

ASIA/OCEANIA REPORT

Takehito Yoshida · Tatsuki Sekino · Motomi Genkai-Kato
Natalia P. Logacheva · Nina A. Bondarenko
Zen'ichiro Kawabata · Tamara V. Khodzher
Natalia G. Melnik · Shuji Hino · Kentaro Nozaki
Yoko Nishimura · Toshi Nagata · Masahiko Higashi
Masami Nakanishi

Seasonal dynamics of primary production in the pelagic zone of southern Lake Baikal

Received: October 9, 2002 / Accepted: December 24, 2002

Abstract We measured primary production by phytoplankton in the south basin of Lake Baikal, Russia, by in situ ^{13}C -bicarbonate incubations within the period March–October in two consecutive years (1999 and 2000). Primary production was highest in the subsurface layer, possibly due to near-surface photoinhibition of photosynthesis, even under 0.8 m of ice cover in March. Areal primary production varied from $79\text{ mg Cm}^{-2}\text{ day}^{-1}$ (March) to $424\text{ mg Cm}^{-2}\text{ day}^{-1}$ (August), and annual primary production was roughly estimated as $75\text{ g Cm}^{-2}\text{ year}^{-1}$, both of which are within the lower range of previous estimates. Size fractionation measurements revealed that phytoplankton in the $<20\mu\text{m}$ fraction accounted for 72%, 96%, and 85% of total primary production in March, August, and October, respectively. The contribution of picophytoplankton ($<2\mu\text{m}$) to total primary production ranged from 41% to 62%. A large fraction (82%–98%) of particulate organic carbon was associated with particles in the $<20\mu\text{m}$ fraction. These results suggest that nano- and picophytoplankton play an important role as primary producers in the pelagic ecosystem of Lake Baikal.

Key words Phytoplankton · Photosynthesis · Size-fractionated production · Particulate organic carbon · Microbial food chain

Introduction

Studies on primary production by phytoplankton are essential for understanding energy and material flows in pelagic ecosystems. In Lake Baikal, the world's deepest freshwater lake, located in the great Baikal Rift of eastern Siberia, seasonal changes in phytoplankton biomass and composition have received much attention (e.g., Kozhova 1987; Bondarenko et al. 1996; Goldman et al. 1996). These studies have revealed clear seasonal patterns in the dynamics of phytoplankton, which are characterized by a periodical bloom of diatoms and/or dinoflagellates under the condition of ice cover in early spring (Antipova 1963; Kozhova 1987) and by a massive propagation of picocyanobacteria in summer (e.g., Bondarenko and Guselnikova 1989b; Boraas et al. 1991; Nagata et al. 1994). Primary production of phytoplankton has been measured since the 1960s by the use of oxygen change and ^{14}C -tracer methods (Moskalenko and Votintsev 1972; Votintsev et al. 1975; Bul'on 1983; Kozhova 1987; Bondarenko and Guselnikova 1989a; Back et al. 1991; Goldman et al. 1996). Based on particular previous data on primary production and estimates of deep water renewal and oxygen consumption, Weiss et al. (1991) suggested that the pelagic ecosystem of Lake Baikal resembles that of oligotrophic open oceans, characterized by intensive recycling of nutrients within the upper water column (Eppley and Peterson 1979). However, previous production estimates that adopted different methods varied substantially. The last published results on primary production go back to the beginning of the 1990s (Goldman et al. 1996), and primary production was not measured over the last decade. Moreover, size-fractionated measurement has rarely been performed, although such information has fruitful implications for the food web structure and biogeochemical fate of primary production.

T. Yoshida¹ (✉) · T. Sekino² · M. Genkai-Kato² · Z. Kawabata ·
Y. Nishimura · T. Nagata · M. Higashi · M. Nakanishi
Center for Ecological Research, Kyoto University, Otsu, Japan

N.P. Logacheva · N.A. Bondarenko · T.V. Khodzher · N.G. Melnik
Limnological Institute, Russian Academy of Sciences, Irkutsk, Russia

S. Hino
Faculty of Science, Yamagata University, Yamagata, Japan

K. Nozaki
School of Environmental Science, University of Shiga Prefecture,
Hikone, Japan

Present addresses:

¹Department of Ecology and Evolutionary Biology, Corson Hall,
Cornell University, Ithaca, NY 14853, USA
Tel. +1-607-254-4273; Fax +1-607-255-8088
e-mail: ty59@cornell.edu

²Research Institute for Humanity and Nature, Kyoto, Japan

This paper reports our modern measurements of primary production in the pelagic area of the south basin of Lake Baikal. Our aim was to provide seasonal estimates of the primary production rate and its size structure and to compare the present estimate with previous data in order to discuss the appropriateness of any representative value of primary production as a long-term average.

Methods

Measurements were carried out at stations located 5 km south of Listvyanka (ca. 1400 m depth) or 4.5 km southwest of Ivanovsky Cape (ca. 1450 m depth), near the coast of the south basin, during seven expeditions conducted between 1999 and 2000 (Table 1). Vertical profiles of water temperature were obtained with a CTD profiler (SBE-25, SeaBird Electronics, Bellevue, WA, USA). Underwater light intensity (PAR) was measured with a quantum meter (LI-1000, Li-Cor, Lincoln, NE, USA) at intervals of 1 m from the surface to a depth of 20 m. During the ice-cover season (March), the light intensity just below the ice was measured with the aid of a SCUBA diver who held the sensor near the bottom of the ice. Water samples for measurements of dissolved nutrients, particulate organic carbon (POC), and primary production were collected with 10-l Niskin bottles or 3-l Van Dorn bottles at five to seven depths within the upper 50 m. The concentrations of NO_3 , PO_4 , and SiO_2 were determined by the hydrazine reduction (Mullin and Riley 1955b), molybdate (Murphy and Riley 1962), and Si-molybdate complex (Mullin and Riley 1955a) methods, respectively.

The concentrations of POC collected on precombusted (at 450°C for 2 h) Whatman GF/F glass fiber filters were measured with a CHN analyzer (2400 II, Perkin Elmer, Wellesley, MA, USA). In order to determine the size distribution of POC, sample waters were filtered through either 20- μm -mesh-size screens or 2- μm -pore-size Nuclepore filters using the force of gravity. The particles contained in each filtrate were collected by the GF/F glass fiber filters to

measure POC (see above). The concentrations of POC in different size fractions (>20 μm , 2–20 μm , and <2 μm) were estimated by subtraction.

The primary production rate was measured by the ^{13}C -tracer method (Hama et al. 1983). Sample waters were contained in either 300-ml (1999 expeditions) or 1-l capacity (2000 expeditions) Nalgene polycarbonate bottles and spiked with $\text{NaH}^{13}\text{CO}_3$ at a final concentration that did not exceed 10% of the total inorganic carbon (TIC) concentration in the lake water (mean, 10.8 mg C l^{-1} ; range, 8.5–12.7 mg C l^{-1}). The bottles were filled to the top with sample water so that the headspace in the bottles was minimized. Zooplankton in the sample waters was not removed, as recommended by Wetzel and Likens (2000). One clear and one dark bottle was prepared for each depth. After in situ incubation for 24 h (except for measurements conducted in March and June 1999; see Table 1), the water samples were filtered through precombusted (at 450°C for 2 h) Whatman GF/F glass fiber filters. The filters were stored frozen for later analysis. To remove inorganic carbon, the filters were treated with HCl fumes and then dried in a desiccator. The concentration of POC and the isotope ratio of ^{13}C to ^{12}C were quantified with a $^{13}\text{CO}_2$ analyzer (EX-130S, Jasco, Hachioji, Japan). Inorganic carbon in the lake water was determined with a total organic carbon analyzer (TOC-500, Shimadzu, Kyoto, Japan). The carbon uptake rate (photosynthetic production rate) was calculated according to Hama et al. (1983). Daily primary production in March 1999 was calculated by doubling the value obtained from the half-day incubation (noon to sunset, Table 1). During the expeditions conducted in 2000, we determined size-fractionated primary production. After in situ incubation of samples (see above), a portion of the sample water was filtered through either 20- μm mesh-size screens or 2- μm pore-size Nuclepore filters using the force of gravity. Then the filtrates were further filtered through precombusted Whatman GF/F filters for the measurements of the isotope ratio (see above). The contributions of different size fractions of phytoplankton (>20 μm , 2–20 μm , and <2 μm) to total primary production were estimated by subtraction.

Table 1. Location of the sampling site, incubation time of primary production measurements, and limnological properties at the study site

| Date | Position | Incubation time | Surface water temperature (°C) | Attenuation coefficient of PAR ^a (m^{-1}) |
|-------------|-------------------|------------------------------|--------------------------------|---|
| 21 Mar 1999 | 51°45'N, 104°25'E | 12:00–17:00 (0.5 daytime) | 0.3 | 0.422 |
| 14 Jun 1999 | 51°48'N, 104°55'E | 8:30–19:30 (1 daytime) | 3.8 | 0.105 |
| 25 Aug 1999 | 51°48'N, 104°55'E | 24 h | 14.3 | 0.256 |
| 23 Oct 1999 | 51°48'N, 104°55'E | 24 h | 5.9 | 0.226 |
| 5 Mar 2000 | 51°45'N, 104°25'E | 24 h | 0.4 | 0.323 |
| 12 Aug 2000 | 51°48'N, 104°55'E | 24 h | 13.0 | 0.281 |
| 13 Aug 2000 | 51°48'N, 104°55'E | 24 h | 13.0 | 0.281 |
| 2 Oct 2000 | 51°48'N, 104°55'E | 24 h | 10.1 | 0.423 |

^a PAR, photosynthetically active radiation

Results

The seasonal change of the thermal structure of the upper 50 m of the water column exhibited a typical dimictic pattern (Fig. 1). A weak inverse thermal stratification was observed under the condition of ice cover in March, with a water temperature of 0.3°–0.4°C just below the ice. After the loss of ice cover, the temperature was vertically uniform at 3.8°C from the surface to a depth of 50 m in June. Thermal stratification was well established in August, with the highest temperature of 14°C in the epilimnion. In late October, fall turnover was indicated by a vertically homogeneous distribution of temperature (5°–6°C). The euphotic depth at which the relative irradiance was 1% of the surface incident PAR ($Z_{1\%}$) varied from 10.9 m in March 1999 to 44 m in June 1999 (Fig. 1). The measurement conducted in March 1999 revealed that PAR at the bottom of the ice

(0.8 m in thickness) was 40% of the irradiance measured at the top of the ice.

The concentrations of inorganic nutrients were determined on 21 March, 25 August, and 23 October 1999 (Fig. 2). The depletion of NO_3 and PO_4 in the euphotic zone was most pronounced in August, and to a lesser extent in October. In March, relatively high concentrations of PO_4 (0.22 μM) and NO_3 (4.9 μM) were detected in the euphotic zone. The SiO_2 concentration was always high (>7.8 μM) within the upper water column.

The primary production integrated over the euphotic zone was high in August (average, 344 $\text{mg C m}^{-2} \text{ day}^{-1}$, $n = 3$) and low in March (average, 96 $\text{mg C m}^{-2} \text{ day}^{-1}$, $n = 2$) (Table 1). Intermediate values were obtained in June (259 $\text{mg C m}^{-2} \text{ day}^{-1}$, $n = 1$) and October (average, 129 $\text{mg C m}^{-2} \text{ day}^{-1}$, $n = 2$). Vertically, primary production was highest in subsurface layers (2.5–10 m) where the light intensity was 28%–50% of the surface value, except for 23

Fig. 1. Depth profiles of daily primary production and water temperature at the pelagic sampling site in Lake Baikal. Dotted lines are the euphotic depths ($Z_{1\%}$) where light intensity was 1% of that at the surface, derived from the measurement of underwater light intensity (PAR). $Z_{1\%}$ deeper than 20 m on 14 June 1999 was calculated by extrapolation, assuming a constant light attenuation coefficient, which is given in Table 1

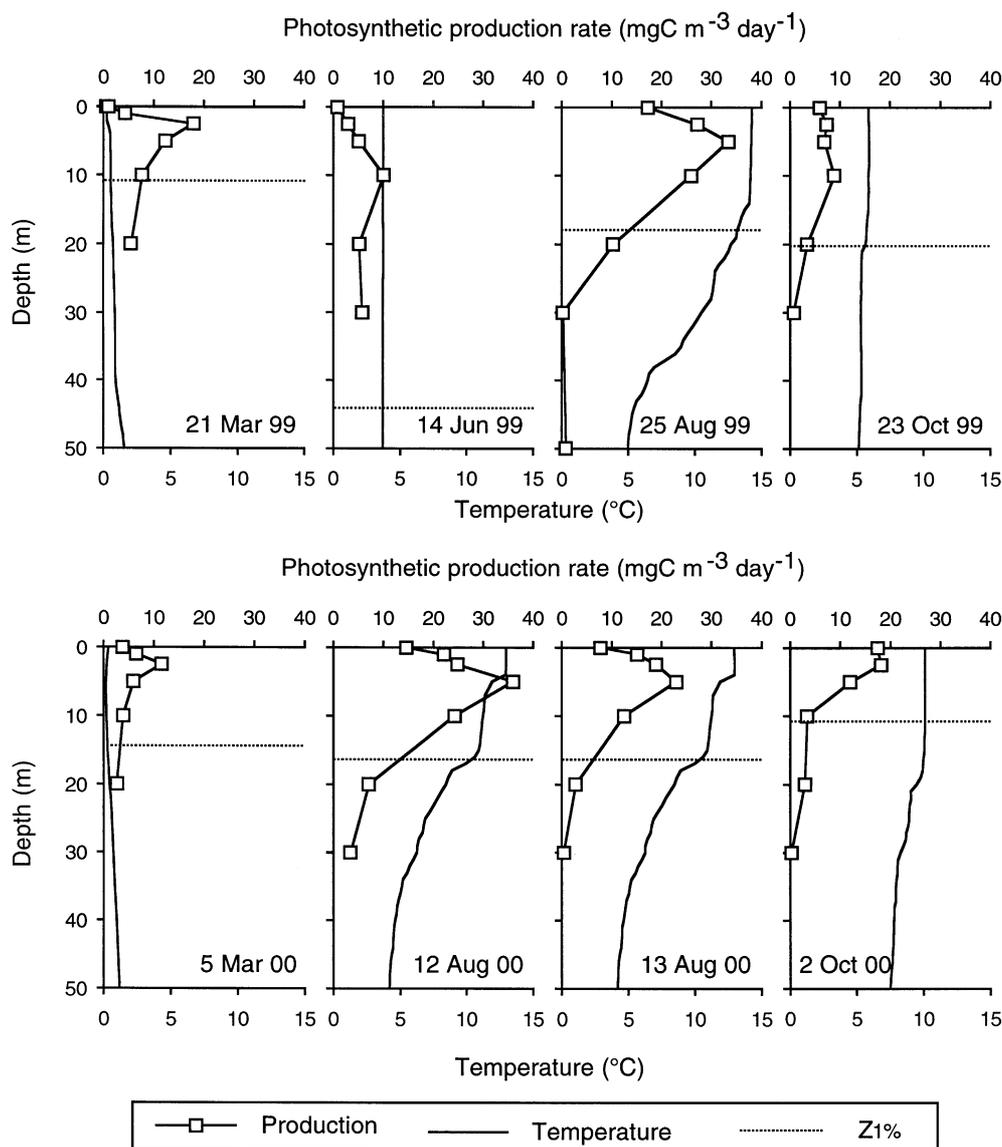
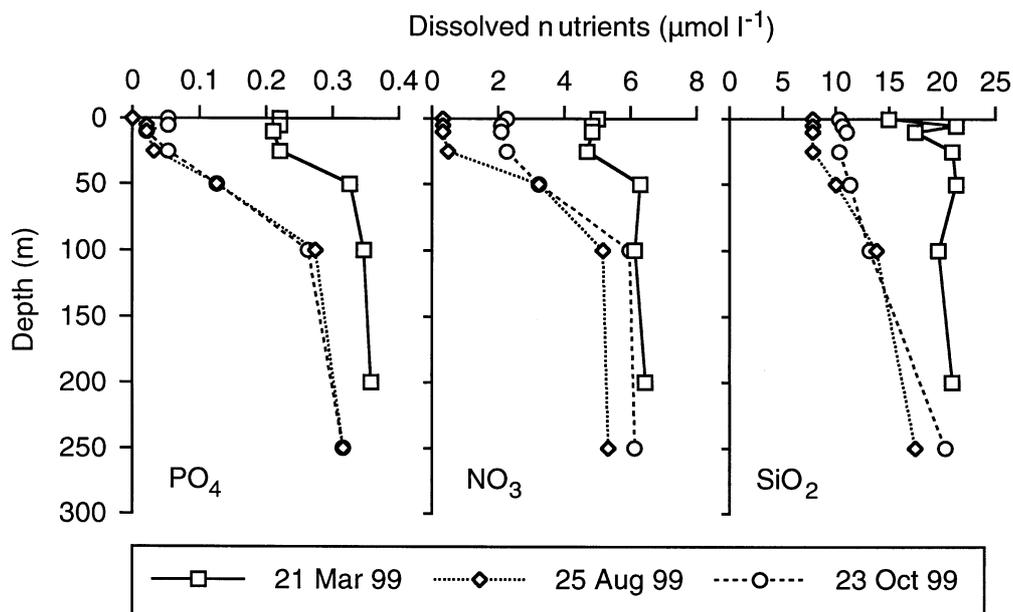


Fig. 2. Depth profiles of PO_4 , NO_3 , and SiO_2 concentrations



October 1999 and 2 October 2000, when primary production did not show a subsurface peak but was still not the highest at the surface (0 m) (Fig. 1). Size-fractionated measurements of primary production were conducted on 5 March, 12 August, and 2 October 2000. The results indicated that phytoplankton in the cell-size category under $20\mu\text{m}$ dominated primary production: the sum of the $<2\mu\text{m}$ -size fraction and the $2\text{--}20\mu\text{m}$ -size fraction accounted for 72%, 96%, and 85% of total primary production in March, August, and October, respectively (Table 3 and Fig. 3). The contributions of $<2\mu\text{m}$ fraction to total primary production varied from 41% to 62%. Notably, the contribution of large phytoplankton ($>20\mu\text{m}$) was lowest (4%) in August when the $<2\mu\text{m}$ fraction accounted for the largest portion of primary production, whereas the $>20\mu\text{m}$ fraction contributed significantly (28%) to total primary production in March, when the contribution of the $<2\mu\text{m}$ fraction was relatively low.

The concentrations of total POC in the euphotic zone varied from 4.0 to 12gCm^{-2} , with the highest value on 12 August 2000 and the lowest on 2 October 2000 (Table 2). The POC concentration was not correlated with the primary production rate ($P > 0.1$, $n = 8$). We calculated the potential turnover time of POC (T_{POC} , days) by dividing the depth-integrated values of POC by the primary production rates. T_{POC} can be considered as a maximum estimate of the turnover time of phytoplankton, because POC includes not only phytoplankton but also heterotrophs and detritus. T_{POC} was generally short in August (15–41 days) and long in March (55–106 days). The size-fractionated measurements of POC indicated that the largest portion (51%–59%) of total POC was attributable to the $<2\mu\text{m}$ fraction (Table 3 and Fig. 4). The $2\text{--}20\mu\text{m}$ and the $>20\mu\text{m}$ fractions accounted for 28%–43% and 2%–18% of total POC. The T_{POC} values calculated for each size fraction varied from 17 to 144 days: the shortest values were found in

the $>20\mu\text{m}$ fraction in March (25 days) and August (17 days).

Discussion

Pelagic primary production of Lake Baikal

Our estimates of the primary production rates, determined in the pelagic area of the south basin between 1999 and 2000, varied from 79 to $424\text{mgCm}^{-2}\text{day}^{-1}$, yielding a seasonal average value of roughly $207\text{mgCm}^{-2}\text{day}^{-1}$ or an annual primary production rate of $75\text{gCm}^{-2}\text{year}^{-1}$ (Table 2). A seasonal pattern was detected, with the highest value in August and the lowest in March (Fig. 1), consistent with the notion that the primary production is, in general, highest in summer in Lake Baikal (Kozhova 1987). However, it should be noted that the interannual variability of the abundance of phytoplankton is large, particularly in spring. Previous work found that the maximum biomass of a dominant diatom, *Aulacoseira baicalensis*, in spring varies from year to year by more than two orders of magnitude (from $<10^3$ to $>10^5$ cells l^{-1}) (Kozhova 1987), for reasons that are not entirely clear (Kozhova 1987). In our study, the abundance of *Aulacoseira* was low in samples collected on 19 March 1999 ($<0.15 \times 10^3$ cells l^{-1}) and 4 March 2000 ($<8.4 \times 10^3$ cells l^{-1}). Thus, our estimates of primary production in March do not represent those for an *Aulacoseira* (*Melosira*) bloom.

Comparisons of our estimates of primary production with those obtained by previous studies are hampered by differences in measurement techniques. The oxygen change method obtained relatively high estimates compared with the ^{14}C and ^{13}C tracer method, and the difference was sometimes larger than an order of magnitude, although the

Fig. 3. Depth profiles of primary production rate in different size fractions (<2 μm , 2–20 μm , and >20 μm) of lake water, and the relative contribution of each size fraction to total primary production

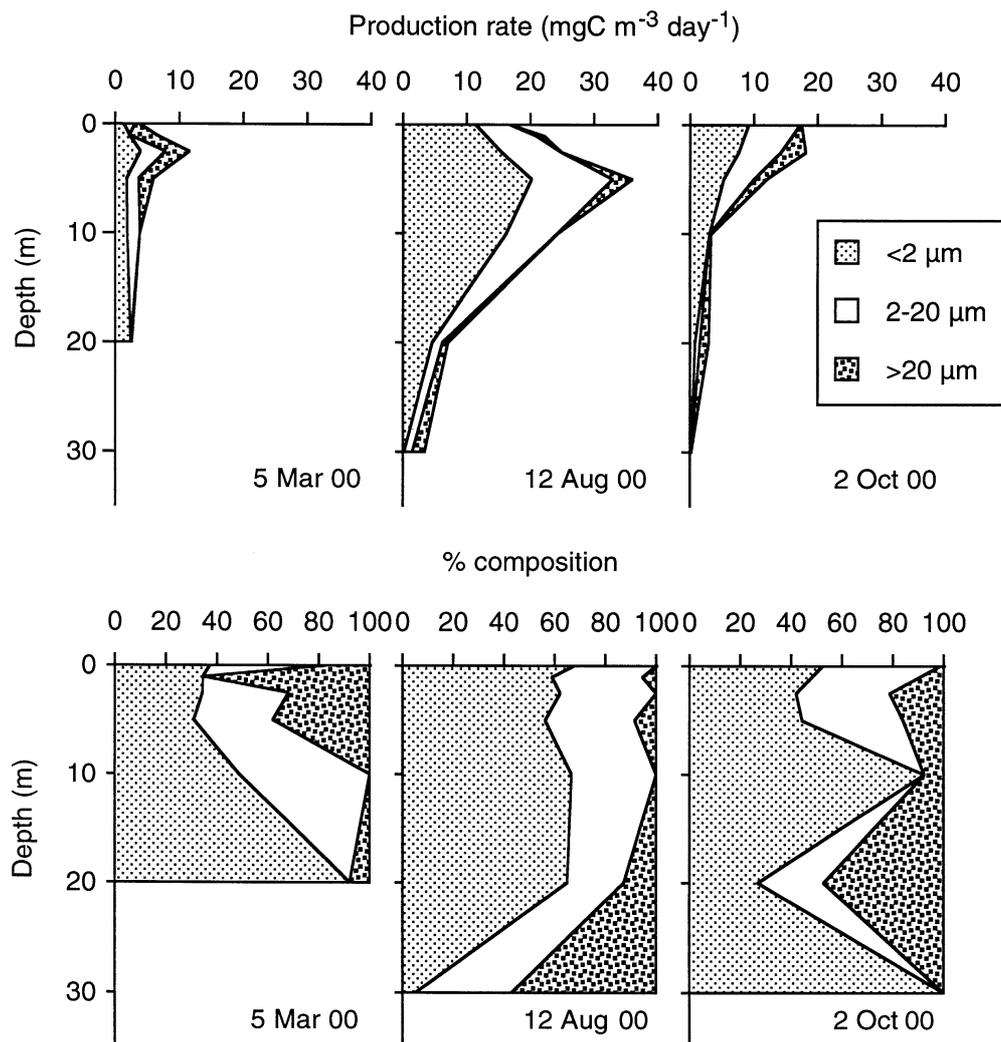


Table 2. Seasonal changes in daily primary production (PP), particulate organic carbon (POC), and potential turnover time of POC (POC/PP) in the euphotic zone

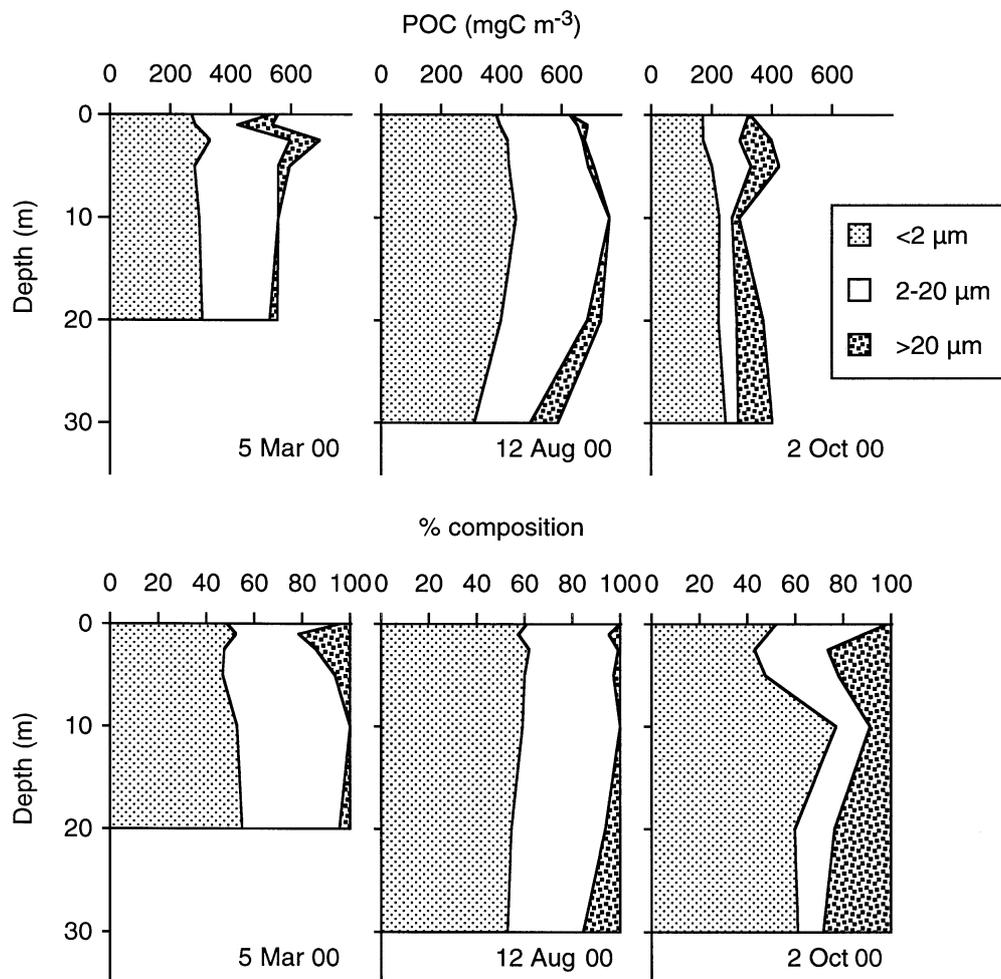
| Date | PP (mg C m^{-2} day^{-1}) | PP (monthly average) ($\text{mg C m}^{-2} \text{ day}^{-1}$) | POC (g C m^{-2}) | POC (monthly average) (g C m^{-2}) | POC/PP (days) | POC/PP (monthly average) (days) |
|-----------------|---|--|--------------------------------|---|------------------|---------------------------------------|
| March | | | | | | |
| 21 Mar 1999 | 113 | | 6.23 | | 55 | |
| 5 Mar 2000 | 78.9 | 95.8 | 8.35 | 7.29 | 106 | 76 |
| June | | | | | | |
| 14 Jun 1999 | 259 | 259 | 9.67 | 9.67 | 37 | 37 |
| August | | | | | | |
| 25 Aug 1999 | 424 | | 6.44 | | 15 | |
| 12 Aug 2000 | 381 | | 11.8 | | 31 | |
| 13 Aug 2000 | 227 | 344 | 9.27 | 9.17 | 41 | 27 |
| October | | | | | | |
| 23 Oct 1999 | 135 | | 8.56 | | 63 | |
| 2 Oct 2000 | 123 | 129 | 4.02 | 6.29 | 33 | 49 |
| Overall average | | 207 | | 8.11 | | 47 |

interannual variation in these estimates was quite large, even within the same method (Table 4). The range of 120–130 $\text{g C m}^{-2} \text{ year}^{-1}$ based on the data collected by the oxygen change method (Moskalenko and Votintsev 1972;

Votintsev et al. 1975) has been cited in order to develop the argument of biogeochemical cycling of this lake (Weiss et al. 1991; Granina 1997). This estimate is, however, larger than our estimate of 75 $\text{g C m}^{-2} \text{ year}^{-1}$. Moreover, Kozhova

Table 3. Daily PP, POC, and potential turnover time of POC (POC/PP) in different size fractions in the euphotic zone

| Date | Size fraction (μm) | PP | | POC | | POC/PP (days) |
|-------------|---------------------------------|---|---------|-------------------------|---------|---------------|
| | | ($\text{mg C m}^{-2} \text{ day}^{-1}$) | % total | (g C m^{-2}) | % total | |
| 5 Mar 2000 | >20 | 21.9 | 27.7 | 0.54 | 6.5 | 25 |
| | 2–20 | 24.8 | 31.5 | 3.58 | 42.9 | 144 |
| | <2 | 32.2 | 40.8 | 4.22 | 50.6 | 131 |
| | Total | 78.9 | | 8.35 | | |
| 12 Aug 2000 | >20 | 15.8 | 4.1 | 0.27 | 2.3 | 17 |
| | 2–20 | 130 | 34.2 | 4.63 | 39.1 | 36 |
| | <2 | 235 | 61.6 | 6.94 | 58.6 | 30 |
| | Total | 381 | | 11.8 | | |
| 2 Oct 2000 | >20 | 18.4 | 14.9 | 0.73 | 18.1 | 39 |
| | 2–20 | 44.9 | 36.4 | 1.13 | 28.2 | 25 |
| | <2 | 60.0 | 48.6 | 2.16 | 53.7 | 36 |
| | Total | 123 | | 4.02 | | |

Fig. 4. Depth profiles of particulate organic carbon (POC) concentrations in different size fractions (<2 μm , 2–20 μm , and >20 μm) of lake water, and the relative contribution of each size fraction to total POC

(1987) reported a wide range of 28–124 $\text{g C m}^{-2} \text{ year}^{-1}$ for the period from 1977 to 1980, and Bondarenko and Guselnikova (1989a) reported 87–246 $\text{g C m}^{-2} \text{ year}^{-1}$ for 1981–1985, both of which were obtained by the ^{14}C tracer method (Table 4). Several factors, including the incubation

time and the method of measurement (i.e., oxygen vs. ^{14}C or ^{13}C tracer), can affect the estimate of primary production (Wetzel and Likens 2000). The long incubations used in most of the tracer methods may have allowed considerable respiratory loss of the labeled carbon by phytoplankton

Table 4. Primary production measured by previous studies and this study using different methods at the pelagic sites of the south basin of Lake Baikal

| Month | Year | Method | | PP ^b | | Reference ^c |
|-------------|-----------------------|--|-----------------|---|---|------------------------|
| | | Oxygen ^a , ¹⁴ C or ¹³ C | Incubation time | (mg C m ⁻² day ⁻¹) | (g C m ⁻² year ⁻¹) | |
| February | 1966 | Oxygen (gross) | 24 h | 59–275 | | 6 |
| March | 1965 | Oxygen (gross) | 24 h | 281 | | 6 |
| | 1965 | Oxygen (gross) | 24 h | 625–2500 | | 6 |
| | 1966 | Oxygen (gross) | 24 h | 63–238 | | 6 |
| | 1969 | Oxygen (gross) | 24 h | 281–781 | | 6 |
| | 1982 | ¹⁴ C | 6 h × 3 times | 86 | | 2 |
| | 1984 | ¹⁴ C | 6 h × 3 times | 67 | | 2 |
| | 1985 | ¹⁴ C | 6 h × 3 times | 70 | | 2 |
| | 1999 | ¹³ C | 5 h | 113 | | This study |
| | 2000 | ¹³ C | 24 h | 79 | | This study |
| April | 1966 | Oxygen (gross) | 24 h | 50–275 | | 6 |
| | 1969 | Oxygen (gross) | 24 h | 313–2094 | | 6 |
| May–June | 1964 | Oxygen (gross) | 24 h | 1000–1375 | | 6 |
| | 1965 | Oxygen (gross) | 24 h | 313–469 | | 6 |
| | 1967 | Oxygen (gross) | 24 h | 500–750 | | 6 |
| | 1967 | Oxygen (gross) | 24 h | 63–250 | | 6 |
| June | 1968 | Oxygen (gross) | 24 h | 750–1313 | | 6 |
| | 1969 | Oxygen (gross) | 24 h | 156–1313 | | 6 |
| | 1981 | ¹⁴ C | 6 h × 3 times | 321 | | 2 |
| | 1983 | ¹⁴ C | 6 h × 3 times | 700 | | 2 |
| | 1984 | ¹⁴ C | 6 h × 3 times | 271 | | 2 |
| | 1985 | ¹⁴ C | 6 h × 3 times | 780 | | 2 |
| | 1999 | ¹³ C | 11 h | 259 | | This study |
| | July | 1964 | Oxygen (gross) | 24 h | 31 | |
| 1966 | Oxygen (gross) | 24 h | 72–1106 | | 6 | |
| 1990 | ¹⁴ C | 3–3.5 h × 4 times | 2640–3360 | | 4 | |
| July–August | 1968 | Oxygen (gross) | 24 h | 281–766 | | 6 |
| August | 1964 | Oxygen (gross) | 24 h | 313–813 | | 6 |
| | 1964 | Oxygen (gross) | 24 h | 1750–2374 | | 6 |
| | 1966 | Oxygen (gross) | 24 h | 63–678 | | 6 |
| | 1975 | ¹⁴ C | 24 h | 282 | | 3 |
| | 1975 | ¹⁴ C | 24 h | 142 | | 3 |
| | 1975 | ¹⁴ C | 24 h | 77 | | 3 |
| | 1975 | ¹⁴ C | 24 h | 80 | | 3 |
| | 1982 | ¹⁴ C | 6 h × 3 times | 1033 | | 2 |
| | 1983 | ¹⁴ C | 6 h × 3 times | 1223 | | 2 |
| | 1984 | ¹⁴ C | 6 h × 3 times | 516 | | 2 |
| | 1985 | ¹⁴ C | 6 h × 3 times | 613 | | 2 |
| | 1999 | ¹³ C | 24 h | 424 | | This study |
| | 2000 | ¹³ C | 24 h | 381 | | This study |
| 2000 | ¹³ C | 24 h | 227 | | This study | |
| September | 1964 | Oxygen (gross) | 24 h | 313 | | 6 |
| | 1965 | Oxygen (gross) | 24 h | 313 | | 6 |
| | 1966 | Oxygen (gross) | 24 h | 119–325 | | 6 |
| | 1968 | Oxygen (gross) | 24 h | 250–719 | | 6 |
| | 1981 | ¹⁴ C | 6 h × 3 times | 360 | | 2 |
| | 1982 | ¹⁴ C | 6 h × 3 times | 299 | | 2 |
| | 1983 | ¹⁴ C | 6 h × 3 times | 380 | | 2 |
| | September –October | 1989 | ¹⁴ C | 1 h | 88 | |
| 1989 | ¹⁴ C | 1 h | 183 | | 1 | |
| 1989 | ¹⁴ C | 1 h | 358 | | 1 | |
| October | 1964 | Oxygen (gross) | 24 h | 406 | | 6 |
| | 1964 | Oxygen (gross) | 24 h | 156–313 | | 6 |
| | 1966 | Oxygen (gross) | 24 h | 144–444 | | 6 |
| | 1968 | Oxygen (gross) | 24 h | 344–938 | | 6 |
| | 1983 | ¹⁴ C | 6 h × 3 times | 901 | | 2 |
| | 1999 | ¹³ C | 24 h | 135 | | This study |
| | 2000 | ¹³ C | 24 h | 123 | | This study |
| November | 1964 | Oxygen (gross) | 24 h | Near 0 | | 6 |

Table 4. *Continued*

| Month | Year | Method | | PP ^b | | Reference ^c |
|------------|-----------|--|-----------------|---|---|------------------------|
| | | Oxygen ^a , ¹⁴ C or ¹³ C | Incubation time | (mg C m ⁻² day ⁻¹) | (g C m ⁻² year ⁻¹) | |
| Year round | 1964 | Oxygen (gross) | | | 175 | 6 |
| | 1965 | Oxygen (gross) | | | 94 | 6 |
| | 1966 | Oxygen (gross) | | | 75 | 6 |
| | 1967 | Oxygen (gross) | | | 128 | 6 |
| | 1968 | Oxygen (gross) | | | 187 | 6 |
| | 1977 | ¹⁴ C | | | 42 | 5 |
| | 1978 | ¹⁴ C | | | 39 | 5 |
| | 1979 | ¹⁴ C | | | 124 | 5 |
| | 1980 | ¹⁴ C | | | 28 | 5 |
| | 1981 | ¹⁴ C | | | 98 | 2 |
| | 1982 | ¹⁴ C | | | 246 | 2 |
| | 1983 | ¹⁴ C | | | 240 | 2 |
| | 1984 | ¹⁴ C | | | 87 | 2 |
| | 1985 | ¹⁴ C | | | 146 | 2 |
| | 1999–2000 | ¹³ C | | | 75 | This study |

^a Oxygen production rate was converted to carbon production assuming a photosynthetic quotient of 1.2 (Wetzel and Likens 2000)

^b PP data represent either a single measurement or a range of multiple measurements

^c References: (1) Back et al. 1991; (2) Bondarenko and Guselnikova 1989a; (3) Bul'on 1983; (4) Goldman et al. 1996; (5) Kozhova 1987; (6) Votintsev et al. 1975

respiration. The lower estimate obtained by the use of the tracer method might be due in part to the production of dissolved organic carbon (DOC) during the incubation, which cannot be accounted for by the measurement of tracer associated with particles collected on filters. Phytoplankton can release 10%–20% of primary production as DOC (Baines and Pace 1991). In addition, a large portion of particulate primary production can be rapidly transformed to DOC during incubation due to excretion and egestion by grazers (Nagata 2000). Moreover, the absence of any *Aulacoseira* bloom data in our records would result in an underestimate in comparison with long-term averages.

Subsurface maxima of primary production rate

Our data indicated that primary production rates were generally highest at depths where the light intensity was 28% to 50% of that at the surface (Fig. 1). POC concentrations were relatively high immediately under the ice, and it therefore seems unlikely that this was an effect of low algal biomass relative to the rest of the water column. A lower production rate at the surface has often been observed in lakes and oceans and is generally explained by the inhibition of photosynthesis by high light (PAR) intensity and/or UV radiation (e.g., Vincent et al. 1984; Neale and Richerson 1987). In our measurements of primary production, however, we used polycarbonate bottles that block most UV radiation (Wulff et al. 1999). The observed lower production rate at the surface might have been caused by harmfully high PAR.

It is interesting to note that strong depression of primary production at the surface was observed even in March when the lake surface was entirely covered by ice (Fig. 1). Most strikingly, the daily primary production rate at the surface (or at the bottom of the ice) was 0.7 mg C m⁻³ day⁻¹ on 21 March 1999, and this value was only 4% of the primary

production rate measured at a depth of 2.5 m (Fig. 1). In Lake Baikal, we found that the light intensity (PAR) just below the ice (0.8 m in thickness) was 40% of that measured at the top of the ice. The large wind fetch of Lake Baikal means that the lake ice is swept relatively clear of snow, which can have a major shading effect on PAR transmission (Belzile et al. 2001). The light inhibition of photosynthesis might have occurred even under the ice due to high penetration of solar radiation through the clear ice.

Size-fractionated primary production and its implications for food web structure and biogeochemical cycling in Lake Baikal

Our data showed that the contribution of small (<20 μm) phytoplankton to total photosynthetic production was high, ranging from 72% (March) to 96% (August) (Table 3 and Fig. 3). More than half of this primary production in the small-cell-size category was accounted for by the smallest cell-size fraction (<2 μm) or picophytoplankton. These data confirm and add to previous results obtained in Lake Baikal. Votintsev et al. (1972) and Back et al. (1991) found that the <10-μm fraction accounted for 60%–100% of total production during the warm season (July–October). Nagata et al. (1994) reported that 80% of total primary production was attributable to phytoplankton in the <3-μm fraction in late July. Our data from seasonal measurement of size-fractionated primary production indicate that nanophytoplankton (2–20 μm) and picophytoplankton (<2 μm) are the dominant primary producers not only in summer (August), but also in fall (October) and spring (March) (Table 3). A similar seasonal pattern was found by Bondarenko and Guselnikova (1989b). In addition, our measurements revealed that a large portion (82%–98%) of POC was associated with particles in the small (<20 μm) size fraction (Table 3 and Fig. 4). These data suggest that

nano- and picophytoplankton played an important role in organic carbon cycling throughout the studied years in Lake Baikal. The dominance of small algae in primary production in Lake Baikal is consistent with data obtained from other large lakes (e.g., Lake Superior; Fahnenstiel et al. 1986) and oligotrophic open oceans (e.g., the subarctic Pacific; Miller et al. 1991). In these environments, the dominance of small cells in primary production has been generally explained by the competitive advantages of smaller cells (or cells with higher surface-to-volume ratio) in nutrient uptake under oligotrophic conditions (Hecky and Kilham 1988), although other factors (e.g., the low sinking loss rate of small cells in stagnant water) also affect the size composition of phytoplankton in the euphotic zone.

The high contributions of pico- and nanophytoplankton to primary production have fruitful implications in the planktonic food webs of Lake Baikal. Along with heterotrophic bacteria, picophytoplankton constitute the first trophic level of the microbial food chain, where various protists, such as flagellates and ciliates, are the main consumers (e.g., Azam et al. 1983; Nagata 1990). It has been reported that the relative importance of the microbial food web in pelagic energy and material flows is generally higher in oligotrophic than in eutrophic lakes (Porter et al. 1988; Weisse 1991). The high primary production of picophytoplankton found in the present and previous studies in Lake Baikal suggests that picophytoplankton contribute significantly to the pelagic food web of Lake Baikal. In addition, a high biomass of ciliates, one of the major consumers of picoplankton, was found during our investigation period (Sekino et al., in preparation). These circumstances suggest that microbial trophic interactions play a central role in the planktonic food web of Lake Baikal.

Acknowledgments This paper is dedicated to Masahiko Higashi, who passed away in March 2000. We thank W.F. Vincent, T. Miyajima, and two anonymous reviewers for their comments that improved the manuscript. We are also grateful to M.A. Grachev, O.A. Timoshkin, E. Wada, and T. Kawai for the arrangement of this Japan-Russia collaboration, and to I.V. Khanaev, A.I. Tanihev, A.A. Zhdanov, E. Tereza, L.A. Gorbunova, T. Koitabashi, I. Shimizu, F. Nagao, K. Yoshiyama, H. Haga, T. Minamoto, and H. Miyasaka for their support in the field and laboratory. This expedition was supported by a Grant-in-Aid for Scientific Research from the Japan Ministry of Education, Science, Sports, Culture and Technology (09NP1501).

References

- Antipova N (1963) Seasonal and annual variations of phytoplankton in Lake Baikal. In: Galaziy GI (ed) Proceedings of the Limnological Institute. 2 (22). USSR Academy of Sciences Publishers, Moscow-Leningrad, pp 12–28
- Azam F, Fenichel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. *Mar Ecol Prog Ser* 10:257–263
- Back RC, Bolgrien DW, Gusel'nikova NE, Bondarenko NA (1991) Phytoplankton photosynthesis in southern Lake Baikal: size-fractionated chlorophyll *a* and photosynthetic parameters. *J Great Lakes Res* 17:194–202
- Baines SB, Pace ML (1991) The production of dissolved organic matter by phytoplankton and its importance to bacteria – patterns across marine and freshwater systems. *Limnol Oceanogr* 36:1078–1090
- Belzile C, Vincent WF, Gibson JAE, Van Hove P (2001) Bio-optical characteristics of the snow, ice and water column of a perennially ice-covered lake in the high Arctic. *Can J Fish Aquat Sci* 58:2405–2418
- Bondarenko NA, Guselnikova NE (1989a) Production of phytoplankton in southern Lake Baikal. *Proc Siberian Branch USSR Acad Sci* 1:77–81
- Bondarenko NA, Guselnikova NE (1989b) Importance of the contribution of pico- and nanoplankton to primary production in Lake Baikal. *J Biol Sci* 12:34–36
- Bondarenko NA, Guselnikova NE, Logacheva NF, Pomazkina GV (1996) Spatial distribution of phytoplankton in Lake Baikal. *Spring 1991. Freshwat Biol* 35:517–523
- Boraas ME, Bolgrien DW, Hølen DA (1991) Determination of eubacterial and cyanobacterial size and number in Lake Baikal using epifluorescence. *Int Rev Ges Hydrobiol* 76:537–544
- Bul'on VV (1983) Plankton primary production of inland waters. Nauka Press, Leningrad
- Eppley RW, Peterson BJ (1979) Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* 282:677–680
- Fahnenstiel GL, Sickoog L, Scavia D, Stoermer EF (1986) Importance of picoplankton in Lake Superior. *Can J Fish Aquat Sci* 43:235–240
- Goldman CR, Elser JJ, Richards RC, Reuter JE, Prisco JC, Levin AL (1996) Thermal stratification, nutrient dynamics, and phytoplankton productivity during the onset of spring phytoplankton growth in Lake Baikal, Russia. *Hydrobiologia* 331:9–24
- Granina L (1997) The chemical budget of Lake Baikal: a review. *Limnol Oceanogr* 42:373–378
- Hama T, Miyazaki T, Ogawa Y, Iwakuma T, Takahashi M, Otsuki A, Ichimura S (1983) Measurement of photosynthetic production of a marine phytoplankton population using a stable ¹³C isotope. *Mar Biol* 73:31–36
- Hecky RE, Kilham P (1988) Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. *Limnol Oceanogr* 33:796–822
- Kozhova OM (1987) Phytoplankton of Lake Baikal: structural and functional characteristics. *Arch Hydrobiol Beih* 25:19–37
- Miller CB, Frost BW, Wheeler PA, Landry MR, Welshmeyer N, Powell TM (1991) Ecological dynamics in the subarctic Pacific, a possibly iron-limited ecosystem. *Limnol Oceanogr* 36:1600–1615
- Moskalenko BK, Votintsev KK (1972) Biological productivity and balance of organic substance and energy in Lake Baikal. In: Kajak Z, Hillbricht-Ilkowska A (eds) Productivity problems of freshwaters. PWN-Polish Scientific Publishers, Krakow, pp 207–226
- Mullin JB, Riley JP (1955a) The colorimetric determination of silicate with special reference to sea and natural waters. *Anal Chim Acta* 12:162–176
- Mullin JB, Riley JP (1955b) The spectrophotometric determination of nitrate in natural waters, with particular reference to sea water. *Anal Chim Acta* 12:464–480
- Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphorus in natural waters. *Anal Chim Acta* 27:31–36
- Nagata T (1990) Contribution of picoplankton to grazer food chain in Lake Biwa. In: Tilzer M, Serruya C (eds) Large lakes – ecological structure and function. Springer Verlag, Berlin, pp 526–539
- Nagata T (2000) Production mechanisms of dissolved organic matter. In: Kirchman D (ed) Microbial ecology of the oceans. Wiley, New York, pp 121–152
- Nagata T, Takai K, Kawanobe K, Kim DS, Nakazato R, Guselnikova N, Bondarenko N, Mologawaya O, Kostrnova T, Drucker V, Satoh Y, Watanabe Y (1994) Autotrophic picoplankton in southern Lake Baikal: abundance, growth and grazing mortality during summer. *J Plankton Res* 16:945–959
- Neale PJ, Richerson PJ (1987) Photoinhibition and the diurnal variation of phytoplankton photosynthesis – I. Development of a photosynthesis-irradiance model from studies of in situ responses. *J Plankton Res* 9:167–193
- Porter KG, Paerl H, Hodson R, Pace M, Prisco J, Riemann B, Scavia D, Stockner J (1988) Microbial interactions in lake food webs. In: Carpenter SR (ed) Complex interactions in lake communities. Springer Verlag, New York, pp 209–227
- Vincent WF, Neale PJ, Richerson PJ (1984) Photoinhibition: algal responses to bright light during diel stratification and mixing. *J Phycol* 20:201–211

- Votintsev KK, Mesheryakova AI, Popovskaya GI (1972) The importance of ultrananoplanktonic algae in the primary production in Lake Baikal in the summer. *Hydrobiol J* 8:13–18
- Votintsev KK, Mesheryakova AI, Popovskaya GI (1975) Circulation of organic matter in Lake Baikal. Nauka Press, Novosibirsk
- Weiss RF, Carmack EC, Koropalov VM (1991) Deep-water renewal and biological production in Lake Baikal. *Nature* 349:665–669
- Weisse T (1991) The microbial food web and its sensitivity to eutrophication and contaminant enrichment: a cross-system overview. *Int Rev Ges Hydrobiol* 76:327–337
- Wetzel RG, Likens GE (2000) *Limnological analyses*, 3rd edn. Springer Verlag, New York
- Wulff A, Nilsson C, Sundbäck K, Wängberg S-A, Odmark S (1999) UV radiation effects on microbenthos – a four year field experiment. *Aquat Microb Ecol* 19:269–278