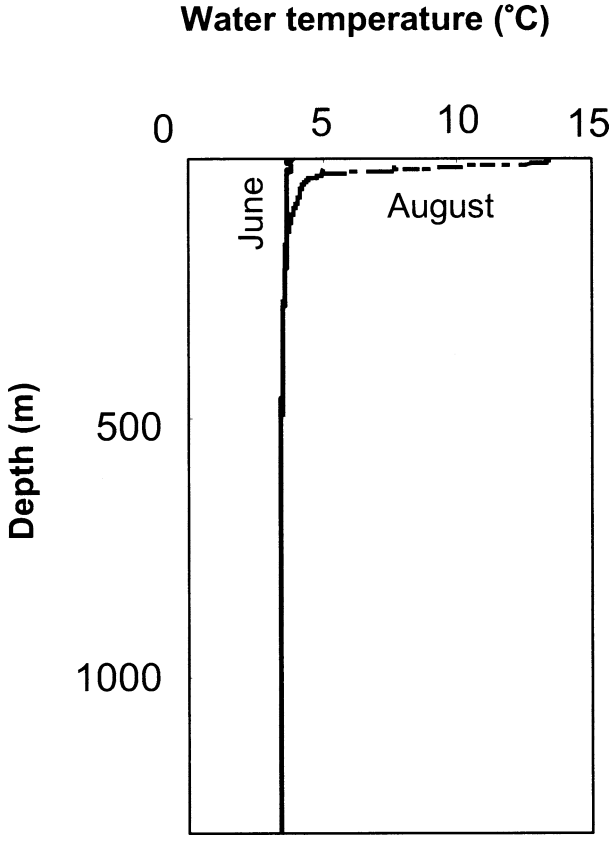

Fig. 1. Vertical profiles of water temperature at the sampling station

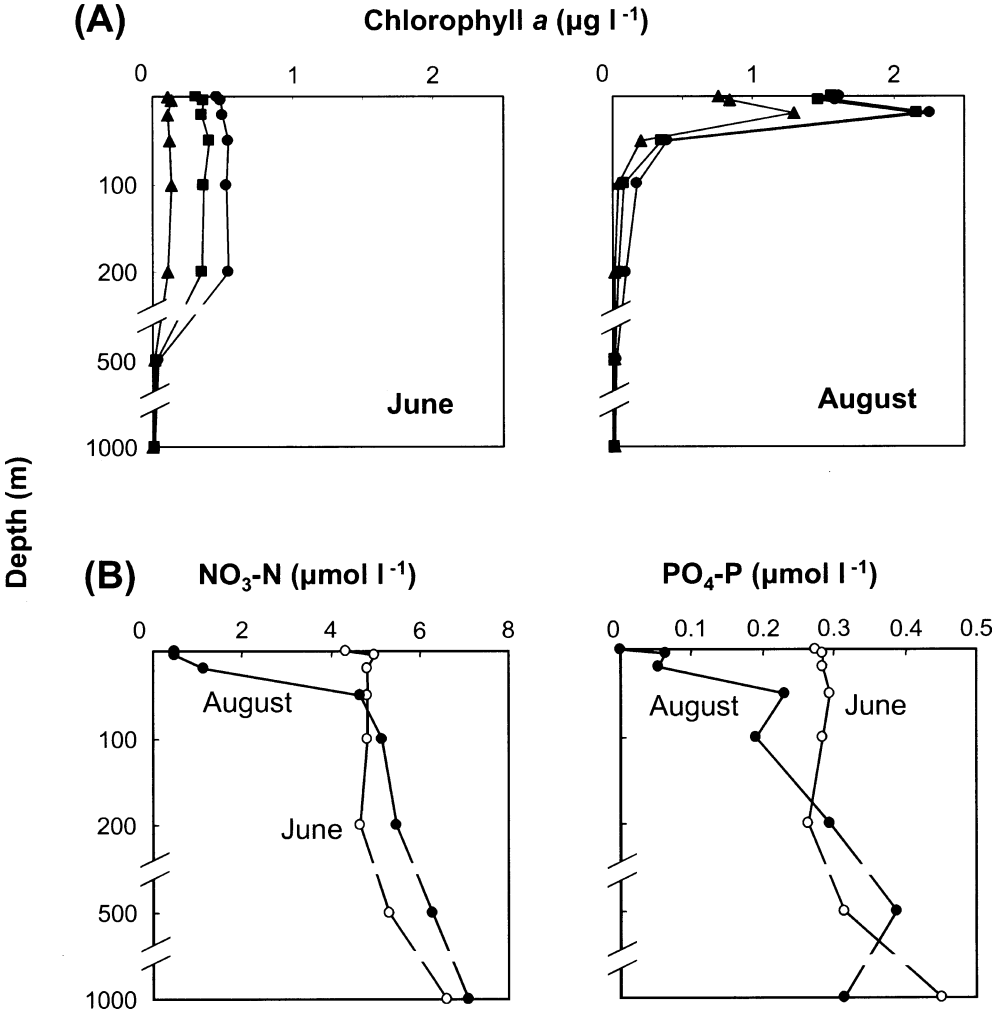

Fig. 2. (**A**) Vertical profiles of chlorophyll *a* concentrations in unfiltered lake water samples (*circles*) and those in samples size-fractioned by using a 20-µm-mesh screen (*squares*) and 2-µm-pore-size filters (*triangles*). (**B**) Vertical profiles of dissolved inorganic nutrients (nitrate and phosphate)

Table 1. Areal levels of chlorophyll *a* ($mg\,m^{-2}$) in the upper water column (0–200 m for June, 0–50 m for August)

	Phytoplankton			
	Pico (<2 µm)	Nano (2–20 µm)	Micro (>20 µm)	Total
June	24	49	33	106
August	43	30	4	77

In June, the community composition of nano- and microphytoplankton varied little in the upper 200 m and was characterized by high contributions of three phyla, including Bacillariophyceae, Dinophyceae, and Chlorophyceae (Fig. 3). In deep waters (500 and 1,000 m) a large fraction (>75%) of total phytoplankton biomass was accounted for by Bacillariophyceae. In August, the diversity at the phylum level was high in the surface layer (5 m); five phyla including Bacillariophyceae, Dinophyceae, Chlorophyceae, Cryptophyceae, and Chrysophyceae contributed significantly to the total biomass (Fig. 3). The phylum diversity decreased with depth with a successional shift toward dominance by Bacillariophyceae (Fig. 3).

We measured ^{13}C-uptake by phytoplankton collected from different depths after incubation under various light conditions (Fig. 4). To compare the potential of photosynthetic activities among phytoplankton collected from different depths, we calculated the carbon-specific production rate (P_c) by dividing the rate of ^{13}C-fixation by the concentration of particulate organic carbon. Note that this index, P_c, can be biased by the presence of detritus and heterotrophs, which contribute to the concentration of particulate organic carbon. The carbon fixation rate normalized by chlorophyll *a* concentration was not examined because of large errors associated with chlorophyll *a* determinations for deep water samples caused by low chlorophyll *a* concentrations ($<0.04\,\mu g\,l^{-1}$, Fig. 2A). In both June and August, our data on relationships between P_c and light intensity (average value during the incubation period, Fig. 4) indicate that phytoplankton cells in deep water (500 m) are capable of photosynthesis when they are exposed to surface levels of irradiance (Fig. 4). It is interesting to note that in August, P_c decreased gradually from the surface to a depth of 100 m, to reach undetectable levels at 200 m, but then increased to detectable levels once more at a depth of 500 m (Fig. 4). In both months, *Cyclotella baicalensis* and *C. minuta* were the

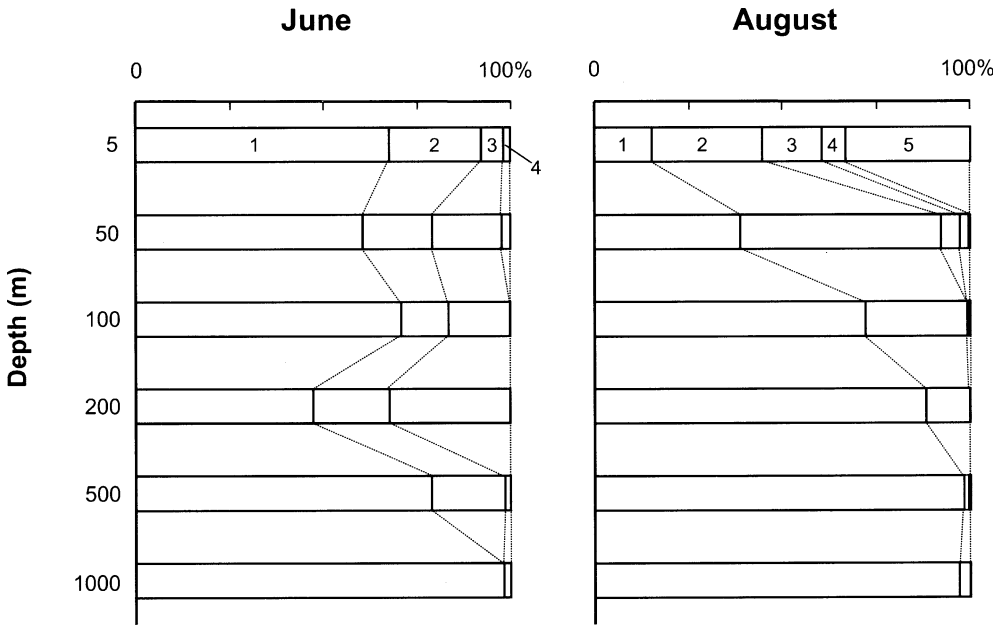

Fig. 3. Relative occurrence of five observed phyla based on biomass at each depth. *1*, Bacillariophyceae [including *Cyclotella minuta* (Skv.) Antipova, *Cyclotella baicalensis* (Meyer) Skv., *Synedra acus* (Kütz.) var. *radians* (Kütz.) Hust., and *Aulacoseira skvortzowii* Edlund et al. as relatively abundant species in June; *Cyclotella minuta*, *C. baicalensis*, *Aulacoseira baicalensis* (Meyer) Simonsen, and *Synedra acus* in August]. *2*, Dinophyceae (*Gymnodinium coeruleum* Antipova and *Glenodinium* spp. in June and August). *3*, Chlorophyceae [*Monoraphidium contortum* (Thur.) Komarkova-Legnerova, *Monoraphidium arcuatum* (Korsch.) Hindak, and *Koliella longiseta f. variabilis* Nygaard in June and August]. *4*, Cryptophyceae (*Chroomonas acuta* Utermohl in June and August). *5*, Chrysophyceae (*Dinobryon cylindricum* Imhof and *Dinobryon bavaricum* Imhof in August)

dominant species at a depth of 500 m. Photosynthetic activity was not detected for samples collected at a depth of 1000 m (Fig. 4).

Discussion

Our data indicate that phytoplankton at a depth of 500 m are capable of photosynthesis when they are exposed to the irradiance prevalent in the upper layer (Fig. 4). Nano- and microphytoplankton communities in this water layer were dominated by Bacillariophyceae in both June and August (Fig. 3), suggesting active transport and survival of this phylum in the deep water. This could be explained by a fast sinking rate of Bacillariophyceae due to the possession of silicon frustules. Alternatively, the surface phytoplankton community could be transported down to the deep water as a result of vertical mixing. Consistent with this hypothesis, Weiss et al. (1991) and Shimaraev et al. (1993) have reported that thermal baric instability causes rapid transport of surface water to deep layers in spring. Thus, spring Bacillariophyceae communities proliferating in the surface waters might be rapidly transported to the deep layers with minimal loss of photosynthetic function during transit.

One interesting finding of our study was that the photosynthetic potential of phytoplankton was detected at 500 m but not at 200 m in August. This result suggests that the photosynthetic potential at a depth of 500 m in August could be a remnant of the previous spring bloom, rather than an indication of transport of the overlying community in August (if the latter were the case, we should have observed higher photosynthetic potential at a depth of 200 m than at a depth of 500 m). The most probable reason for the survival of phytoplankton under aphotic conditions is that they can enter a state of reduced metabolism by which all catabolic processes are slowed (Hellebust and Terborgh 1967). Although phytoplankton in Lake Baikal in June were exposed to a gradual decline in light intensity during downward transport, other conditions such as temperature (Fig. 1) and nutrients (Fig. 2B) varied little with depth. The consistency in temperature and nutrients might facilitate the physiological adaptation of phytoplankton. In contrast, the summer phytoplankton community proliferating in the surface layer would likely experience a drastic shift in temperature (Fig. 1) during vertical transport, which could result in the rapid loss of photosynthetic potentials. If the above interpretation is correct, the viable phytoplankton stock in the deep water of Lake Baikal could be largely derived from the spring bloom.

Our data are consistent with the finding of Kiefer et al. (1972) who observed the viability of phytoplankton in deep layers (>300 m) of Lake Tahoe. Although we failed to detect photosynthetic potentials for samples collected in the deeper layer (1000 m), it awaits future research to determine whether such activity can be detected by the use of more sensitive techniques. It also remains to be seen if the

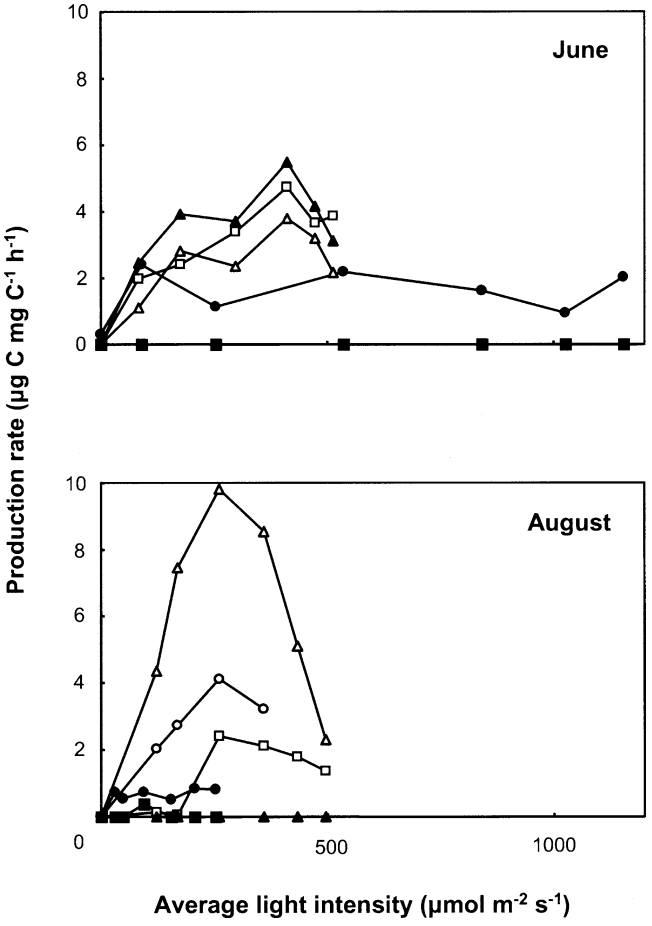

Fig. 4. Carbon-specific production rate versus irradiance relationships of phytoplankton collected from different depths. The average light intensity was dependent upon the weather condition (i.e., cloudy or sunny) when the bottles were incubated. The light intensity for the incubation depth was calculated using the average light intensity on the deck during the incubation period and the light attenuation coefficient determined at the beginning of the incubation. *open triangles*, 5 m; *open circles*, 50 m; *open squares*, 100 m; *solid triangles*, 200 m; *solid circles*, 500 m; *solid squares*, 1000 m

stock of viable phytoplankton in the huge volume of deep water in Lake Baikal can play a role as a "seed bank" for phytoplankton populations that may contribute to the maintenance of biodiversity.

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