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Abundance, growth and grazing loss rates of picophytoplankton in Barguzin Bay, Lake Baikal

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Abstract

The abundance, growth, and grazing loss rates of picophytoplankton were investigated in August 2002 in Barguzin Bay, Lake Baikal. Water samples for incubation were taken once at a near-shore station and twice at an offshore station. Contributions of picophytoplankton to total phytoplankton were high (56.9–83.9%) at the offshore station and low (5.8–6.8%) at the near-shore station. The picophytoplankton community in the offshore station comprised mainly phycoerythrin (PE)-rich cyanobacteria, with eukaryotic picophytoplankton being less abundant. In contrast, as well as PE-rich cyanobacteria and eukaryotic picophytoplankton, phycocyanin (PC)-rich cyanobacteria were found in the near-shore station. At the offshore station, growth and grazing loss rates on 25 August were 0.56 and 0.43 day^{-1}, respectively, and on 29 August, 0.69 and 0.83 day^{-1}, respectively. At the near-shore station, growth and grazing loss rates were 1.61 and 0.70 day^{-1}, respectively. These results show that there is a difference in the abundance, composition, and ecological role in the microbial food web of picophytoplankton between the near-shore and the offshore areas in Barguzin Bay.

Introduction

Lake Baikal, located in central Siberia, Russia, is the world's deepest large lake (Kozhov 1963). Primary production in the lake is usually high during the summer (Kozhova 1987; Yoshida et al. 2003), with picophytoplankton accounting for a significant portion of the total primary production in its southern basin (Nagata et al. 1994; Yoshida et al. 2003). Several groups of investigators have studied

the abundance of picocyanobacteria in Lake Baikal (Boraas et al. 1991; Nagata et al. 1994; Belykh and Sorokovikova 2003). Belykh and Sorokovikova (2003) found that the small (pico) phytoplankters are abundant from the northern to the southern basin during the summer, with the density of picocyanobacteria in the southern basin reaching as high as 2×10^6 cells ml^{-1} (Nagata et al. 1994).

Picophytoplankton consist of eukaryotic and prokaryotic organisms.

Synechocystis limnetica was the first picophytoplankter in Lake Baikal to be described (Popovskaya 1968). Subsequent investigations involving the use of molecular biological techniques have resulted in the identification of the eukaryotic and prokaryotic picoalgae *Choricystis* (green alga) and *Synechococcus* (cyanobacterium), respectively (Belykh et al. 2000; Semenova et al. 2001). At the present time, the *Synechococcus* identified by Semenova et al. (2001) is assigned to *Cyanobium*, as suggested by Boone et al. (2001) and Ernst et al. (2003). However, information on their ecological role in the planktonic food web is limited.

Barguzin Bay, in the central basin of Lake Baikal, receives inflow from the Barguzin River. Recently, Nakano et al. (2003) reported that picocyanobacteria are present in abundance in this bay also, however they did not investigate the growth and grazing loss rates of the picophytoplankton. The river water flowing into the bay contains significant amounts of inorganic and organic matter and, consequently, there is an environmental gradient from near-shore areas to offshore areas. It is expected that the structure and function of the plankton community will change in relation to this gradient. Further, the composition of the picophytoplankton community may also change from near-shore to offshore areas in the bay.

The aim of the present study was to determine possible differences in the abundance, growth, and grazing loss rates of picophytoplankton in the near-shore and offshore areas.

Materials and methods

Study site and sampling

The study was conducted at two stations in Barguzin Bay in August 2002 (Figure 1). Water depths at these stations were: 6 m for Sta. 1 (53°25′48″ N; 108°58′24″ E) and 61 m, at Sta. 4 (53°25′17″ N; 108°46′47″ E). Water was sampled with a 10-l Van-Dorn water sampler at depths of 0 and 3 m for Sta. 1 and at 0, 5, 10, 15, 20 and 50 m for Sta. 4. The near-shore station (Sta. 1) was located so as to directly receive the inflow of the Barguzin River. Water temperature and photosynthetically active radiation (PAR) were measured with a thermometer and a quantum sensor (Li-193A; Li-Cor, Lincoln, Neb.), respectively. On the basis of the PAR measurements at depths of up to 28 m, we calculated the attenuation coefficient (K).

Chlorophyll a *measurements*

Size-fractionated chlorophyll *a* (Chl. *a*) concentrations were determined using a 2-μm Nuclepore filter (Whatman, N.J.) and a 10-μm plankton net. Between 100 and 300 ml of the water samples was filtered through a GF75 glass-fiber filter with a mean mesh size of approximately 0.3 μm (Advantec, Tokyo, Japan). The filters were then stored in a freezer (−20°C) for analysis for a maximum of 4 days. The Chl. *a* was extracted from the filter with methanol (Wako, Osaka, Japan) overnight at room temperature and the concentrations of the extracted Chl. *a* determined fluorometrically (APHA, AWWA, WPCF 1985) with a 10-AU fluorometer (Turner Designs, Sunnyvale, Calif.) calibrated with pure Chl. *a* (Wako, Osaka, Japan).

Determination of nutrient concentration

In addition to the samples taken at Stations 1 and 4, we sampled water at a 0-m depth at the mouth of the Barguzin River for determination of the phosphate concentration. A portion of this water was filtered through a GF/F filter, and the ammonia, nitrate, and phosphate concentrations in the filtrate were determined by the indophenol method (Sagi 1966), the hydrazinium reduction method (Mitamura 1997) and the molybdenium blue method (Murphy and Riley 1962), respectively.

Picophytoplankton counting

Picophytoplankton cells were counted by epifluorescence microscopy (Maclsaac and Stockner

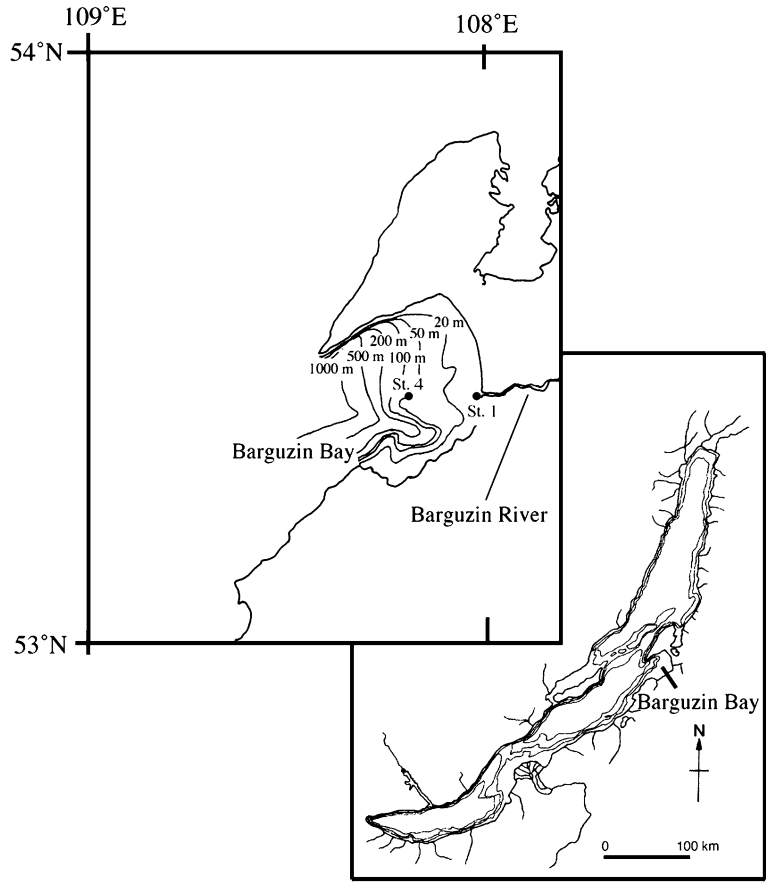

Figure 1. Map of sampling stations in the Barguzin Bay, Lake Baikal.

1993). Water samples were fixed with glutaraldehyde (Wako) at a final concentration of 1% and stored in a refrigerator. Aliquots (5–30 ml) of the fixed water samples were filtered through 0.2-μm Nuclepore filters and the filters mounted on slides with immersion oil (Olympus, Tokyo, Japan). Picophytoplankton cells were counted with an Olympus BHS-EF (Tokyo, Japan) equipped with an epifluorescence illumination system using blue (excitation filter, BP490; barrier filter, AFC + 0515; dichromic mirror, DM500) and green (BP545, O590, DM580) filter sets. Eukaryotic picophytoplankton cells fluoresce red under blue light excitation and very weak red or not at all under green light excitation (Maclsaac and Stockner 1993). Phycoerythrin (PE)-rich and phycocyanin (PC)-rich picocyanobacteria, respectively, fluoresce orange and dull red under blue light excitation and bright orange and red under green light excitation (Maclsaac and Stockner 1993). According to the fluorescence characteristics as mentioned above, we separately enumerated these three types of picophytoplankton. At least 100 cells of picophytoplankton were counted for each sample. All of the samples were counted within 5 days of collection.

Dilution experiments

Growth and grazing loss rates of picophytoplankton were determined by the dilution technique of Landry and Hassett (1982). One experiment was conducted at the near-shore station (August 28), and two experiments were conducted at the offshore station (August 26 and 29).

The filtrates of the water samples (< 150 μm and < 0.2 μm) were mixed in different ratios: 1.20 l, 1.00 l, 0.90 l, 0.75 l, 0.60 l, 0.40 l, 0.25 l, and 0.10 l (volume of the < 150-μm filtrate in a total of 1.20 l). The diluted lake water samples thus prepared were poured into 1.2-l polycarbonate bottles and supplemented with nitrogen (NH_4Cl) and phosphorus (K_2HPO_4) nutrients at final concentrations of 15 μmol N l^{-1} and 1 μmol P l^{-1}, respectively. These eight bottles were incubated in a container with a flow-through surface lake water system on shipboard for 24 h. To mimic the *in situ* light environment, a neutral density filter that reduces light intensity uniformly from 400 to 700 nm was used (data not shown). Water temperature and light intensity that passed through the filter were measured every 2–3 h during the daytime. Following the 24-h incubation, Chl. *a* concentration in the < 2-μm fraction was determined as previously described. The apparent specific growth rates were calculated from changes in the Chl. *a* concentrations assuming exponential growth according to the following equation: $\mu = \ln (Nf/N0)/t$, where N0 and Nf are Chl. *a* concentrations at time zero and after the 24-h incubation, respectively, and t is the incubation period of 1 day. Growth and grazing loss rates ± the standard error were calculated from the apparent specific growth rates in each bottle using linear regression analysis according to Landry and Hassett (1982).

Results

Water temperature, attenuation of PAR, and nutrient concentrations

The water temperature at the surface was slightly higher at Sta. 1 (17.3 °C) than that at Sta. 4 (15.9 °C; Figure 2). Thermal stratification did not develop at Sta. 1, but it did develop at Sta. 4, with a thermocline that was between 8 and 20 m in depth. The attenuation coefficients were 1.11 and 0.56 m^{-1} at Stations 1 and 4, respectively. The concentrations of inorganic nitrogen were low at both stations (Table 1): while phosphate concentrations (0.15–0.16 μmol P l^{-1}) were higher at Sta. 1 than at Sta. 4. The much higher phosphate concentration (0.22 μmol l^{-1}) in the water of the Barguzin River suggested that the river was the source of the phosphorous supply.

Abundance, composition, and contribution of picophytoplankton

At Sta. 1, the Chl. *a* concentrations in the < 2-μm fraction ranged from 0.73 to 0.81 μg l^{-1} (Figure 2) at depths of 0–3 m, while at Sta. 4, the Chl. *a* concentrations in the < 2-μm fraction ranged from 1.20 to 1.65 μg l^{-1} at depths of 0–20 m and was 0.18 μg l^{-1} at 50 m. Chl. *a* concentrations in the total fraction at Sta. 1 were higher than those at St. 4, whereas Chl. *a* concentrations in the < 2-μm fraction at Sta. 4 were higher than those at Sta. 1. Hence, the contribution of picophytoplankton was low at Sta. 1 (5.3–6.8%) and high at Sta. 4 (58.9–83.5%).

Cell densities of picophytoplankton at Sta. 4 ($47.3–57.1\times10^4$ cells ml^{-1}) were approximately sevenfold higher than those at Sta. 1 ($7.6–8.5\times10^4$ cells ml^{-1}; Figure 2). However, the densities of eukaryotic picophytoplankton were similar between the stations (Sta. 1: $1.8–2.1\times10^4$ cells ml^{-1}; Sta. 4: $1.0–5.1\times10^4$ cells ml^{-1}). Most of the picophytoplankton found at Sta. 4 were coccoid PE-rich cyanobacteria. The eukaryotic cells were slightly larger than prokaryotics ones based on visual observation; the cells were not measured. Epifluorescence microscopy revealed the presence of *S. limnetica*-type cells at Sta. 4 but not at Sta. 1. PC-rich picocyanobacteria as well as PE-rich picocyanobacteria were present at Sta. 1; in this respect – the presence of PC-rich picocyanobacteria at Sta. 4 – the compositions of picophytoplankton differed between the two stations.

Incubation experiments

Water temperature and light intensities in the container during incubation ranged from 13.1 to 18.7 °C and from 30 to 270 μE m^{-2} s^{-1}, respectively (Table 2). Incubation conditions were similar among the incubation experiments.

At Sta. 1, the growth rate and grazing loss of picophytoplankton (< 2-μm fraction) were, respectively, 1.61 and 0.70 day^{-1} (Figure 3). The grazing loss accounted for 44% of the growth rate in the < 2-μm fraction. At Sta. 4, the growth and

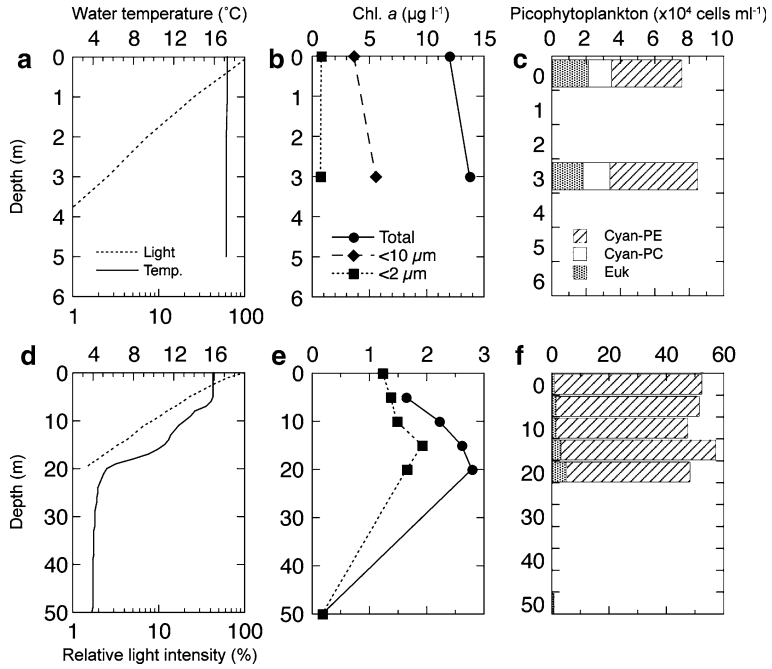

Figure 2. Vertical distributions of water temperature and relative light intensity (**a** and **d**), Chl. *a* concentrations in the different size fractions (**b** and **e**), and picophytoplankton abundance (**c** and **f**) at Stations 1 and 4. **a–c** Sta. 1, **d–f** Sta. 4.

Table 1. Nutrient concentrations in Barguzin Bay (nd not determined).

	Depth (m)	NH_4-N (µmol l^{-1})	NO_3-N (µmol l^{-1})	PO_4-P (µmol l^{-1})
Barguzin River	0	nd	nd	0.22
Station. 1	0	0.22	0.33	0.16
	3	0.02	0.36	0.15
Station 4	0	0.22	0.35	0.03
	5	0.19	0.32	0.01
	10	0.48	0.34	0.01
	15	0.27	0.32	0.02
	20	0.30	1.97	0.02
	50	0.21	8.75	0.41

grazing loss rates on August 25 were 0.56 and 0.43 day^{-1}, respectively, and those on August 29 were 0.69 and 0.83 d^{-1}, respectively. Thus, the grazing loss was 77% of the growth rate on August 26 and 120% on August 28.

Discussion

Although picophytoplankton has been shown to be a dominant primary producer in the pelagic zone of Lake Baikal (Nagata et al. 1994), its ecological importance in the near-shore areas of Lake Baikal has been neglected area of research. The present study has demonstrated that picophytoplankton in these near-shore areas of the lake has a high growth rate although it is more abundant in the offshore area. Picophytoplankton abundance in Lake Baikal is highest during the summer (Belykh and Sorokovikova 2003). The picophytoplankton cell densities that we measured at offshore Sta. 4 were at levels similar to those reported by Nakano et al. (2003), but lower than those in the southern basin (Nagata et al. 1994) during summer. Belykh and Sorokovikova (2003) also reported that the abundance of picophytoplankton was higher in the southern basin. Thus, It would appear that the population of picophytoplankton in Barguzin Bay may be slightly smaller than that in the southern basin, although the reason for this difference is currently unknown.

The composition and abundance of picophytoplankton differed between the offshore (Sta. 4) and near-shore (Sta. 1) stations. Epifluorescence microscopy revealed that the picophytoplankton composition at Sta. 4 was similar to that in the southern basin (Nagata et al. 1994; Belykh and

Table 2. Incubation conditions.

	Experiment 1	Experiment. 4-1	Experiment 4-2
Water temperature (°C)	16.1–18.7	13.1–17.7	13.3–17.0
Light intensity ($\mu E\ s^{-1}\ m^{-2}$)	45–235	40–270	30–266

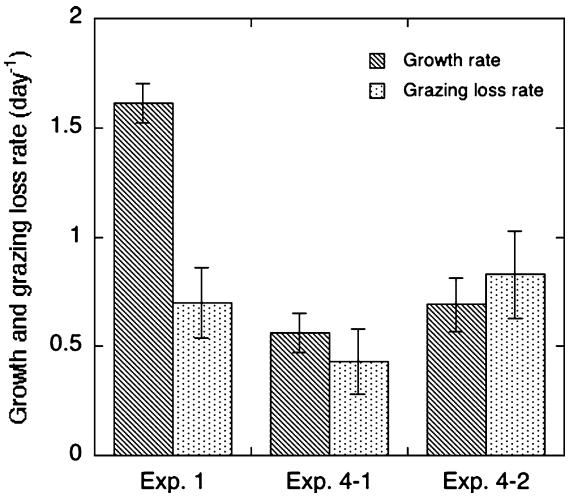

Figure 3. Growth and grazing loss rates of picophytoplankton at Sta. 1 (near-shore, Exp. 1) and Sta. 4 (offshore, Exps. 4-1 and 4-2). Experiments 4-1 and 4-2 were conducted on August 26 and 29, respectively. *Error bars* indicate the standard error.

Sorokovikova 2003). In contrast, PC-rich picocyanobacteria were found only near-shore (Sta. 1), although their densities were low. PC-rich picocyanobacteria are generally found in eutrophic and hypertrophic lakes (Pick 1991; Carrick and Schelske 1997; Vörös et al. 1998). Vörös et al. (1998) found that the underwater light climate was the most important environmental factor affecting the contribution of PC-rich picocyanobacteria to total picocyanobacteria in lakes: when the attenuation coefficient was higher than 2.25 m^{-1}, PC-rich types predominated among the picocyanobacteria; at attenuation coefficients ranging between 0.55 and 2.25 m^{-1}, PC- and PE-rich types co-occurred; at a coefficient below 0.55 m^{-1}, only the PE-rich type bacteria were found. At Stations 1 and 4, the attenuation coefficients were 1.11 m^{-1} and 0.56 m^{-1}, respectively. Thus, our results were consistent with those of Vörös et al. (1998).

The growth rate of picophytoplankton at Sta. 1 was distinctly higher than that at Sta. 4 (Figure 3), possibly due to differences in the composition of the picophytoplankton community. The presence of both PC-rich picocyanobacteria and eukaryotic picophytoplankton may have contributed to the higher growth rates. Both of these types of picophytoplankton are generally found in eutrophic and hypertrophic lakes (Vörös et al. 1998 and Søndergaard 1991; Stockner and Shortreed, 1991, respectively). Picophytoplankton may grow rapidly by using the nutrients, especially phosphorus, supplied by the Barguzin River. In addition to the attenuation coefficient, the nutrient supply was probably another important factor affecting the presence of the PC-rich types at Sta. 1.

Ueno et al. (2005) enumerated the heterotrophic nanoflagellates (HNF) and ciliates and found that the abundance of HNF was similar between the stations (5.4–10.4×10^3 cells ml^{-1}). The cell densities of ciliates at Stations 1 and 4 were 345–649 and 89–245 cells l^{-1}, respectively, with suspension feeders such as *Strombidium* and *Strobilidium* being numerically dominant at both stations. The HNF and suspension feeders of ciliates may be grazers of picophytoplankton, as suggested by many researchers (Caron et al. 1991; Sherr et al. 1991a, b).

Our results indicate that the loss processes of picophytoplankton between the two stations differed. Growth and grazing loss rates of picophytoplankton were very similar at Sta. 4 (Figure 3), which is consistent with studies in temperate lakes (Fahnenstiel et al. 1991; Weisse 1993) and in the southern basin of Lake Baikal (Nagata et al. 1994). Thus, grazing may be a major loss process of picophytoplankton in the pelagic zone of Lake Baikal. However, as the grazing loss rate accounted for only 44% of the growth rate at Sta. 1 (Figure 3), the fate of more than one-half of the picophytoplankton production is currently unknown.

Since the composition of the picophytoplankton community in the near-shore area differs from those in the pelagic zone and their sinking loss is considered to be negligible (Takahashi and Bienfang 1983; Raven 1998), it is a logical assumption that PC-rich

picocyanobacteria should be consumed by grazers in the near-shore area. Moreover, as mentioned above, PE-rich picocyanobacteria were less abundant at Sta. 1 than that at Sta. 4 (Figure 2) even though the growth rate at Sta. 1 was higher than that at Sta. 4 (Figure 3). In addition to biological processes such as grazing, physical processes should be studied in order to understand the loss process of picophytoplankton in the near-shore areas. Flushing with water from the Barguzin River may contribute to the loss of picophytoplankton at Sta. 1. The effects of the mixing process of river water and lake water in the near-shore area and inflowing current of river water in the bay should be studied in the future.

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