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Primary production and microbial activity in the euphotic zone of Lake Baikal (Southern Basin) during late winter

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Abstract

Three years of regular weekly/biweekly monitoring of seasonal changes in temperature, transparency, chlorophyll *a* (CHL) and bacteria [erythrosine-stained microscopic counts and cultivable colony forming units (CFUs)] at the vertical profile in the South basin of Lake Baikal (51°54′195″ N, 105°04′235″ E, depth 800 m) were evaluated. In more detail, the structure and function of phytoplankton and the microbial loop in the euphotic layer at the same site were investigated during the late-winter–early-spring period under the ice. The depth of euphotic zone (up to 1% of surface irradiation) was 35 to 40 m. Primary production was measured three times a week with the ^{14}C method in 2, 10, 20, 30 and 40 m. Maximum production was found in 10 m, with lower values towards the surface (light inhibition) and towards the lower layers. The total production in cells larger than 1 μm in the column (0–40 m) was 204–240 mg C d^{-1} m^{-2}, 30–40% of it being in cells 1–3 μm (mostly picocyanobacteria), which represented roughly 9% of the total chlorophyll *a* (estimated from pigment analyses). A major part of phytoplankton biomass was formed by diatoms (*Synedra acus* Hust., *Asterionella formosa* Hass. and *Stephanodiscus meyerii* Genkal & Popovskaya). Total production (including extracellular, dissolved organic matter) was 235–387 mg C day^{-1} m^{-2}, and the exudates were readily used by bacteria (particles 0.2–1 μm). This part amounted to 1–5% of cellular production in 2 to 20 m and 11–77% of cellular production in 20–40 m, i.e., in light-limited layers. From 0 to 30 m, chlorophyll *a* concentration was 0.8 to 1.3 μg l^{-1}, wherefrom it decreased rapidly to 0.1 μg l^{-1} towards the depth of 40 m. Bacteria (DAPI-stained microscopic counts) reached 0.5–1.4×10^6 ml^{-1}; their cell volumes measured via image analysis were small (average 0.05 μm^{-3}), often not well countable when erythrosine stain was used. Bacterial biomasses were in the range of 6–21 μg C l^{-1}. Numbers of colony forming units (CFUs) on nutrient fish-agar were c. 3–4 orders lower than DAPI counts. The amounts of heterotrophic protists were low, whereby flagellates reached 6 to 87 ml^{-1} and ciliates, 0.2–1.2 ml^{-1} (mostly Oligotrichida). Bacterial production was measured in the same depths as primary production using ^3H-thymidine (Thy) and ^{14}C-leucine (Leu) uptake. Consistently, bacterial abundances, biomasses, thymidine and leucine production were higher by 30–50% in layers 2, 10 and 20 m compared

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with that in the deeper 30 and 40 m, where cellular primary production was negligible. Leucine uptake in the deeper layers was even three times lower than in the upper ones. From the comparison of primary and bacterial production, bacteria roughly use 20–40% of primary production during 24 h in the layers 2 to 20 m.

Keywords: pelagial; primary production; bacterial production; phytoplankton; bacteria

1. Introduction

Ancient Lake Baikal, with the largest volume of water among world freshwater lakes, is an oligotrophic ecosystem and has been studied by limnologists since the beginning of last century (Kozhova and Izmest'eva, 1998). Despite human activities in the catchment, the Lake still seems to conserve a healthy status. Recent studies (Goldman et al., 1996; Genkai-Kato et al., 2002) documented that Lake Baikal, like portions of the oceans, is not phosphorus limited and, in some cases, nitrogen limitation might be probable. Its oligotrophy is mainly due to its peculiar geomorphometry, in combination with climatic factors. The volume of the hypolimnion of the lake is enormous, and the period of summer temperature stratification with surface water warming in the euphotic layer is very short. Thus, the primary production per area unit remains low compared with the aerial rates of heterotrophic bacterial production and decomposition in the total water column above the sediment (compare Cimbleris and Kalff, 2003). The attempts were made to evaluate the organic matter cycling and budget in the whole lake based on production and decomposition measurements with the oxygen method (Votintsev et al., 1975). It was concluded that not only the autochthonous primary production, but also a part of organic matter imported by the inflows, is decomposed in the water column and not reaching sediments.

Some warning alterations with an increasing human impact and global warming have been noticed. During the last 20 years, a decrease in ice cover duration occurred (referred by Shimaraev et al., 1994), and a significant coupling between winter NAO and Arctic oscillation indices and events in the lake have been observed (Straile et al., 2003; Todd and Mackay, 2003). A recent long-term increase in air temperature measured at south Baikal was significant, especially in winter and spring, viz. by 0.8 °C during 1990–2000 (Shimaraev et al., 2002). During the same period, ice duration at Lake Baikal shortened, and the ice-free season became longer by 18 days. The late-winter–early-spring period is also considered as important "trigger" determining the following seasonal cycle (Zavoruyev et al., 1992; Kozhova and Izmest'eva, 1998; Popovskaya, 2000).

The spatial and temporal variabilities of phytoplankton biomass and chlorophyll *a* (CHL) have been well described (Kozhova, 1987; Bondarenko et al., 1996; Kozhova and Izmest'eva, 1998). In phytoplankton, several characteristic endemic species were found, mainly from the groups of dinophytes and diatoms. The representatives of the latter group, large species *Aulacoseira* (formerly known as *Melosira*) *baicalensis* (Meyer) Simonsen and *Aulacoseira skwortsovii* Edlund, Stoermer and Taylor occurred periodically (Kobanova and Izmest'eva, 2003), every third or fourth year in high biomasses, even by one order higher than in the intervening periods. These years are called "high productive" or "melosira" years. During the last two decades, however, some alterations of characteristic interannual variations in phytoplankton structure and biomass were reported (Bulygin et al., 1998; Kozhova and Kobanova, 2001), possibly as a consequence of human impacts and/or warming.

The role of autotrophic picoplankton (APP) in primary production and its share in the total phytoplankton biomass were also investigated (Votintsev et al., 1972; Boraas et al., 1991; Nagata et al., 1994; Popovskaya, 2000). From long-term data, it was reported that the proportion of smaller phytoplankton species, especially of picocyanobacteria, has been increasing, although the biomass did not rise significantly. Some activity parameters of

the whole phytoplankton assemblage, and of its particular components measured in the past, suffer from the inadequacy of methods (see Kozhova and Pautova, 1985). A comparison of data between those on primary production with those on bacterial decomposition, which were acquired with methods of low sensitivity, revealed that decomposition rates in the water column largely exceeded production (Votintsev, 1992), as is true of all inland waters. The concept that all lakes are heterotrophic systems and that bacterial production in the water column often greatly exceeds that possible from organic matter produced by phytoplankton was first developed by Wetzel et al. (1972) and later discussed in detail (Wetzel, 1995, 2001).

Lake Baikal is likely the lake where total abundances of pelagic aquatic bacteria were studied first time in the history of aquatic microbiology and limnology. Bacterial abundance and distribution in the pelagic region of the lake were evaluated by Kuznetsov (1951) and by Kozhova and Kazantseva (1961). Bacteria in littoral parts of the lake were also studied, as referred by Goman (1973). Since 1969, bacterioplankton in Lake Baikal has been systematically monitored and its structure, vertical and horizontal distribution and relations to other components of pelagic biomass analyzed (see Maksimova, 1973, 1976; Maksimova and Maksimov, 1989; and references in Kozhova and Izmest'eva, 1998). In the huge volume of water, immense bacterial biomasses were found, which can reach 8–10 mg org. C in m^3, i.e., 6.4–8 g org. C under m^2 of 800-m-deep water column.

Our study explored the abundances and fluxes among heterotrophic microbes and size-fractionated primary producers during the early spring phytoplankton development under the ice, with a special emphasis on the coupling between bacterial and phytoplankton production. As a background assessment, 3-year seasonal changes of chlorophyll and bacteria, followed by regular monitoring, were evaluated. Several methodological approaches, hitherto not applied at the site, were used and compared with the more traditional methods. As a result, estimates of the organic matter input through vernal primary production and its bacterial decomposition in the water column were derived for an important period of the seasonal cycle and compared with historical data.

2. Area description, methods and material studied

2.1. Site

Lake Baikal is an oligotrophic lake with a volume of 22,160 km^3, an area of 31,500 km^2, mean depth of 688 m. It is the deepest lake of world, located between 104° to 110° E and 51° 30′ to 55° 30′ N in the Asian part of the Russian Federation, in Irkutsk district and in Buryat Republic. The largest inflows—Selenga, Upper Angara and Barguzin rivers and many other smaller inflows—supply the lake with 60 km^3 yearly, and the outflow of the lake into the Irkutsk Reservoir-Angara River carries out 60.4 km^3, which amounts roughly to 0.25% of the total lake volume exchange per year. The upper 250 m of the lake is dimictic, the whole lake is meromictic. Summer temperature stratification is very short (2 to 3 weeks), and ice cover extends from December–January to March–April. Underwater ridges divide the lake into three basins: north, central and south. A description of various limnological parameters and characteristics of the lake is summarized by Kozhova and Izmest'eva (1998).

Investigations were performed at the site Bolshie Koty in the Southern basin (the long-term monitoring site No. 1 of the Research Institute of Biology at the Irkutsk State University-RBI ISU), coordinates 51°54′195″ N, 105°04′235″ E located 2.2 km from the western shore against the Baikal Biological Station of RBI-ISU. The depth at the site is 800 m.

2.2. Sampling

Regular monitoring at the station Bolshie Koty, site No.1 by RBI-ISU started in 20th century: phytoplankton and zooplankton since 1946, bacterioplankton since 1969 and chlorophyll since 1979. The following parameters have been monitored in 1–4 week' intervals up to now: chlorophyll and phytoplankton at 9 depths up to 250 m, microscopic bacterial counts, colony forming units (CFUs) and bacterial production at 13 depths up to 500 m and zooplankton in the columns 0–10 and 0–200 m. Since February 2003, autotrophic picoplankton (APP) counts have been followed at weekly intervals in 5 m depth. Regular monitoring always was interrupted for 4–5 weeks during the period of freezing (December–January) and

ice melting (end of March–April) when the site is not accessible either by ship or by car on ice.

Intense measurements were performed during March 11–17, 2003, at five depths (2, 10, 20, 30 and 40 m). Primary production was measured three times, while bacterial abundances, biomass and production were measured four times during a week. Abundances of heterotrophic protists were determined three times. During the same week, also the regular monitoring was done (March 13), which allowed comparison of the compatibility of methods.

2.3. Methods

2.3.1. Microscopic bacterial counts and biomass

For regular monitoring, samples were fixed with formaldehyde (2% final concentration), filtered through 0.2 μm pore size membrane filters and stained by erythrosine (Razumov, 1932). Filters were cleared by immersion oil and counted.

During intense investigations, preserved samples were filtered through 0.2 μm pore size black Nuclepore filters, stained by DAPI, counted in epifluorescent microscope (Porter and Feig, 1980) and sized with image analysis (Lucia, Laboratory Imaging; Psenner, 1993). The carbon content of individual cells was calculated according to Norland (1993), the bacterial carbon was then calculated by multiplying the bacterial abundance and average cell-carbon content.

2.3.2. Saprophytic bacteria (colony forming units—CFU)

During regular monitoring, the colonies on 10% fish-peptone-agar were counted after 7 days incubation at 18 °C.

2.3.3. Bacterial production

For regular monitoring, bacterial production was estimated by the dark ^{14}C-carbonate fixation method (Romanenko and Kuznetsov, 1974; Sorokin and Kadota, 1972). Samples were kept for 5 h in the darkness (to suppress uptake by phytoplankton), then labelled carbonate was added, and samples were incubated in the darkness at the ambient temperature for 24 h. After incubation, the samples were filtered through 0.2-μm-pore-size membrane filters and measured by Geiger counter. Inorganic C uptake by bacteria was calculated from the percent of radioactivity retained on the filters and from the initial DIC concentration. Total C assimilation was calculated assuming that bacteria take 6% of the total C as CO_2.

During intense investigations, bacterial production was measured by ^{3}H-thymidine (Thy) and ^{14}C-leucine (Leu) uptake (described in Straškrábová et al., 1999). Twenty nanomoles per l of labelled compound was added, and five 10-ml subsamples were incubated from each sample and for each compound. Two of the five subsamples were preserved by formaldehyde (2% final concentration) at the start (control), the other three, after 3 h incubation in the dark at the ambient temperature. Samples were then filtered through 0.2-μm polycarbonate filters and washed on filters 10× with 1 ml of ice-cold 5% TCA. Radioactivity was measured by liquid scintillation. The conversion factors used were the following: mol Leu/kg C=3.1 (Kirchman, 1993) and mol Thy/10^{-15}cells=2.0 (Bell, 1993). Bacterial cells produced were expressed in carbon using per cell carbon content from bacterial biomass measurement (Section 2.3.1).

2.3.4. Chlorophyll a concentration

Samples for regular monitoring were filtered through 0.7-μm-pore-size Nuclepore© polycarbonate filters, dried in cold and dark places and stored frozen. They are extracted by 96% acetone, centrifuged, and the absorbance was measured at wavelengths 750, 665, 645 and 630 nm. Calculation was according to SCOR-UNESCO (1964).

During intense measurement, vertical chlorophyll profile was measured with a submersible fluorescence probe (bbe Moldaenke, Kiel).

2.3.5. Phytoplankton: counting and biomass

Samples were preserved by Lugol's iodine solution and examined in chambers with an inverted microscope, taxa determined, counted and converted to volume biomass from respective cell volumes.

2.3.6. Autotrophic picoplankton

Samples from regular monitoring were fixed with formaldehyde (0.7% final concentration) and filtered through black Nuclepore© polycarbonate filters (0.2 μm pore size). The filter was placed on a microscope slide, briefly dried and covered with a drop of

fluorescence-free immersion-oil and a cover slip. Slides were stored frozen and later counted and measured by epifluorescence microscopy using chlorophyll autofluorescence.

Samples from the intensive March investigations were fixed with formaldehyde (2% final concentration) and stored at 3–5 °C before filtering. APP were counted on DAPI-stained black polycarbonate filters (0.2 μm pore size) by epifluorescence microscopy using chlorophyll autofluorescence.

2.3.7. Heterotrophic protists

Heterotrophic nanoflagellates (HNF) were determined in formaldehyde-preserved samples (2% final concentration) after filtration, through polycarbonate filters (1 μm pore size) and DAPI stain. The epifluorescent microscope was used, and each DAPI-stained flagellated cell was controlled for the absence of chlorophyll autofluorescence.

Samples for ciliates were fixed by Lugol's iodine, decolorized by thiosulphate, preserved by formaldehyde (4% final concentration) and concentrated by sedimentation (Sherr and Sherr, 1993). The taxa were determined and counted.

2.3.8. Primary production

The method used in mountain lakes and described by Straškrábová et al. (1999) was applied. The depth profiles of the photosynthetically active radiation (PAR) intensity were measured with the Li-Cor model LI-250 Light Meter with the PAR spherical sensor. Five layers within the euphotic layer (estimated as 1% of the surface irradiation) were sampled for analyses. From each layer, two black and two light quartz-glass flasks (130 ml) with added ^{14}C-bicarbonate were exposed for 4 h (between 9 and 14 h) in the respective depth in the lake. The assimilated ^{14}C was fractionated using a combination of filtration and acidification into the following fractions: [Aa] >3 μm nanophytoplankton; [Ab] 1–3 μm autotrophic picoplankton; [B] 0.2–1 μm bacteria; [C] <0.2 μm dissolved organic C. The gross primary production was calculated as Aa+Ab+B+C, the cellular production as Aa+Ab, and the extracellular production as B+C. To obtain carbon fluxes (μg C l^{-1} h^{-1}), the rates of ^{14}C incorporation into each fraction (in percent of the added inorganic ^{14}C) were multiplied by the DIC concentration estimated from pH and alkalinity (using Gran titration with correction for temperature).

3. Results and analyses

3.1. Seasonal changes during the years 2001–2003

From the last 3 years of regular monitoring at site No. 1, the seasonal changes of the selected parameters were evaluated. The inverse stratification under the ice was observed each year: in 2001, it lasted 6 weeks, in 2002, only 4 weeks, and in 2003, it lasted 7 weeks (Fig. 1). Ice cover duration was the longest in 2001, and the shortest, in 2002. Summer temperature at the water surface increased to its maximum in August 2001, just to a short peak of 15 °C, whereas in 2002, maximum values reached 18 °C, and temperatures ca. 15 °C lasted almost 5 weeks. Temperature at the layer at 50 m reached a maximum later (September–October), with the onset of the decrease in surface temperature and starting of mixing. A short (1 week) temperature maximum in 50 m of 8–9 °C occurred both in 2001 and 2002.

Regularly, after the onset of early summer warming at the surface of up to 9–12 °C (see the difference in both layers since July), a cooling event occurred between July and August. This decrease was observed in all 3 years, and the surface temperature always declined to 6 °C for 1–3 weeks. Cooling event was very short in 2002.

Seasonal changes of chlorophyll *a* (CHL) and transparency (shown in Fig. 2) were in concordance with the temperature dynamics. The sum of CHL in the column 0–50 m increased under the ice in all years and reached the highest value in 2003. Maximum CHL concentrations in winter reached 1.3, 1.6 and 3.8 μg l^{-1} in 2001, 2002 and 2003, respectively. The highest values were observed in the 0-, 5- or 10-m depths. At the maximum CHL per area, the concentrations per volume unit usually were high in the whole column 0–50 m. Summer maximum concentrations (per volume) were not substantially higher than those of winter, reaching 2.15, 2.88 and 2.67 μg l^{-1} in 2001, 2002 and 2003, respectively. Transparency (Secchi disc) varied between 25 and 5 m and was inversely correlated to CHL concentrations.

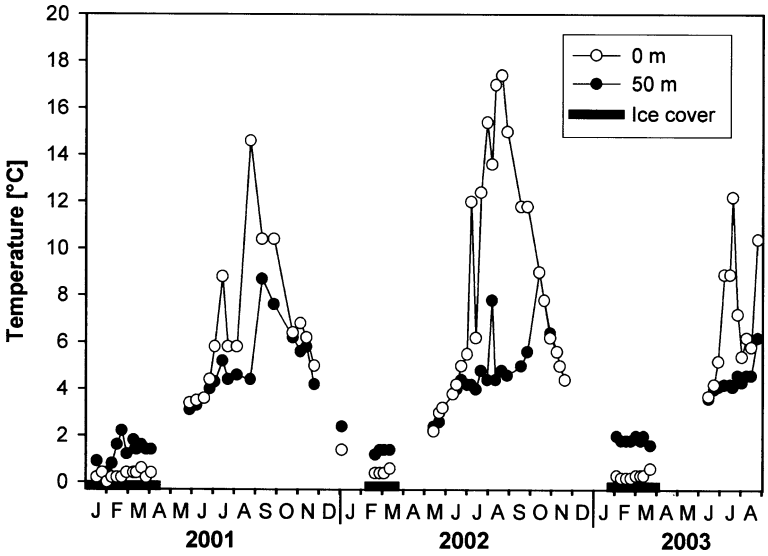

Fig. 1. Seasonal changes of temperature in the 0- and 50-m layers during January 2001 to August 2003.

The total abundances of bacteria (microscopic counts) were followed biweekly up to 500 m depth. They are expressed as total abundances in the column under 1 m^2 (Fig. 3). In the layers 0–50 m, the maximum abundances per ml found were 1.1, 1.3 and 0.5×10^6 cells/ml in the years 2001, 2002 and 2003, respectively. In the layers between 50 and 250 m, the respective values were 0.5, 0.3 and 0.3×10^6 cells/ml, and in the layers 250–500 m, 0.2, 0.3 and 0.2×10^6 cells/ml. The respective summer values were two to three times higher in all layers. Variations of bacterial abundances during summer was correlated directly to variations of CHL concentration, showing a maxima in 2001 and 2002. In summer 2003, there were no summer data from depths greater than 250 m. The relative maxima were

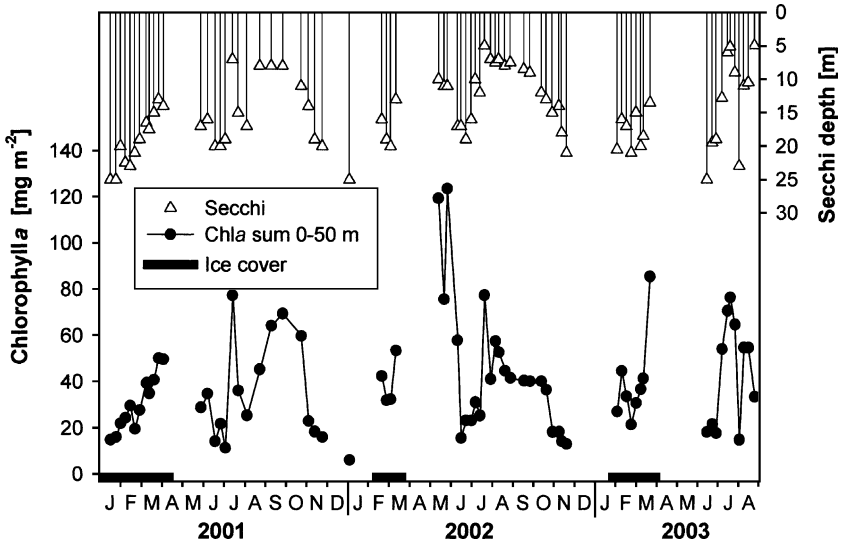

Fig. 2. Seasonal changes of transparency (Secchi) and chlorophyll *a* in the column 0 to 50 m during January 2001 to August 2003.

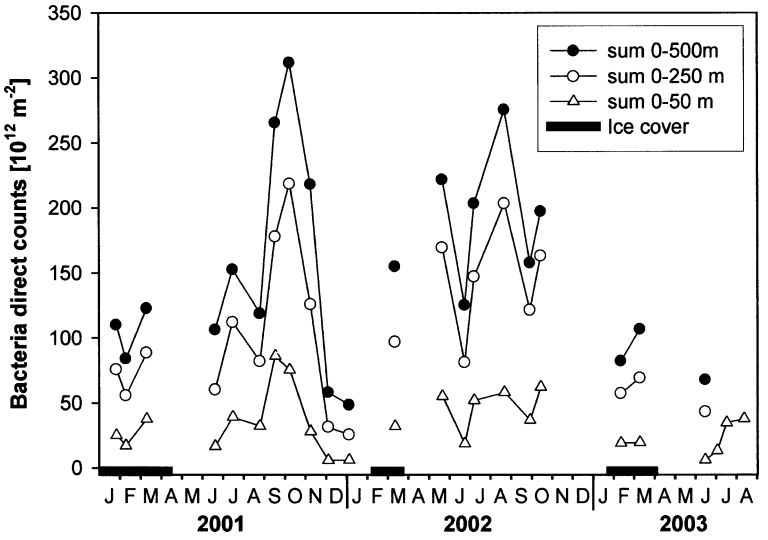

Fig. 3. Seasonal changes of bacteria microscopic counts (erythrosine stain) summed per columns 0 to 50, 0 to 250 and 0 to 500 m during January 2001 to August 2003.

not correlated with CHL. While for CHL, the spring maximum was higher than the summer maximum; for bacteria, the opposite is true.

Simultaneously with microscopic counts, heterotrophic bacteria growing on agar plates (CFU) were investigated weekly (Fig. 4). In general, CFU were four orders less abundant than the microscopic counts, but their seasonal changes were similar. During summer, in 2001 and 2002, two distinct maxima, separated by a deep depression, were found in the layers deeper than 50 m. In the upper 50 m, the decline was less distinct in 2001, and in 2002, only one maximum occurred in August. Both in winter and in summer, tens to hundreds of colony-forming cells per milliliter were found in layers as deep as 200 m, and in 500 m, still 5 to 60 CFU/ml occurred regularly.

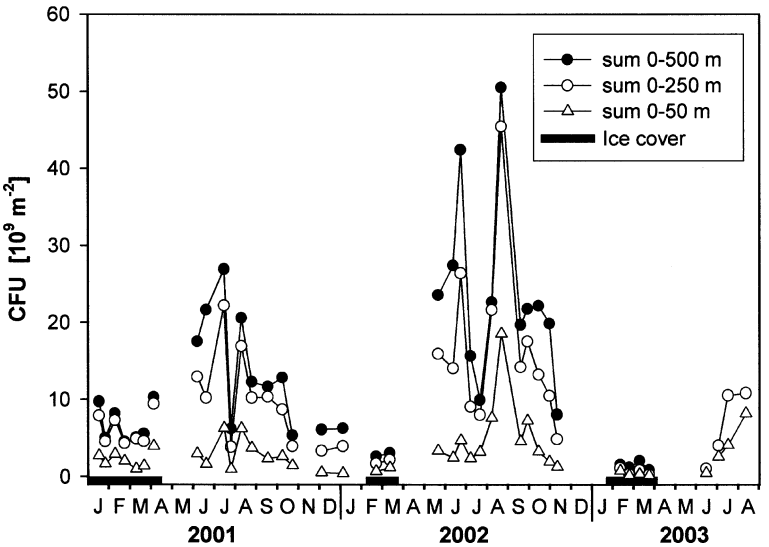

Fig. 4. Seasonal changes of bacterial plate counts (CFU=colony forming units) summed per columns 0 to 50, 0 to 250 and 0 to 500 m during January 2001 to August 2003.

Table 1
Changes in the euphotic layer during February to March 2003 under the ice

	Units	Febr. 4	Febr. 11	Febr. 18	Febr. 25	March 4	March 10	March 11	March 12	March 15	March 25
T_{av} 0-25 m weighted	° C	0.45	0.40	0.44	0.44	0.45	0.49*	0.49	0.52*	0.57	0.84
Chl_{av} 0-25 m weighted	µg . l^{-1}	0.72	1.50	0.97	0.67	0.85	0.88*	0.88	1.00*	1.09	2.00
TPP_{sum} 0-40 m	mgC $h^{-1}m^{-2}$	n.d.	n.d.	n.d.	n.d.	n.d.	38.7	n.d.	23.5	32.7	n.d.
Cell PP_{sum} 0-40 m	mgC $h^{-1}m^{-2}$	n.d.	n.d.	n.d.	n.d.	n.d.	24.0	n.d.	20.7	20.4	n.d.
BP Thy_{ave} 0-40 m	pmol $l^{-1}h^{-1}$	n.d.	n.d.	n.d.	n.d.	n.d.	0.90	0.65	0.53	0.55	n.d.
BP Leu_{ave} 0-40 m	pmol $l^{-1}h^{-1}$	n.d.	n.d.	n.d.	n.d.	n.d.	42.4	16.3	8.2	n.d.	n.d.

T_{av}: average (weighted) temperature in the layers 0, 5, 10, 15 and 25 m. Chl_{av}: average (weighted) chlorophyll *a* in the layers 0, 5, 10, 15 and 25 m. Values with asterisks evaluated from continuous recording with Fluoroprobe. TPP_{sum}: sum of total primary production hourly rate (measured in 2, 10, 20, 30 and 40 m) per square meter. Cell PP_{sum}: sum of cellular primary production hourly rate (measured in 2, 10, 20, 30 and 40 m) per square meter. BP Thy_{ave}: hourly rate of bacterial thymidine uptake, average from 2, 10, 20, 30 and 40 m. BP Leu_{ave}: hourly rate of bacterial leucine uptake, average from 2, 10, 20, 30 and 40 m. Part in the frame: week of intense measurements.

3.2. Changes under the ice in winter 2003

Monitoring under the ice started on February 4, 2003, and lasted until March 25, 2003. First week after the full freezing, temperature in upper layers decreased and CHL increased (Table 1). This latter change was mostly due to a 10-fold increase (in 5-m depth) in the biomass of *Asterionella formosa*, *Stephanodiscus meyerii* and *Synedra acus* (Bacillariophyta; Table 2). In the rest of February, temperature did not change much or increased only very slowly, and both CHL and phytoplankton biomass were decreasing. After March 4, temperature increased, and so did CHL and phytoplankton biomass. The predominant groups in phytoplankton biomass were Bacillariophyta and Dinophyta. The former group was represented by the same dominant species as in the preceding month (see above). Among the latter group, *Gymnodinium baicalense* Antip. appeared and grew all the time. At the end of March, cryptophytes (*Cryptomonas* spp., *Rhodomonas* spp.) and chrysophytes (*Chrysidalis* sp., *Dinobryon cylindricum* Imh. and *Pseudopedinella* sp.) increased considerably. Autotrophic picoplankton (APP) included both procaryotic and eucaryotic cells. Abundances of APP were increasing during the whole period below ice, procaryotic APPs from 2100 up to 44,000 per ml, and eucaryotic, from 134 to 6700. Because of higher cell volume, eucaryotic APPs reached comparable biomass with the procaryotic ones by the end of March.

Intense measurements of vertical profiles was performed during the week from March 10 to March

Table 2
Biomass wet weight in mg m^{-3} of phytoplankton groups in 5 m layer during late winter 2003

Date	Feb. 4	Feb. 11	Feb. 18	Feb. 25	Mar. 4	Mar. 11	Mar. 15	Mar. 25
Bacillariophyta	31.6	303.7	52.5	65.1	28.8	74.0	243.1	592.8
Dinophyta	0.0	7.5	0.3	4.2	14.6	202.3	194.5	92.4
Chlorophyta	0.3	0.2	1.4	0.8	1.4	2.1	0.9	1.6
Cryptophyta	0.0	3.8	2.0	1.5	6.9	17.0	30.6	57.3
Chrysophyta	0.0	0.4	0.2	5.4	0.3	0.5	3.0	22.7
APP	1.9	n.d.	20.9	5.4	27.5	11.3	n.d.	60.1
Total excl. APP	31.9	315.6	56.4	71.6	52.0	278.9	472.1	766.8

APP—autotrophic picoplankton.

15, i.e., during the period of increase in temperature, CHL and phytoplankton biomass (see the frame in Tables 1 and 2). Ice thickness was 0.8 m, with almost no snow cover, and the weather was sunny without clouds. Two representative profiles of temperature, light and CHL were shown in Fig. 5. Except that of the surface (cca 1 m below the ice), temperatures increased very slowly, up to the depth of 30 m (less than 0.1 °C/10 m). From 30 to 50 m, the temperature increase was three times faster. Secchi disc transparency was 20 m, and in the depth of 35 m, there was 1% of surface irradiance of photosynthetic active irradiation (PAR). The depth of the euphotic layer thus corresponded to 1.7× Secchi. The highest CHL concentrations (1.2–1.5 mg.m^{-3}) were found between 5 and 30 m, and they decreased sharply down to 0.1 mg m^{-3} in 30 m. All parameters were measured in five layers, starting at 2 m (the near-surface layer, which was not disturbed by ice breaking) up to 40 m.

The abundances of bacteria (DAPI), heterotrophic nannoflagellates (HNF) and autotrophic picoplankton (APP) are shown in five layers with increasing scales from March 10 to March 15 (Fig. 6). Except at the 40-m depth, the abundances of microbes increased during the week, with slight fluctuations among the depths. From 2 to 30 m on March 15, bacterial abundances were 1 to 1.5×10^6 cells/ml, HNF reached 20–80 ind. per ml. APP were at maximum (28–68×10^3 cells/ml) in the middle of the period. In the lowest stratum measured, abundances remained low for the whole period, especially APP (not surpassing 2×10^3 per ml).

Bacterial cell volumes (mean per sample) varied during the period (0.034–0.104 μm^3), and, consequently, the biomass variations (5.88–21.15 μg C l^{-1}) were not always correlated with abundances (0.53–1.61×10^6 cells/ml). On March 12, the lowest bacterial biomass (mean from all layers) was found. Usually, but not always, bacterial abundances and biomasses were lower in the deeper layers. The mean biomass for the upper strata from 0 to 20 m from all dates was 14.6 μg C l^{-1}, whereas that from layers 30 and 40 m was 11.1 μg C l^{-1}.

When evaluating bacterial abundances during the comparative measurements, DAPI counts (Fig. 6) were, on the average, 2.8 times higher than the counts with erythrosine stain (Fig. 3).

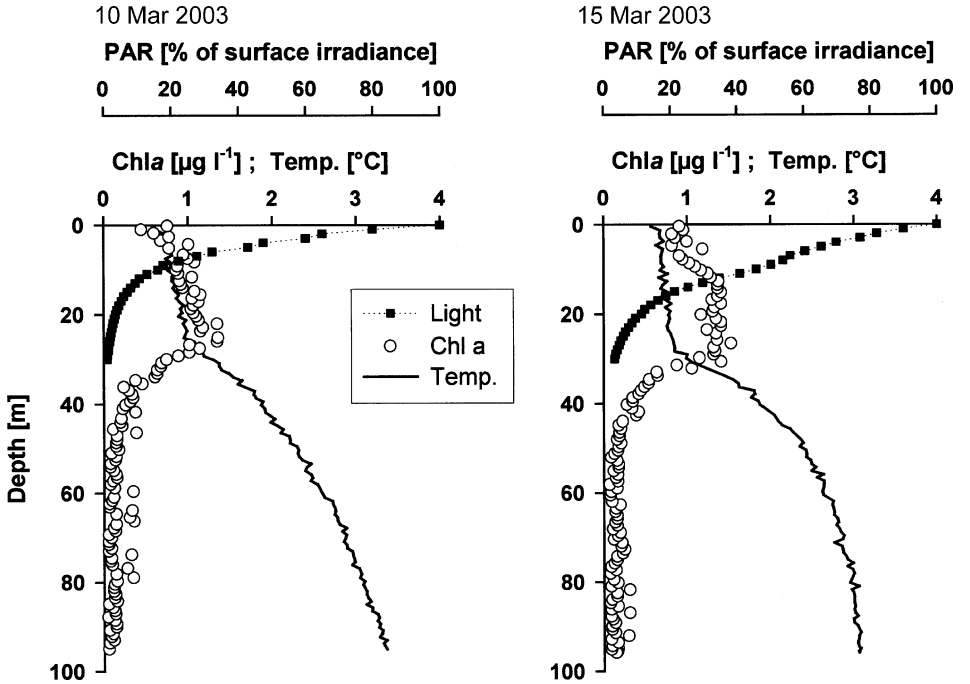

Fig. 5. Vertical profiles of photosynthetically active radiation (PAR in % of surface irradiance), water temperature and chlorophyll *a* (Fluoroprobe measurements) in March 2003.

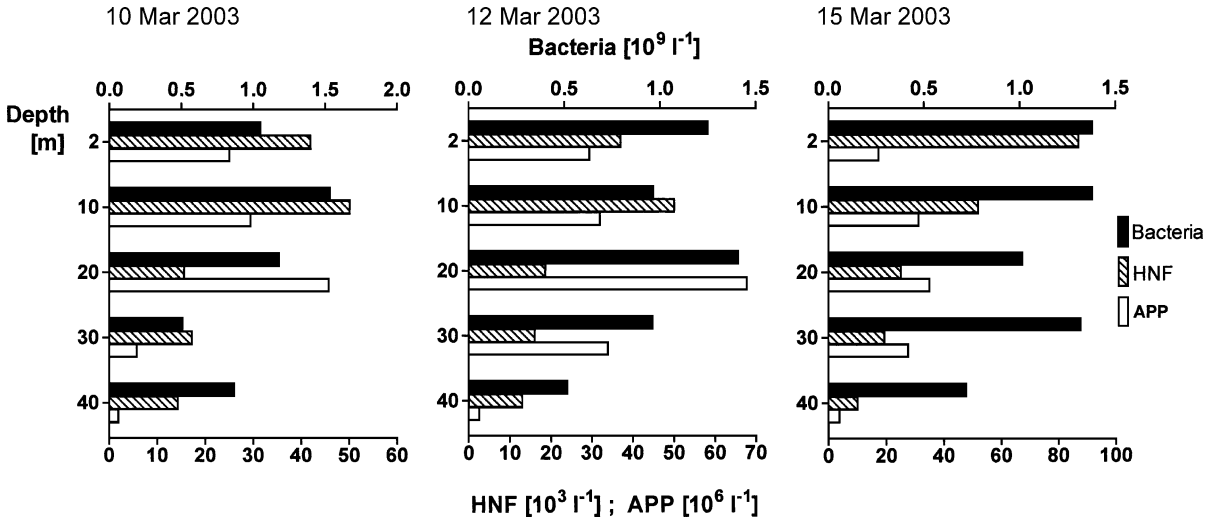

Fig. 6. Vertical profiles of microbial abundances (bacterial microscopic counts DAPI stained; HNF=heterotrophic nanoflagellates; APP=autotrophic picoplankton) in March 2003.

Ciliates were found in small numbers—increasing from 0.5 to 1.2 ind. per ml from 2 towards 30 m, and in 40 m, they were scarce (0.2 ind. per ml). Most frequently, the representatives of Oligotrichida were determined: *Rimostrombidium hyalinum* (Mirabdullaev) Petz & Foissner, *Limnostrombidium viride* (Stein) Krainer, *Pelagostrombidium* sp. and *Tintinnidium* sp. Whereas the first species is picoplanktivorous, the others are coarse filter feeders. There was a considerable abundance of potentially picoplanktivorous and nanoplanktivorous microzooplankton in the water column of 0–50 m (Table 3), especially the nauplii of *Epischura baicalensis* Sars (0.3 ind. per ml).

An important nano- and microplanktivorous flagellate was the apochloric representative of Dinophyta—*Gymnodinium coeruleum* Antip. In Lake Baikal, chloroplasts were never observed in this species, and its feeding on *Asterionella* was frequently recorded. During February and March 2003, its abundance in the 5-m layer varied from 0.3 to 8.5 ind. per ml (biomass wet weight=8–300 mg m^3).

Table 3
Zooplankton abundance (10^3 ind m^{-2}) in the upper 50 m and in the column from 50 to 500 m on March 11, 2003

Taxon	0–50 m	50–500 m
Epishura baicalensis Sars, nauplii	157.4	5.87
Epishura baicalensis Sars, copepodits	4.18	2.46
Epishura baicalensis Sars, adults	14.28	6.6
Notholca grandis Vor.	0.37	0
Synchaeta pachypoda Jaschn.	3.0	0
Kellicottia longispina (Kell.)	0.9	0
Cyclops kolensis Lill., nauplii	0.2	0

3.3. Primary production and bacterial production

Primary production was measured three times during the week (March 10, 12 and 15). In the same period, the amount of light (photosynthetically active radiation, PAR) showed a slight increase in all measured depths (Table 4). Due to ice cover and sampling arrangement, the PAR at 0 m could not be measured directly, and it was estimated by extrapolation from the curve measured in the depths from 2 to 30 m. The depths of 10% and 1% surface PAR varied just slightly during the week (12 to 15 and 30 to 35 m, respectively). Primary production (Fig. 7) reached the maximum values in the 10-m depth, viz.

Table 4
Vertical profiles of light (PAR) during March 8 to March 15

Depth (m)	March 8	March 10	March 12	March 15
2	87.3	142	174	173
5	74.9	133	132	147
10	33.6	50.0	57.0	103
20	8.75	10.9	15.3	25.6
30	3.00	3.30	4.92	7.50

Values in μmol photon m^{-2} s^{-1}, measured at 10 a.m.

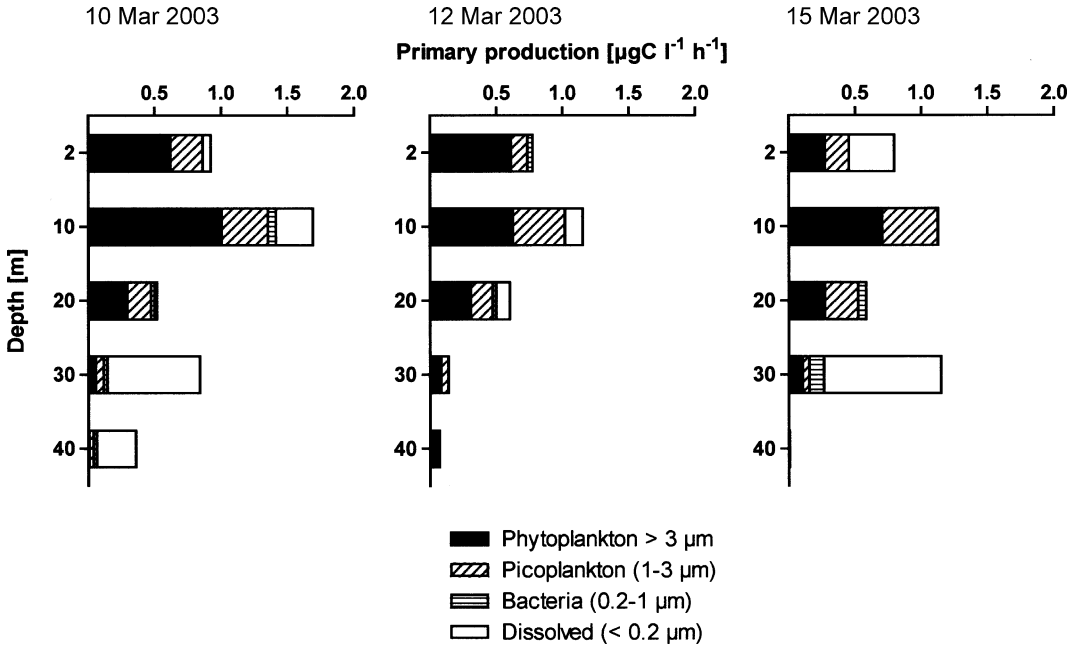

Fig. 7. Vertical profiles of primary production separated into size fractions (nano- and picoplankton assimilation, bacterial uptake, dissolved exudates) in March 2003.

1-1.5 µg C $l^{-1}h^{-1}$. The assimilation numbers also were the highest in that layer (hourly rates 0.9–2.0 µg C/µg Chl*a*). Assimilation numbers were lower both in 2 and in 20 m, with hourly rates of 0.8–1.0 and 0.5–0.6 µg C/µg Chl*a*, respectively. In 30 and 40 m, at the lower end of euphotic zone, primary production was negligible for mostly the cellular production, i.e., in particles larger than 1 µm. Dissolved extracellular products (empty parts of bars) could not be determined accurately due to the small volumes measured; the results are erratic and variable, especially in the layers with low light. Only the part of extracellular production immediately used by bacteria during the exposition was measured accurately and was the lowest in 2 and 10 m—less than 10% of cellular production. However, in 30 and 40 m, it equaled 25–90% of cellular production, indicating that the exudation in light-limited depths might be high compared with that in the upper layers.

The major part of primary production was due to phytoplankton larger than 3 µm—mostly diatoms and dinophytes—in the layers 2 to 20 m. Production by APP (1–3 µm) was 26–38% of the total cellular production in layers 2 to 20 m during the first measurement, but its rates increased during the week and its share increased up to 37–48%. From pigment analyses (Fietz and Nicklisch, 2004) calibrated by taxonomic determination, it can be derived that about 8% of total CHL was in cyanobacterial APP, whereas 60–70% was in diatoms and dinophytes.

The hourly production rate per area (Table 1), including both the total (with possibly erratic values of extracellular production) and the cellular production, showed a clear decrease occurring from March 10 to 15, although the phytoplankton biomasses increased and CHL did not change much. However, the part of production in the cells between 1 and 3 µm increased from 7.25 to 8.14 mg C $h^{-1}m^{-2}$ between March 11 and 15.

Bacterial production by thymidine (Thy) and leucine (Leu) uptake was measured in the same layers like primary production (Fig. 8 and Table 1). On March 11, 2003, the vertical profile of bacterial production was measured in the layers 0, 10, 30, 50 and 100 m by three methods: Thy, Leu and dark carbon fixation (Fig. 9). Similarly, like primary production, bacterial production in 0–40 m decreased during the 5 days of measurement in all depths. In

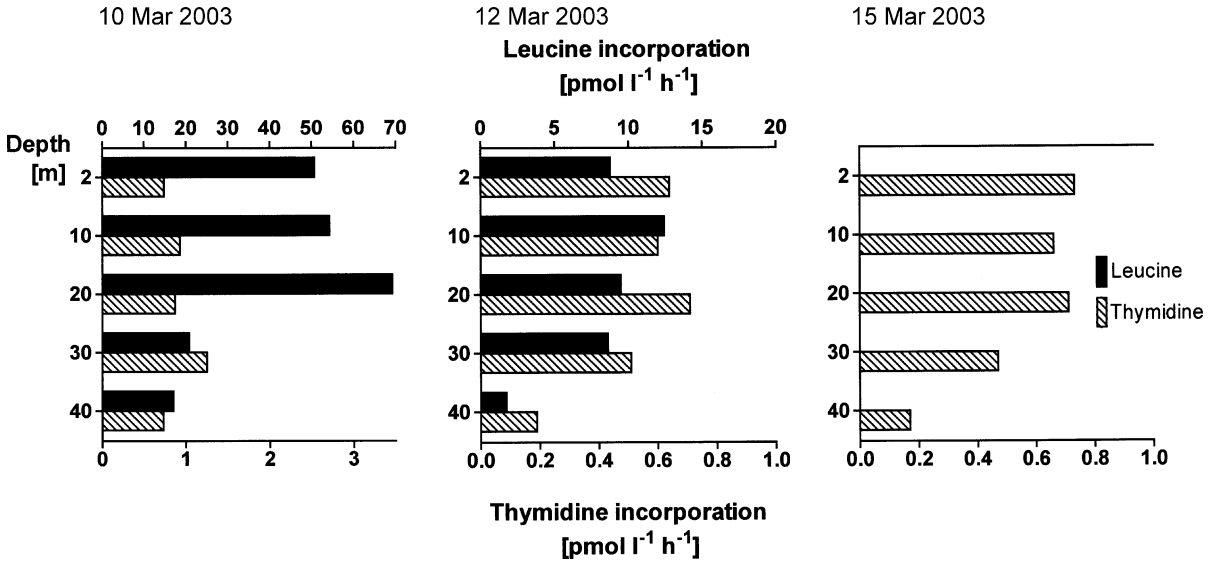

Fig. 8. Vertical profiles of bacterial production (leucine and thymidine uptake) in March 2003.

Leu, the decrease during 3 days was considerable. The shape of the vertical profiles also changed during that period, especially that of Thy. On March 10 and 11, Thy uptake rates did not differ much from the surface towards the deeper layers, whereas on March 12 and 15, distinctly lower values in the 30- to 40-m layers were found compared with the upper ones.

For comparison with dark carbon fixation method, Thy and Leu were converted to carbon (Fig. 9).

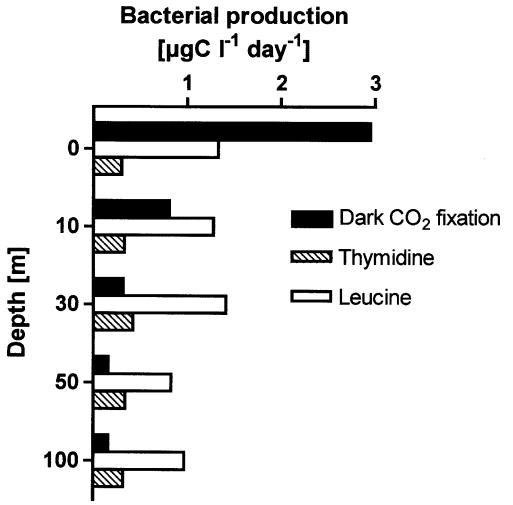

Fig. 9. Vertical profile of bacterial production measured by three methods on March 11, 2003.

Conversion from Thy yielded values just 30% to 40% of those converted from Leu. Compared with dark carbon uptake, not only the absolute values differ, but also the relative proportion of production in particular layers. The carbon method showed maximum values at the surface, with a very sharp decrease with increasing depth.

4. Discussion

4.1. Spring phytoplankton maximum under the ice in the South Basin

At the end of March 2003, chlorophyll *a* values were the highest observed during the last three seasons. However, compared with historical data, both the chlorophyll *a* concentrations (86 mg m^{-2} summed in 0–50 m, see Fig. 2, and maximum concentration 3.8 mg m^3 at the surface on March 25) and phytoplankton biomasses (766.8 mg m^{-3} in 5 m, see Table 2) were in the range of interannual variations, recorded from the past in Lake Baikal. Izmest'eva (in Kozhova and Izmest'eva, 1998) recorded a vernal maxima of chlorophyll *a* (0 m) at Bolshie Koty station as high as 16 mg m^{-3} in 1979 and 9 mg m^{-3} in 1994. In the years 1982, 1983 and 1995, in contrast, the maxima were below 2 mg m^{-3}. During long-term monitoring, a

considerable interannual variation in phytoplankton biomass has been observed between "low production" and "high production" (melosira) years (Kozhova and Izmest'eva, 1998). The former years showed vernal maximum values in depths 0–50 m lower than 300 mg m^{-3}, whereas in the latter years, the maxima reached 550–4469 mg m^{-3}, all at the Bolshie Koty station. Popovskaya (2000) listed the peak values of phytoplankton biomasses during spring in the South Basin from 1964 to 1990, and she showed 11 values above 1000 mg m^{-3} in layers from 0 to 25 m. Those high values (up to 4163 mg m^{-3} in 1968) were found periodically during the whole period. On the other hand, there were 7 years with biomasses below 100 mg m^{-3}, also during the whole period. However, the years with the highest biomasses were not always the years with mass occurrence of *Aulacoseira*. During the period evaluated by Popovskaya (2000), only six "high-biomass" years are melosira years, whereas the other five high-biomass years were characterized by high abundance of small *Nitzschia acicularis* W. Smith.

In the past, dominant vernal diatom species varied during the melosira years. *Aulacoseira baicalensis* and *Cyclotella baicalensis* dominated in the 1950s and 1960s, whereas the proportion of *Aulacoseira skwortsovii* was increasing from the 1970s to the 1980s. Then, also the smaller diatoms, *Synedra acus*, *Nitzchia acicularis*, *Stephanodiscus meyerii* and *Cyclotella minuta*, became more abundant in the 1990s and later. Consequently, with smaller species prevailing, a long-term increase in cell numbers was observed (Kozhova and Izmest'eva, 1998), although the biomasses remained in the same range (Bulygin et al., 1998).

A comparison between two 5-year periods at the south Baikal monitoring station (1979–1983 and 1996–2000) by Izmest'eva et al. (2000) revealed significant increases in chlorophyll *a* concentrations. Both periods represented comparable interannual cycles from one melosira year to the next. Both the mean concentrations and ranges rose from averages of 0.83 (0.06–1.70) to 1.28 (0.30–4.03) mg m^{-3}.

From the three investigated years, 2001 and 2003 were not melosira years, with no mass occurrence of large *Aulacoseira* species. Their occurrence was mentioned in 2001, during July, but only in the north basin, not in the south (Fietz and Nicklisch, 2004). In 2002, *Aulacoseira* was abundant.

On March 11, dinophytes predominated in phytoplankton biomass (73% of total biomass in the 5-m layer), mainly *Gymnodinium baicalense* (endemic). In all other dates, diatoms dominated. The maximum phytoplankton biomass of 766.8 mg m^3 was reached just on the last sampling date before ice melting, and 77% of total phytoplankton biomass in the 5-m layer consisted of three diatom species (*Synedra acus*, *Asterionella formosa* and *Stephanodiscus meyerii*—endemic), with the predominance of *S. acus* (85% of biomass and 69% of abundance in total diatoms). For the first time in the long-term monitoring history, *A. formosa* was detected as one of dominant diatom species during the vernal peak (12% in total diatom biomass). This may be important because this species is characteristic of more mesotrophic to eutrophic waters (Patrick and Reimer, 1966).

4.2. Primary production

The daily rates of primary production were estimated to be 10× the hourly rates (from Table 1), and they reached 235–387 mg C m^{-2} day^{-1} when the total production is considered. If we neglect the extracellular part, the respective values (cellular production) were 204–240 mg C m^{-2} day^{-1}. Compared with the data gathered by Yoshida et al. (2003), these total production values were in the middle of range found in March 1965–1969 in the south basin of Lake Baikal with the oxygen method after 24 h exposition (Votintsev et al., 1975). The values measured with the ^{14}C method in 1982–1985 by Bondarenko and Guselnikova (referred to in Yoshida et al., 2003) were about three times lower than our cell production values. Yoshida et al. (2003) measured primary production in March 1999 and 2000 by the ^{13}C method in the south basin, approximately 60 km southwest from Bolshie Koty station. Their values were 79 and 113 mg C m^{-2} day^{-1}. Even if we did not consider extracellular production (impossible to be measured by the ^{13}C method), these values were very low compared with our data. A very sharp maximum of production rates in March was found by Yoshida et al. (2003) in the 2.5-m depth (18 and 12 mg C m^{-2} day^{-1}), and this was quite comparable with our maximum rates of cell production, viz. 14, 10 and

12 mg C m^{-2} day^{-1}, found in 10 m. The main discrepancy was the height of column, from which the production was integrated. Yoshida et al. (2003) did not mention the absolute values of irradiance nor the depth of Secchi disc transparency at their site, but they estimated the depth of euphotic zone (1% of the surface irradiance) at 11 and 14 m (compared with our 30–35 m and high transparences always found in March; Fig. 2). There is no explanation of the high attenuation coefficient of PAR (>0.4 m^{-1}) during both spring measurements found by Yoshida et al. (2003), and no reference on chlorophyll *a* concentration or phytoplankton biomass, which might be the reason of low transparency. It can be concluded that at moderate or low biomasses (or chlorophyll *a* concentrations) and high depth of euphotic zone, primary production under the area unit might be even several times higher than in cases with high biomass, but low transparency and lower thickness of euphotic zone.

Izmest'eva et al. (2000) evaluated the production rates in the south basin of Lake Baikal (monitoring station Bolshie Koty) from long-term monitoring and derived that they have been increasing since the 1980s to the 1990s, with seasonal ranges of 180–540 mg C m^{-2} day^{-1} in the former period and of 225–675 mg C m^{-2} day^{-1} in the latter. These values incorporate the ranges of the whole season, not only the spring values, which are always lower.

The production of the smallest fraction (APP 1–3 μm) was in the range of 70–81 mg C m^{-2} day^{-1}, and its share in cell production increased during the week of our measurement, from 30% to 40%. Due to the patchiness of chlorophyll *a* concentrations and permanent currents, even under the ice, the import from other water layers during the weekly measurement could not be excluded (compare Zavoruyev et al., 1992). Yoshida et al. (2003), during March 2000, also found 40% of primary production in the size fraction <2 μm, where they also included that part of extracellular production used by bacteria during incubation.

Assimilation numbers observed by Kozhova and Pautova (1985) with the ^{14}C method, in March, under the ice were in the range of 0.1–0.7 μg C h^{-1} per μg Chl*a* in the years 1977–1981, compared with ours, 20 years later, in the range of 0.5–2.0 μg C h^{-1} per μg Chl*a*. The assimilation numbers of APP in our measurements might be four times higher (i.e., 2–8 μg C day^{-1} per μg Chl*a*) when considering their share in total cell production, 40% (see Results section), and the share in total chlorophyll, just 10% (Fietz and Nicklisch, 2004).

4.3. Bacterial biomass and activity

DAPI-stained bacterial cells during 1 week of measurements in March were small, short rods, with an intense fluorescence, well distinguishable. Apparently, many of them were not readily visible with erythrosine stain without fluorescence, which was the reason of discrepancy between the two methods of counting. In summer (August 2003), the erythrosine counts (ERYT) in the upper 50 m were two times higher than in March (see Fig. 3). These values were comparable with the DAPI counts (from July and August, data not shown): $0.73–1.13\times10^6$ per ml ERYT and $0.77–1.25\times10^6$ DAPI in six samples. Cell volumes measured by image analysis of DAPI-stained cells in the summer samples were by 50% larger, at the average (range 0.05–0.15 μm^3), than in March, and also longer.

In the upper 20–30 m, the biomass of bacteria in terms of carbon was comparable with the biomass of autotrophic picoplankton (assuming 20% of carbon in "fresh weight" estimated from measured cell volumes). Such relationships are referred from oligotrophic lakes and marine systems (Stockner, 1988).

Bacterial production in Lake Baikal has been measured by the method of dark carbon fixation from the last century up to now, whereas Thy and Leu methods likely were used first time in this lake. Short-time Leu and Thy uptake is not readily comparable with the dark carbon fixation method, which used 24-h incubation. The former should be considered as "instantaneous" rate, which might fluctuate during 24 h, whereas the latter was more a "potential" production in a closed system. Shchetinina et al. (1998) and Shchetinina (2003) found fourfold amplitude of daily variations in bacterial production in the upper layers during summer in Lake Baikal. Moreover, the conversion factors to carbon from Leu and Thy uptake might not be valid for the oligotrophic Lake Baikal. When using the factors mostly referred in the literature, unrealistically high production rates resulted from Leu uptake (Fig. 9). Since we measured bacterial production in the dark, a similar phenom-

enon might occur, which was observed by Morán et al. (2001) in oceanic samples. They found an increase in leucine uptake in dark bottles compared with light ones, which was not due to UV inhibition in the light and might be explained by changing nutrient availability for bacteria when transferred from light to dark conditions.

An independent estimate of the instantaneous rate of bacterial production might be derived from the bacterial uptake of algal extracellular products (0.2–1 μm size fraction) during primary production measurements (Fig. 7). In the layers up to 20 m, bacteria assimilate ^{14}C, corresponding roughly to 1–10% of total primary production. Assuming bacterial yield of 50%, this means a consumption of 2–20% of organic C. And considering that bacteria keep the same rate during nighttime, this could result in 4–40% of primary production consumed by bacteria daily (in the euphotic layer). However, bacteria could directly use only extracellular part of production, whereas the cellular production could be used after it is grazed and released in excrements and/or after it is senescent and decaying. Consequently, bacterial decomposition of primary production in the euphotic layer may be positively affected by a considerable percentage of extracellular production in the total and easily grazable APP in cellular production. Apparently, bacterial decomposition rate in the total column of the deep lake during the late-winter phytoplankton maximum is significantly reduced from the euphotic layer towards the deeper strata, and most of it occurs in the upper 30–40 m, although the length of the total water column and the presence of saprophytic bacteria, even in the deepest layers, suggest that the decomposition is almost complete before the material reaches the sediment.

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