

Nutritional diagnosis of phytoplankton in Lake Baikal

MOTOMI GENKAI-KATO,^{1*} TATSUKI SEKINO,¹ TAKEHITO YOSHIDA,¹ HITOSHI MIYASAKA,¹
TAMARA V. KHODZHER,² OLGA A. BELYKH,² NATALIA G. MELNIK,² ZEN'ICHIRO KAWABATA,¹
MASAHIKO HIGASHI¹ AND MASAMI NAKANISHI^{1†}

¹*Center for Ecological Research, Kyoto University, Otsu, Shiga 520-2113, Japan and*

²*Limnological Institute, Siberian Division of the Russian Academy of Sciences, PO Box 4199,
664033, Irkutsk, Russia*

To diagnose the nutritional status of phytoplankton in Lake Baikal, surveys for the determination of concentrations of particulate carbon (PC), nitrogen (PN) and phosphorus (PP) and their ratios were conducted at six stations in March, June, August and October 1999. The concentrations of PC and PN were lower than, and those of PP were similar to, those in another mesotrophic lake except at the station near the mouth of the largest input river, Selenga River, of Lake Baikal. The PC : PN : PP ratio was 102 : 13 : 1, considerably close to the Redfield ratio. The ratio was constant against spatiotemporal changes. These indicate that phytoplankton in Lake Baikal were exposed to no deficiency in nitrogen nor phosphorus. From a viewpoint of the nutritional status of phytoplankton, Lake Baikal might be viewed as an ocean rather than as a lake.

Key words: Lake Baikal; nutrient deficiency; phytoplankton; Redfield ratio.

INTRODUCTION

Primary producers are the indispensable component in food webs. In aquatic systems like lakes, phytoplankton support other organisms such as zooplankton and fish on upper trophic levels. Thus, the nutritional quality of the basal component can affect ways of interaction in food webs. In the present paper, we report the spatial and temporal abundance of phytoplankton in a large, oligotrophic lake, Lake Baikal located in Siberia, Russia. In addition, we report ratios of chemical elements (carbon, nitrogen and phosphorus) of phytoplankton.

Lake Baikal is one of the most attractive lakes in the world for scientists including ecologists.

According to Kozhov (1963), it is the deepest (1637 m) and the oldest (20 million years) lake in the world, and contains as much as 20% of the world's fresh water (23 000 km³). Even in the trend of eutrophication in the world's large lakes, Lake Baikal remains oligotrophic, where a value of 40.2 m of Secchi disk reading was recorded (Shostakovich 1924); human impact is still small. In addition to its physical characteristics, Lake Baikal is biologically diverse and unique: there are 2565 animal species (64% of them are endemic) and about 1000 plant species (Timoshkin 1997).

Lake Baikal is particularly well suited to evaluate the applicability of concepts derived from marine studies because of its large dimensions and oligotrophy. The importance of nitrogen and phosphorus, which potentially regulate phytoplankton abundance, has been highlighted by the oceanic work of Redfield (1958). In lakes, ratios between particulate carbon (PC), particulate nitrogen (PN) and particulate phosphorus (PP) have been established as a good tool for evaluating the nutritional status of phytoplankton (e.g. Healey & Hendzel 1980; Tezuka 1985; Aizaki & Otsuki 1987; Nakanishi *et al.* 1990). Nutritional characteristics

*Author to whom correspondence should be addressed. Email: genkai@ecology.kyoto-u.ac.jp

†Present address: Research institute for Humanity and Nature, Kitashirakawa-Oiwake, Sakyo, Kyoto 606-8502, Japan.

Received 20 June 2001.

Accepted 24 October 2001.

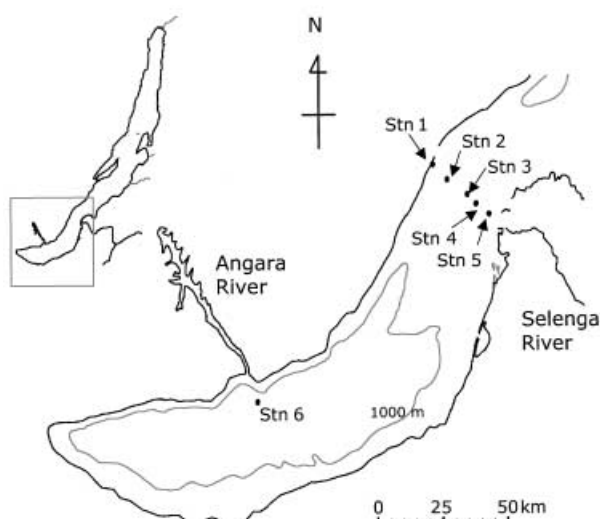


Fig. 1. Lake Baikal and sampling stations (Stn).

of Lake Baikal phytoplankton from a viewpoint of the ratios between PC, PN and PP have not been characterized, although the spatiotemporal variability of phytoplankton abundance has been described (e.g. Kozhova 1987; Bondarenko *et al.* 1996; Goldman *et al.* 1996).

The present study was undertaken to estimate the spatial and temporal changes in the abundance and the nutritional status of phytoplankton in the south basin of Lake Baikal on the basis of PC, PN and PP. The spatial change here is classified into two dimensions: different sampling stations (horizontal change) and depths (vertical change). We set up sampling stations on a transect that lay from the mouth of the Selenga River (east site), the largest inflow, to the opposite shore (west site) (see Fig. 1). The temporal change corresponds to the seasonal one. A previous study indicated that Lake Baikal displayed a noticeable dominance of algal picoplankton in abundance during summer (Nagata *et al.* 1994). We also fractionated particulate matter into three sizes to determine the seasonal change in the size-dependent distribution of phytoplankton at the middle station on the transect.

METHODS

Surveys were conducted on 20 March, 12–13 June, 22–23 August and 21–22 October 1999 at six stations in the south basin (Fig. 1). Taking into account the effect of nutrient inflow from Selenga

River in ice-out seasons (i.e. June, August and October), five of the six stations were arranged on a transect called 'Krasny Yar–Kharauz' from the west site to the east side (the Selenga mouth): Stn 1 (52°25'N, 105°53'E; ca 120 m deep), Stn 2 (52°23'N, 105°60'E; 690 m), Stn 3 (52°20'N, 106°05'E; 270 m), Stn 4 (52°19'N, 106°09'E; 65 m), and Stn 5 (52°18'N, 106°15'E; 15 m). In ice-up season (i.e. March), we set up Stn 6 (5 km off Listvyanka; 51°48'N, 104°55'E; 1430 m deep) as a sampling station because of the difficulty in moving to the transect. Sampling depths were in principle 0, 5, 10, 25, 50, 100 and 250 m. Vertical changes in water temperature were measured with a conductivity, temperature and depth (CTD) probe (SBE-25; SeaBird Electronics Sealogger (SeaBird Electronics, Bellevue, WA, USA)). Using the vertical profile of water temperature, the water column was divided into the epilimnion and the hypolimnion: the boundary of the two layers was determined at the depth where the vertical change of water temperature was maximum. To determine the euphotic zone (from the surface to the 1%-depth of the surface light intensity), underwater light attenuation was measured with a quantameter (LICOR LI-1000; LICOR, Lincoln, NB, USA). Water samples for determining the concentrations of PC, PN and PP were collected vertically at each station using a 10-L Niskin water sampler (General Oceanics, Miami, FL, USA). To remove mesozooplankton, all the water samples were filtered through a 200- μ m mesh-size hand net. At Stns 3 and 6, water samples were divided into three fractions according to the size of particulate matter: <200 μ m, sieved through a 200- μ m mesh-size hand net in which micro-, nano- and picoplankton were supposed to be present; <20 μ m, sieved through a 20- μ m mesh-size hand net in which nano- and picoplankton were present; <2 μ m, sieved through a 2- μ m mesh-size Nuclepore membrane filter (Corning Coster, Cambridge, MA, USA) in which picoplankton were present. Thus, we obtained the concentration of particulate matter (PM) in the microplankton (20–200 μ m) fraction by $[PM < 200 \mu m] - [PM < 20 \mu m]$; [PM in the nanoplankton (2–20 μ m) fraction] = $[PM < 20 \mu m] - [PM < 2 \mu m]$; [PM in the picoplankton fraction (<2 μ m) fraction] = $[PM < 2 \mu m]$.

Particulate carbon, PN and PP were collected on Whatman GF/F glass fiber filters (Whatman

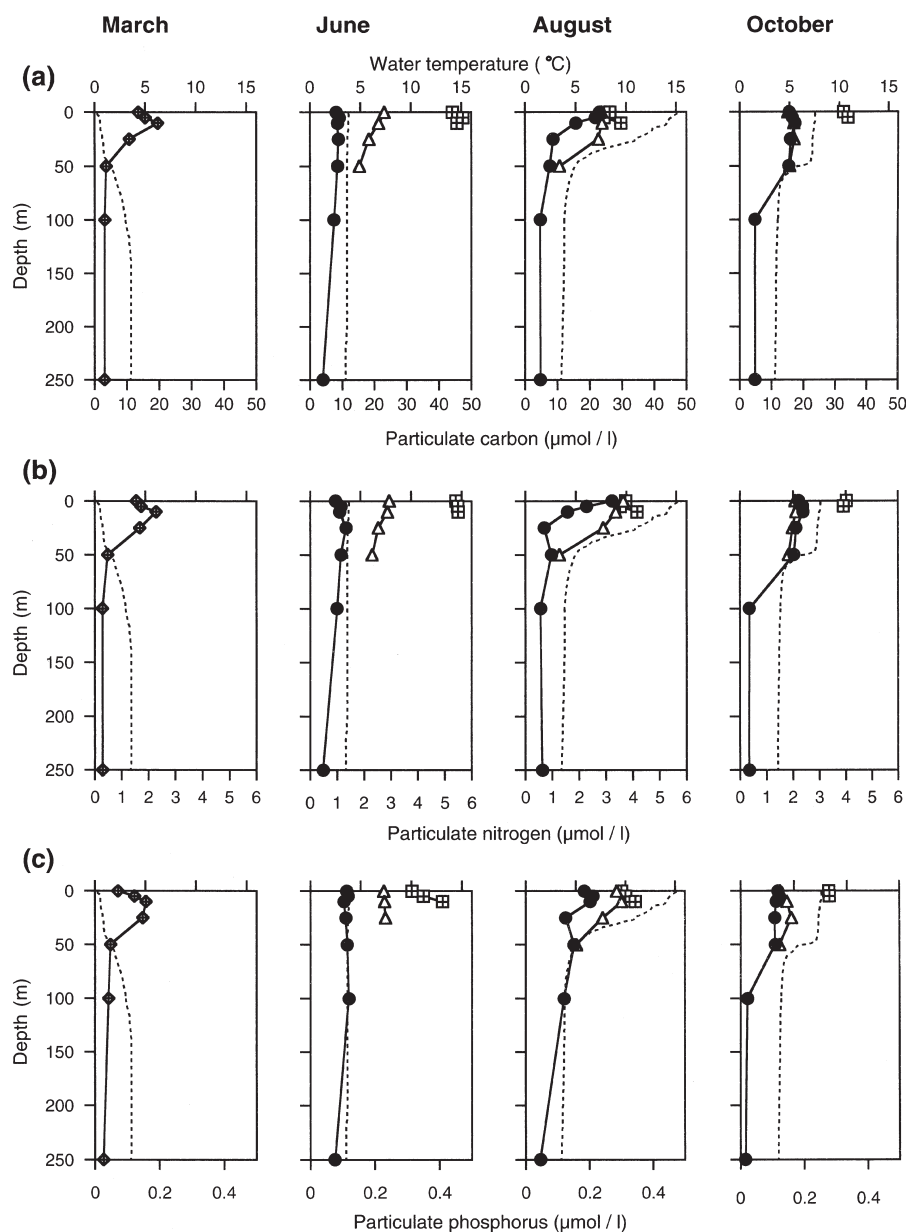


Fig. 2. Seasonal changes in the vertical profiles of particulate (a) carbon, (b) nitrogen and (c) phosphorus concentrations. In March, data at station (Stn) 6 (\diamond) are shown; in June, August and October, data at Stn 3 (\bullet), Stn 4 (\triangle) and Stn 5 (\boxplus) are shown. Vertical profiles of water temperature at Stn 6 in March and at Stn 3 in the other months are expressed by broken lines.

International, Maidstone, England, UK) pre-ignited at 450°C for 2 h. The PC and PN were measured with a carbon, hydrogen, nitrogen (CHN) analyzer (Perkin Elmer 2400 II; Perkin Elmer, Norwalk, CT, USA) and PP was measured by the modified method of Menzel and Corwin (1965).

RESULTS

The PC, PN and PP concentrations <200 μm were always high at Stn 5 (Fig. 2). The concentrations were not so different among Stns 1–3 (only data at Stn 3 are shown in Fig. 2). The concentrations at

Stn 4 had a tendency to take intermediate values of these at Stn 3 and Stn 5. Vertical profiles of PC, PN and PP at open waters (Stns 3 and 6) well reflected the thermal regime. In March, when reverse thermal stratification was established, the concentrations of PC, PN and PP displayed maxima below the surface (the surface of the water was defined as the bottom surface of the ice); in June, when the water was well mixed so that the vertical distribution of water temperature was uniform, the concentrations also displayed uniform patterns; in August and October, when thermal stratification was established, the concentrations were higher in the epilimnion.

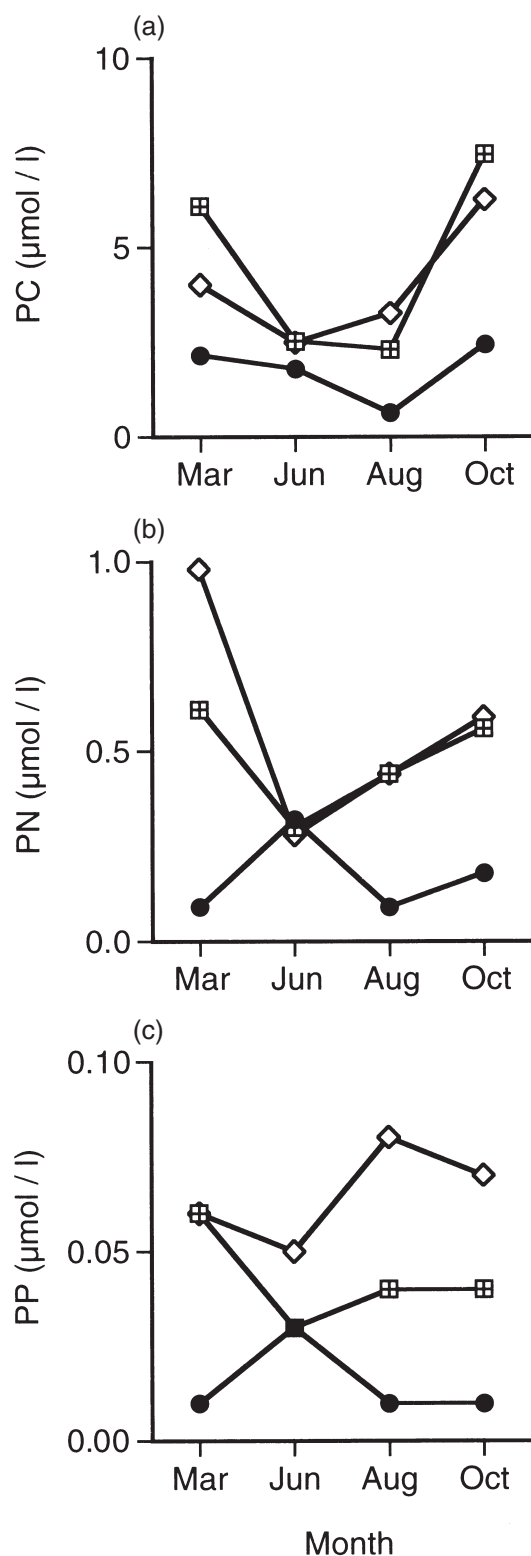


Fig. 3. Size-dependent distribution of the average biomass expressed as: (a) particulate carbon (PC); (b) particulate nitrogen (PN); and (c) particulate phosphorus (PP) in the epilimnion. The data in March were collected at station (Stn) 6 and the others at Stn 3. (●), Microplankton; (⊞), nanoplankton; (◇), picoplankton.

The average concentrations of PC, PN and PP in each fraction ($<2\ \mu\text{m}$ = picoplankton fraction, $2\text{--}20\ \mu\text{m}$ = nanoplankton, $20\text{--}200\ \mu\text{m}$ = microplankton) in the epilimnion (except for June) are shown in Fig. 3. In the mixing period of June, we regarded the layer of 0–250 m deep as the epilimnion because there was no remarkable change in water temperature. The pico- and nanoplankton fractions were dominant and the microplankton fraction was least abundant in terms of PC, PN and PP except for June. Comparing PC, PN and PP between the picoplankton and nanoplankton fractions, the picoplankton fraction was noticeably high in PP.

The ratios (by atoms) between PC, PN and PP $<200\ \mu\text{m}$ in the water collected were calculated using a simple linear regression through the origin (PC : PN, slope = 7.8, $R^2 = 0.99$, $P < 0.001$, $n = 82$; PC : PP, slope = 102.3, $R^2 = 0.94$, $P < 0.001$, $n = 82$; PN : PP, slope = 13.1, $R^2 = 0.94$, $P < 0.001$, $n = 82$; Fig. 4). The seasonal changes in the ratios between PC, PN and PP at Stns 3–5 are shown in Fig. 5. Taking into consideration effects of photosynthetic growth of phytoplankton on the ratios between PC, PN and PP, we divided the water column into the euphotic and aphotic zones ($\leq 250\ \text{m}$). There were no noticeable differences in the ratios between seasons, stations, nor euphotic–aphotic zones. The ratios between PC : PN, PC : PP and PN : PP of each fraction fitted well on the Redfield ratio, although there was a tendency that the PC : PP and PN : PP ratios in the picoplankton fraction were lower than in other fractions (Fig. 6). One-way ANOVA revealed that there were significant differences both in the PC : PP ($F_{2,47} = 3.645$, $P = 0.034$) and PN : PP ($F_{2,42} = 4.847$, $P = 0.013$) ratios between the pico- and microplankton fractions ($P < 0.05$ by Student–Newman–Keuls' tests).

DISCUSSION

We measured concentrations of, and ratios between, PC, PN and PP as a tool for nutritional diagnosis of phytoplankton. However, particulate matter is mainly composed of ciliates, nanoflagellates, bacteria and detritus, as well as phytoplankton. In the microplankton fraction ($20\text{--}200\ \mu\text{m}$), the ciliate biomass was greater than the algal

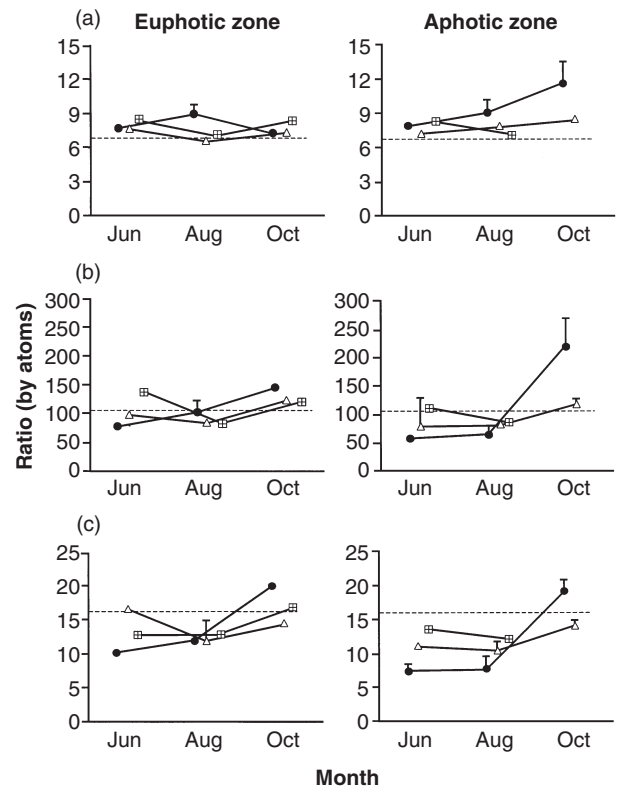
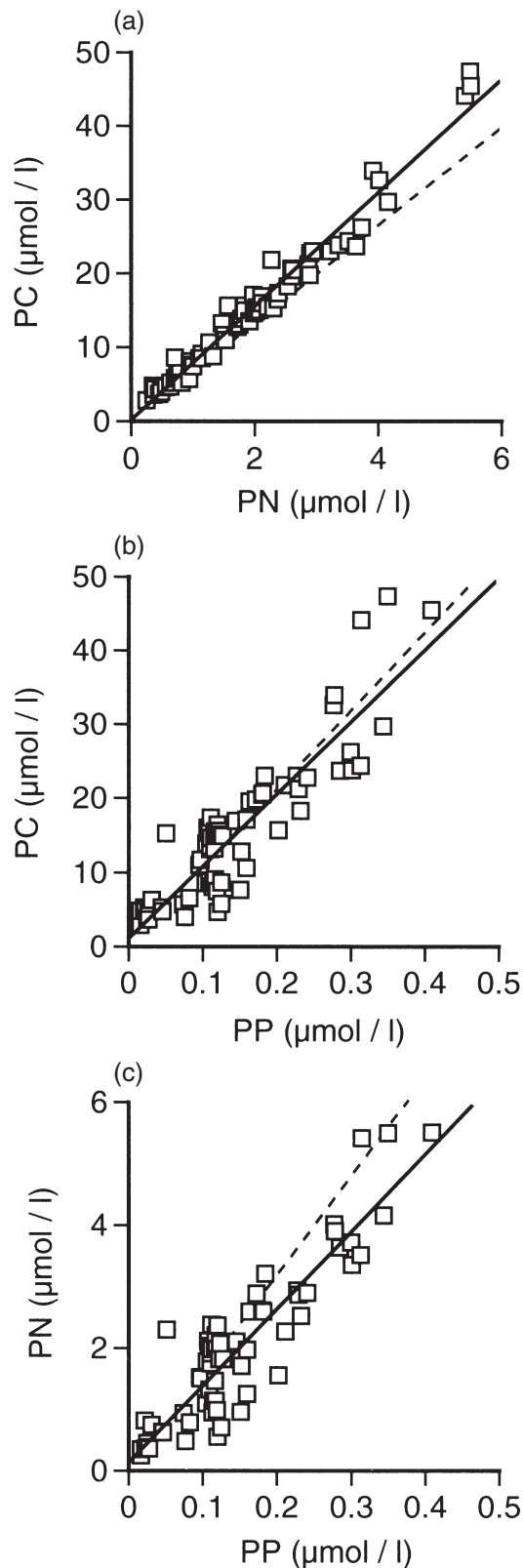
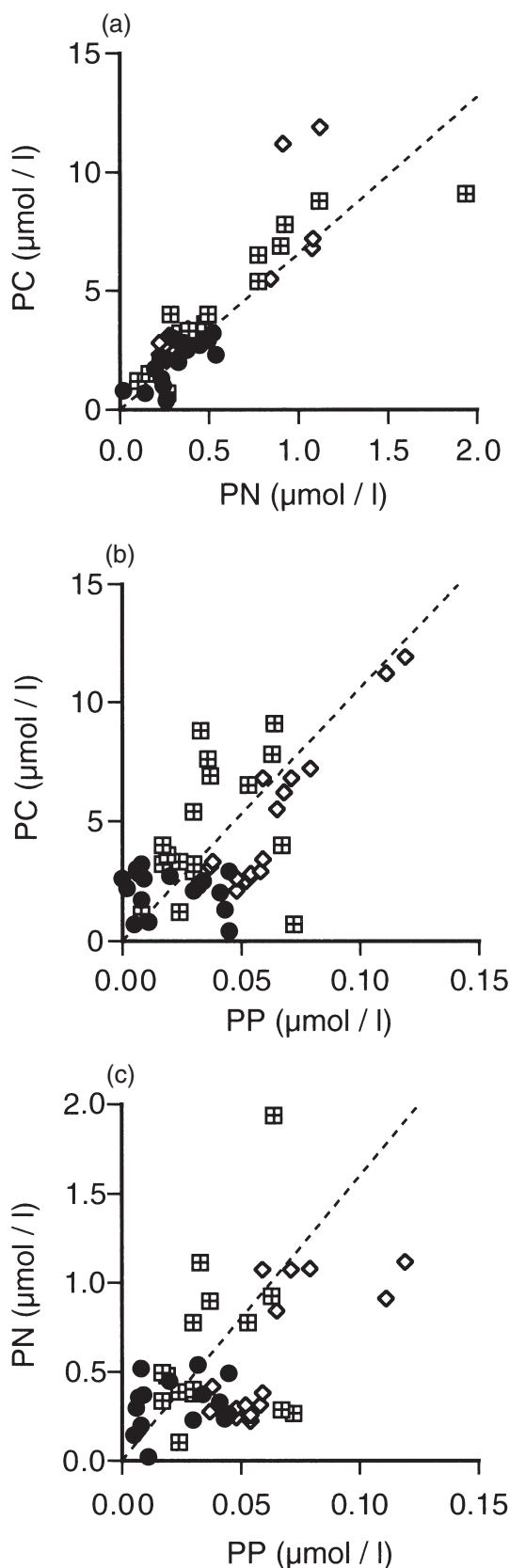


Fig. 5. Seasonal changes in PC : PN, PC : PP and PN : PP ratios (mean \pm SE) in each water column (euphotic or aphotic zone) at station (Stn) 3 (●), Stn 4 (△) and Stn 5 (□). The Redfield ratio is indicated by broken lines. PC, particulate carbon; PN, particulate nitrogen; PP, particulate phosphorus.

biomass; in the nanoplankton fraction (2–20 μm), the algal biomass exceeded the nanoflagellates; in the picoplankton fraction (<2 μm), the bacterial biomass took a similar level to the algal one (T. Sekino, pers. comm., 1999). Because more than 80% of the ciliates were mixotrophs (L. A. Obolkin, unpubl. data, 1999), we viewed the ciliates as autotrophic algae here. Although we do not have direct evidence, considerable amounts of bacteria did not seem to be collected on the filters (Whatman GF/F). For these reasons, it was con-

Fig. 4. PC : PN, PC : PP and PN : PP ratios of phytoplankton <200 μm . Plotted data were gathered together from all seasons, stations and depths. Solid lines were fitted by a simple linear regression. Broken lines represent the Redfield ratio. PC, particulate carbon; PN, particulate nitrogen; PP, particulate phosphorus.



sidered that the particulate matter of each fraction well reflected the algal biomass.

There was a difference in PC, PN and PP concentrations between Stns 3–5, but little difference between Stns 1–3 (Fig. 2). This implies that the Selenga River had a gradual effect from its mouth (Stn 5) towards the off-shore, but the effect almost disappeared in the deep area (Stns 1–3). In another ancient lake, Lake Biwa, central Japan, the concentrations of PC, PN and PP during the most productive periods in its mesotrophic north basin are $50 \mu\text{mol C l}^{-1}$, $7.1 \mu\text{mol N l}^{-1}$ and $0.2 \mu\text{mol P l}^{-1}$, respectively (Tezuka 1985). The maximum concentrations of PC ($48 \mu\text{mol C l}^{-1}$) and PN ($5.5 \mu\text{mol N l}^{-1}$) at Stn 5 in Lake Baikal were lower, whereas that of PP ($0.4 \mu\text{mol P l}^{-1}$) was higher than those in the north basin of Lake Biwa. However, these concentrations at Stn 5 were lower than the average, except for PP ($PC \sim 70 \mu\text{mol l}^{-1}$, $PN \sim 9.6 \mu\text{mol l}^{-1}$, $PP \sim 0.4 \mu\text{mol l}^{-1}$) in the eutrophic south basin of Lake Biwa (Nakanishi *et al.* 1990). At Stn 3 during the thermal stratification period (August and October), the PC and PN concentrations were lower than those in the north basin of Lake Biwa, whereas the PP concentrations were similar to those in the north basin of Lake Biwa. These data suggest that the concentrations of particulate matter in the south basin of Lake Baikal displayed oligotrophic to mesotrophic levels depending on the area.

In spite of wide variation in the PC, PN and PP concentrations, these ratios all showed relatively constant relationships, independent of season, station, and depth (Figs 4,5). This suggests that the ratios between PC, PN and PP of phytoplankton in Lake Baikal are temporally and spatially stable. The average PC:PN:PP ratio (by atoms) in Lake Baikal was 102:13:1. This ratio is close to the representative ratio in the oceans (Redfield ratio, 106:16:1). Certainly, the ratio in oceanic waters varies somewhat. Ranges of 75:1–150:1

Fig. 6. PC:PN, PC:PP and PN:PP ratios of each fraction (\diamond , picoplankton; \boxplus , nanoplankton; \bullet , microplankton) at station 3 (including all seasons and depths). Broken lines represent the Redfield ratio. PC, particulate carbon; PN, particulate nitrogen; PP, particulate phosphorus.

for the PC : PP ratio and 10 : 1–20 : 1 for the PN : PP ratio are still consistent with the concept of uniform chemical composition (Goldman *et al.* 1979). The ratio in Lake Baikal fits within the ranges. On the other hand, ratios in some ancient lakes are different from the Redfield ratio; PC : PN : PP = 150 : 18 : 1 in Lake Victoria and 243 : 19 : 1 in Lake Malawi (Guildford & Hecky 2000); and 217 : 30 : 1 in the north basin of Lake Biwa (Tezuka 1985). The lower ratio of PC : PN : PP in Lake Baikal than the three lakes mentioned above is attributed to the high concentration of PP compared with PC and PN. Good accordance with the Redfield ratio in Lake Baikal conforms to the report by Hecky *et al.* (1993) that N and P deficiency is less likely in arctic and subarctic lakes than in temperate and tropical lakes. They also reported that N and P deficiency is more likely to occur in smaller lakes. Dominance of small-sized phytoplankton (<20 µm) again suggests that Lake Baikal is an oligotrophic lake on the basis of a theoretical prediction that smaller, more vulnerable algae to herbivores are likely to dominate in systems with low degrees of enrichment (e.g. Phillips 1974; Vance 1978; Leibold 1989, 1996).

In conclusion, Lake Baikal is relatively poor in nutrient concentrations, so called an oligotrophic lake, but the nutrients are stably balanced from a viewpoint of the ratios of chemical composition in phytoplankton. The characteristic of the ratios between PC, PN and PP in Lake Baikal displays that of oceans rather than lakes. Such a nearly ideal ratio between PC, PN and PP in phytoplankton may play an important role in matter cycling through food webs.

ACKNOWLEDGEMENTS

This paper is dedicated to Professor M. Higashi who passed away in March 2000. The authors are grateful to M. A. Grachev, O. A. Timoshkin, I. V. Khanaev, N. A. Bondarenko, L. A. Obolkina, I. Shimizu, T. Koitabashi, T. Minamoto, F. Nagao, E. Wada and T. Kawai for their support. Chemical analyses were assisted by K. Yoshiyama and Y. Nishimura. This work was supported by a Grant-in-Aid for Scientific Research from the Japan Ministry of Education, Science, Sports, Culture and Technology (09NP1501). M. Genkai-

Kato is a research fellow of the Japan Society for the Promotion of Science.

REFERENCES

- AIZAKI M. & OTSUKI A. (1987) Characteristics of variations of C : N : P : Chl ratios of seston in eutrophic shallow Lake Kasumigaura. *Japanese Journal of Limnology* 48: S99–S106.
- BONDARENKO N. A., GUSELNIKOVA N. E., LOGACHEVA N. F. & POMAZKINA G. V. (1996) Spatial distribution of phytoplankton in Lake Baikal, Spring 1991. *Freshwater Biology* 35: 517–523.
- GOLDMAN C. R., ELSEY J. J., RICHARDS R. C., REUTER J. E., PRISCU J. C. & LEVIN A. L. (1996) Thermal stratification, nutrient dynamics, and phytoplankton productivity during the onset of spring phytoplankton growth in Lake Baikal, Russia. *Hydrobiologia* 331: 9–24.
- GOLDMAN J. C., MCCARTHY J. J. & PEAVER D. G. (1979) Growth rate influence on the chemical composition of phytoplankton in oceanic waters. *Nature* 279: 210–215.
- GUILD FORD S. J. & HECKY R. E. (2000) Total nitrogen, total phosphorus, and nutrient limitation in lakes and oceans: Is there a common relationship? *Limnology and Oceanography* 45: 1213–1223.
- HEALEY F. P. & HENDZEL L. L. (1980) Physiological indicators of nutrient deficiency in lake phytoplankton. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 442–453.
- HECKY R. E., CAMPBELL P. & HENDZEL L. L. (1993) The stoichiometry of carbon, nitrogen, and phosphorus in particulate matter of lakes and oceans. *Limnology and Oceanography* 38: 709–724.
- KOZHOV M. (1963) *Lake Baikal and its Life*. Dr W. Junk Publishers, The Hague.
- KOZHOVA O. M. (1987) Phytoplankton of Lake Baikal: structural and functional characteristics. *Archiv für Hydrobiologie. Beihefte, Ergebnisse der Limnologie* 25: 19–37.
- LEIBOLD M. A. (1989) Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist* 134: 922–949.
- LEIBOLD M. A. (1996) A graphical model of key-stone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* 147: 784–812.

- MENZEL D. W. & CORWIN N. (1965) The determination of total phosphorus in seawater based on the liberation of organically bound fraction by persulfate oxidation. *Limnology and Oceanography* 10: 280–283.
- NAGATA T., TAKAI K., KAWANOBE K. *et al.* (1994) Autotrophic picoplankton in southern Lake Baikal: abundance, growth and grazing mortality during summer. *Journal of Plankton Research* 16: 945–959.
- NAKANISHI M., MITAMURA O. & MATSUBARA T. (1990) Sestonic C:N:P ratios in the southern basin of Lake Biwa with special attention to nutritional state of phytoplankton. *Japanese Journal of Limnology* 51: 185–189.
- PHILLIPS O. M. (1974) The equilibrium and stability of simple marine systems. II. Herbivores. *Archiv für Hydrobiologie* 73: 310–333.
- REDFIELD A. C. (1958) The biological control of chemical factors in the environment. *American Scientist* 46: 205–221.
- SHOSTAKOVICH V. B. (1924) Water transparency of Lake Baikal. *Notes of Russian Hydrological Institute, Leningrad* 11: 85–87 (in Russian).
- TEZUKA Y. (1985) C:N:P ratios of seston in Lake Biwa as indicators of nutrient deficiency in phytoplankton and decomposition process of hypolimnetic particulate matter. *Japanese Journal of Limnology* 46: 239–246.
- TIMOSHKIN O. A. (1997) Biodiversity of Baikal fauna: state-of-the-art (Preliminary analysis). In: *New Scope on the Boreal Ecosystems in East Siberia* (eds E. Wada, O. A. Timoshkin, N. Fujita & K. Tanida), pp. 35–76. Russian Academy of Sciences, Siberian Branch, Novosibirsk.
- VANCE R. R. (1978) Predation and resource partitioning in one predator–two prey model communities. *American Naturalist* 112: 797–813.