

RESEARCH PAPER

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Role of phytoplankton size distribution in lake ecosystems revealed by a comparison of whole plankton community structure between Lake Baikal and Lake Biwa

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Abstract The influence of the size distribution of phytoplankton on changes in the planktonic food web structures with eutrophication was examined using natural planktonic communities in two world-famous lakes: Lake Baikal and Lake Biwa. The size distribution of phytoplankton and the ratio of heterotrophic to autotrophic biomass (H/A ratio), indicating the balance between primary production and its consumption, were investigated in the lakes of different trophic status. The results revealed that microphytoplankton ($>20\mu\text{m}$) in mesotrophic Lake Biwa, and picophytoplankton ($<2\mu\text{m}$) or nanophytoplankton ($2\text{--}20\mu\text{m}$) in oligotrophic Lake Baikal, comprised the highest proportion of the total phytoplankton biomass. The H/A ratio was lower in Lake Biwa (<1) than in Lake Baikal (>1). The low H/A ratio in Lake Biwa appeared to be the consequence of the lack of consumption of the more abundant microphytoplankton, which were inferior competitors in nutrient uptake under oligotrophic conditions but less vulnerable to grazing. As a result, unconsumed microphytoplankton

accumulated in the water column, decreasing the H/A ratio in Lake Biwa. Our results showed that food web structure and energy flow in planktonic communities were greatly influenced by the size distribution of phytoplankton, in conjunction with bottom-up (nutrient uptake) and top-down (grazing) effects at the trophic level of primary producers.

Key words Eutrophication · H/A ratio · Food webs · Phytoplankton size distribution · Size-selective grazing

Introduction

It is well known that nutritional status of a lake affects energy flow in planktonic food webs. The ratio of primary production to total biomass, reflecting energy turnover, is lower in more eutrophic conditions (Lampert and Sommer 1997). The ratio of total heterotrophic to autotrophic biomass (H/A ratio), indicating the balance between primary production and its consumption, declined with eutrophication (Del Giorgio and Gasol 1995). These changes in food web structure with eutrophication are caused mainly by changes in autotrophic biomass (Del Giorgio and Gasol 1995). The changes in phytoplankton biomass have been studied in relationship to eutrophication. Although these studies have revealed that the biomass is controlled by balance between top-down and bottom-up effects (Burkpile and Hay 2006), most of the studies have not sufficiently considered the mechanism that autotrophic biomass increases more intensively with eutrophication than heterotrophic biomass.

The size distribution of phytoplankton apparently is related to nutritional status (bottom-up effect) and size-selective grazing by zooplankton (top-down effect). Uptake rate of nutrients by phytoplankton through the cell surface depends on cell size, as the surface area to volume (S/V) ratio decreases with increasing cell size (Friebele et al.

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1978). Therefore, nutrient uptake efficiency and growth rate are lower in larger-sized phytoplankton (Smith and Kalff 1983), and larger phytoplankton cannot reach high abundance under low-nutrient concentrations (bottom-up effect; Nakanishi et al. 1999). Size ranges of phytoplankton available for zooplankton are restricted according to grazing mechanisms and are $<50\ \mu\text{m}$ for large cladocerans and copepods and $<20\ \mu\text{m}$ for small cladocerans and rotifers (Lampert and Sommer 1997). Therefore, larger phytoplankton have an advantage to tolerance for grazing pressure (top-down effect).

These top-down and bottom-up effects through size distribution of phytoplankton have the potential to change phytoplankton biomass and to affect the plankton community structure through energy flow of lacustrine food webs in relationship to differences in nutritional status of the lake. Although there are a number of previous studies on size distribution of phytoplankton in relationship to species composition and zooplankton (e.g., Havens 1998), little is known about the influence of difference in size distribution of phytoplankton on the whole food web structure. In this article, the size distribution of phytoplankton and the balance between primary producers and their consumers were investigated in two lakes: oligotrophic Lake Baikal and mesotrophic Lake Biwa. The effect of size distribution of phytoplankton on the structure of whole planktonic food webs was studied in light of nutritional status by comparison between these world-famous lakes.

Methods

Lake Baikal, an oligotrophic lake, with a surface area of $31\,500\ \text{km}^2$ and maximum depth of $1\,741\ \text{m}$, is located at $53^\circ\ \text{N}$ and $106^\circ\ \text{E}$ (ILEC 1995). Sampling was conducted at stations located in the south basin when the lake was covered with ice (Stn. 6 in March 1999 and Stn. 7 in March 2000) and on the Krasny Yar–Kharauz transect located at the boundary between the south and middle basins in other months (Stn. 3) (Fig. 1). These stations were chosen because of our prior accumulation of biological data on the planktonic communities (Genkai-Kato et al. 2002, 2003; Yoshida et al. 2003). Lake Biwa, a mesotrophic lake, with a surface area of $672\ \text{km}^2$ and maximum depth of $104\ \text{m}$, is located at $35^\circ\ \text{N}$ and $136^\circ\ \text{E}$ (ILEC 1995). Sampling in Lake Biwa was conducted at our fixed station (Stn. P) (Nakanishi et al. 1999) in the north basin (Fig. 1).

Sampling was carried out in Lake Baikal in March, June, August, and October 1999, and in March, August, and October 2000; and in Lake Biwa, one to five times a month in June, August, and October 1997 and in March 1998. In both lakes, water temperature and transparency were measured with a CTD profiler (SBE-25; Seabird Electric, Bellevue, WA, USA) and a Secchi disk, respectively. Water samples were collected from depths of 0, 5, 10, 25, 50, 100, and 250 m with a 10-l Niskin water sampler in Lake Baikal, and from depths of 0, 2.5, 5, 10, 20, 30, and 45 m with a modified 10-l Van Dorn water sampler in Lake Biwa.

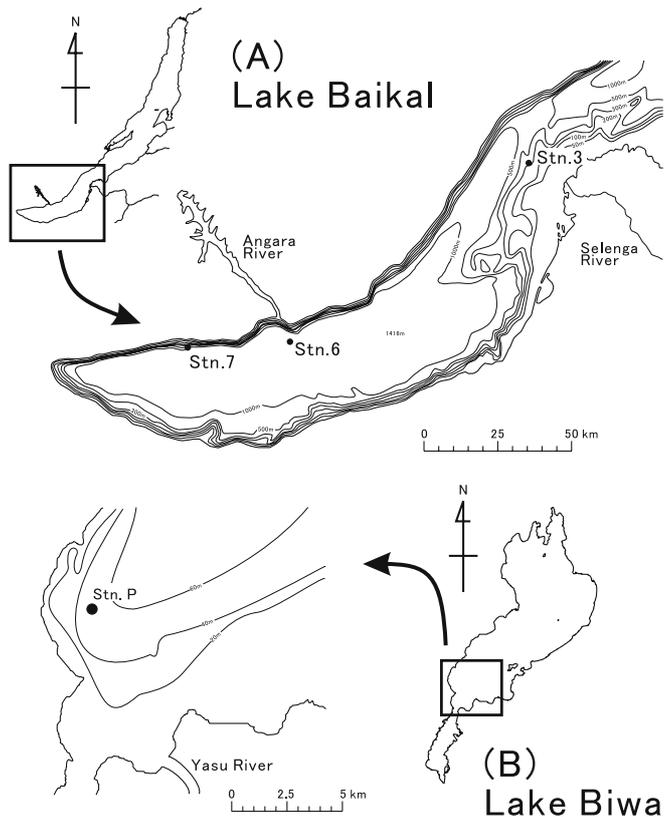


Fig. 1. Sampling stations in Lake Baikal (A) and Lake Biwa (B). Sampling in Lake Baikal was conducted at Station (Stn.) 6 or 7 in March during ice cover and at Stn. 3 in the other months

Using water from each depth, we measured the concentrations of nitrate and soluble reactive phosphorus (SRP) and estimated the biomass of bacteria, flagellates, ciliates, picophytoplankton ($<2\ \mu\text{m}$), nanophytoplankton ($2\text{--}20\ \mu\text{m}$), and microphytoplankton ($>20\ \mu\text{m}$). Samples to estimate biomass of crustaceans and rotifers were collected from the sampled water as already mentioned in Lake Biwa, whereas samples were collected with a Juday plankton net with $100\text{-}\mu\text{m}$ mesh from layers 0–10, 10–25, 25–50, and 50–250 m deep in Lake Baikal.

Water collected for measurement of nitrate and SRP concentrations was filtered through Whatman GF/F filters pretreated with hydrochloric acid, and samples were stored at $-20^\circ\ \text{C}$ until measurement. SRP concentrations of both lakes were determined according to Murphy and Riley (1962). Nitrate concentrations in Lake Baikal and Lake Biwa were determined according to the phenoldisulfonic acid method (Taras 1950) and the hydrazine reduction method (Saijo and Mitamura 1995), respectively.

Bacteria, heterotrophic nanoflagellates (HNF), and picophytoplankton were fixed with glutaraldehyde (2% final concentration). Nano- and microphytoplankton were fixed with Lugol's solution. Rotifers and crustaceans were fixed with sugar-formalin (5% final concentration) (Haney and Hall 1973). Ciliates were fixed with Lugol's solution in Lake Baikal, and with formalin (5% final concentration) in Lake Biwa. Bacteria and HNF were stained with acridine orange

Table 1. Conversion factors to carbon content

Category	Conversion	Reference
Picophytoplankton	0.106 pg C/ μm^3	Nagata (1986)
For Lake Biwa	0.065 pg C/cell ^a	Nagata (1988)
For Lake Baikal	0.045 pg C/cell ^a	Nagata et al. (1994)
Nano- and microphytoplankton		Strathmann (1967)
Diatoms	$C = \exp(-0.422 + 0.758 \times \ln(V))$	
Others	$C = \exp(-0.46 + 0.866 \times \ln(V))$	
Crustaceans	$C = 0.45 \times \text{DW}^c$	Urabe (1988)
Rotifers	$C = 0.5 \times \text{DW}^c$	Latja and Salonen (1978)
Ciliates		Putt and Stoecker (1989)
For Lake Biwa (formalin)	0.14 pg C/ μm^3	
For Lake Baikal (Lugol's)	0.19 pg C/ μm^3	
Flagellates	0.071 pg C/ μm^3	Fenchel and Finlay (1983)
For Lake Biwa	2.1 pg C/cell ^a	Nagata (1988)
For Lake Baikal	5.0 pg C/cell ^a	Mean volume, 70.3 μm^3 ^b
Bacteria	0.106 pg C/ μm^3	Nagata (1986)

C, carbon content (pg); DW, dry weight (pg); V, volume (μm^3)

^aConversion factors based on cell number calculated from mean cell volume were used for estimating carbon content of picophytoplankton and flagellates

^bMean cell volume at Stn. 3 of Lake Baikal in October 1999 (data not shown)

^cDry weight of crustaceans and rotifers was estimated according to McCauley (1984)

and fluorescein isothiocyanate (FITC), and counted using an epifluorescence microscope with a standard B-excitation system. Picophytoplankton without staining were counted using an epifluorescence microscope with a standard B-excitation system. Nano- and microphytoplankton, ciliates, rotifers, and crustaceans were concentrated, counted, and measured for volume estimation under a microscope. Distinction between nano- (2–20 μm) and microphytoplankton (>20 μm) was based on the observed standard size of each species.

In the present study, the plankton food web structure in relationship to energy flow was characterized by the ratio of total heterotrophic to autotrophic biomass (H/A ratio). Biomass was expressed in terms of carbon content as estimated by conversion factors (Table 1). The H/A ratio was calculated on the assumption that autotrophs consist of pico-, nano- and microphytoplankton, and heterotrophs consist of the other organisms (crustaceans, rotifers, ciliates, HNF, and bacteria). In the present study, we focused on the plankton community in the epilimnion. In Lake Biwa, biomass data points for June, August, and October 1997 were averages of several observations (4–5 times) in each month.

Results

Lake Baikal, a dimictic lake, was thermally stratified in March, August, and October 1999, and turnover occurred in June 1999 (Fig. 2), with the thermocline forming around 50 m during the stratification in summer and winter. Secchi depth was 16 m in June 1999 and around 10 m in the other months. Seasonal variations of water temperature and Secchi depth in 2000 (data not shown) were similar to the trend observed in 1999. Lake Biwa, a monomictic lake, was thermally stratified in June, August, and October 1997, and turnover occurred in March 1998 (Fig. 2). The thermocline was around 15 m in June and August and 20 m in October 1997. Secchi depth was 8 m in October 1997 and around 5 m in the other months. Based on the depth of thermocline obtained in both lakes, we here regarded the layers above

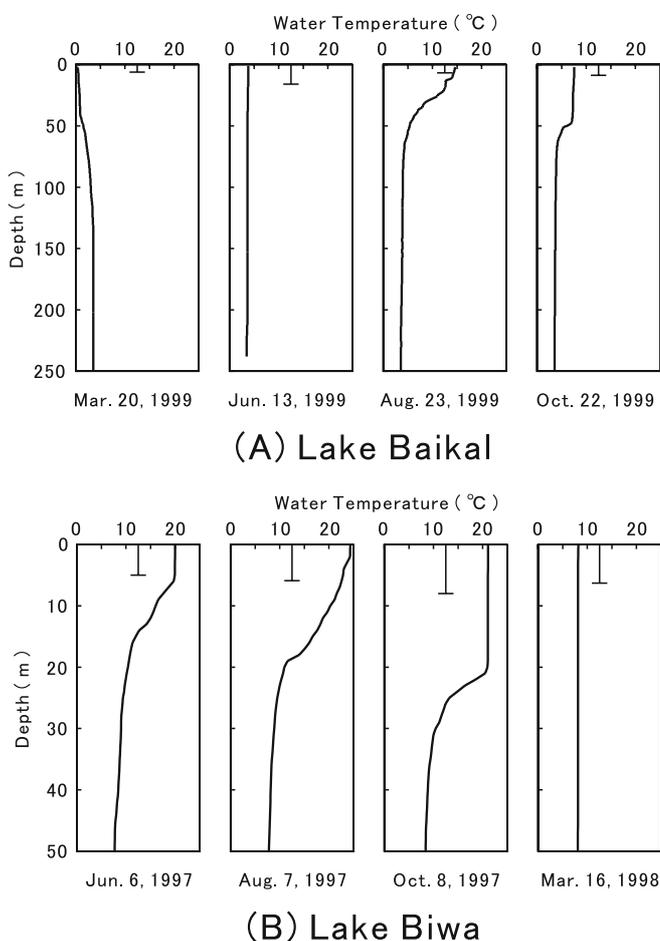


Fig. 2. Seasonal changes in vertical profiles of water temperature with Secchi depth (*bars*) from March 1999 to October 1999 in Lake Baikal (A) and June 1997 to March 1998 in Lake Biwa (B)

50 m and 15 m deep as the epilimnion in Lake Baikal and Lake Biwa, respectively. In the following analyses, data were averaged over the epilimnion.

Nitrate concentrations were higher in Lake Biwa than in Lake Baikal, with the maximum and minimum nitrate concentrations occurring in March and in August, respectively,

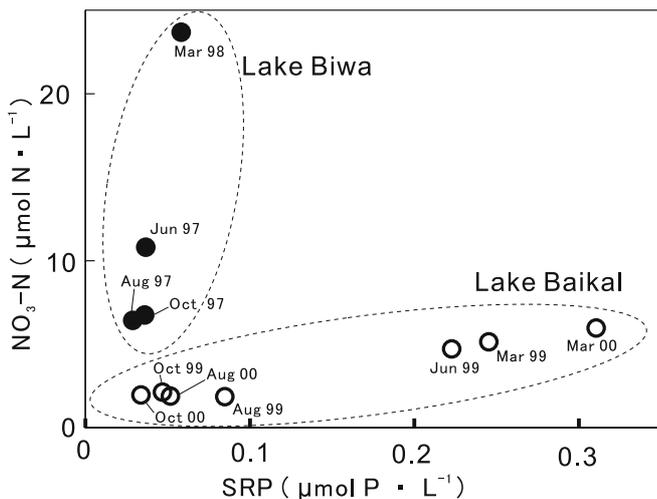


Fig. 3. Nitrate ($\text{NO}_3\text{-N}$) and soluble reactive phosphorus (SRP) concentrations from March 1999 through October 2000 in Lake Baikal (open circles) and from June 1997 through March 1998 in Lake Biwa (solid circles). Data were averaged over the epilimnion

in both lakes (Fig. 3). In contrast, SRP concentrations were lower in Lake Biwa than in Lake Baikal, with the maximum and minimum concentrations occurring in March and in October, respectively, in Lake Baikal and no obvious seasonal variation in Lake Biwa (Fig. 3). The ratio of nitrate to SRP was higher in Lake Biwa (406–187) than in Lake Baikal (19.2–58.4).

Total autotrophic biomass (pico-, nano- and microphytoplankton) was higher in Lake Biwa (ranging from $40.4 \mu\text{g C l}^{-1}$ in March 1998 to $316.0 \mu\text{g C l}^{-1}$ in June 1997) than in Lake Baikal (ranging from $3.2 \mu\text{g C l}^{-1}$ in March 1999 to $19.2 \mu\text{g C l}^{-1}$ in August 1999) (Fig. 4). The percentage of microphytoplankton biomass comprising the total autotrophic biomass was higher than 34.3% and often exceeded 50% in Lake Biwa, whereas the percentage was lower than 18.2% throughout the observation period in Lake Baikal, with the exception of 51.8% observed in March 2000. Dominant species of microphytoplankton were *Uroglena americana* (June 1997), *Staurastrum dorsidentiferum* (August and October 1997), and *Aulacoseira solida* (March 1998) in Lake Biwa and *Synedra acus* (March 1999), *Aulacoseira baicalensis* (June 1999 and March 2000), *Dynobryon* spp. (August 1999 and October 2000), *Cymbella ventricosa* (October 1999), and *Anabaena* spp. (August 2000) in Lake Baikal. Total heterotrophic biomass including crustaceans, rotifers, ciliates, heterotrophic nanoflagellates (HNF), and bacteria, was also higher in Lake Biwa (ranging from $58.9 \mu\text{g C l}^{-1}$ in March 1998 to $126.6 \mu\text{g C l}^{-1}$ in June 1997) than in Lake Baikal (ranging from $10.5 \mu\text{g C l}^{-1}$ in March 2000 to $71.9 \mu\text{g C l}^{-1}$ in October 2000). The differences in the total heterotrophic biomass between the lakes were relatively smaller than that observed for total autotrophic biomass.

The H/A ratio was lower in Lake Biwa than in Lake Baikal (Fig. 4). In Lake Biwa, the H/A ratio was lower than 1 (i.e., autotroph biomass exceeded heterotroph biomass), with the exception of 1.46 observed in March 1998, and ranged from 0.31 in October 1997 to 0.66 in June 1997 (Fig.

4B). On the other hand, the H/A ratio was higher than 1 in Lake Baikal (i.e., autotroph biomass was less than heterotroph biomass), and ranged from 1.77 in March 2000 to 9.77 in March 2000 (Fig. 4A).

Discussion

Transparency, as Secchi depth, was higher in Lake Baikal than in Lake Biwa (see Fig. 2). Nitrate and SRP concentrations imply that Lake Biwa was phosphorus limited whereas Lake Baikal was nitrogen limited (see Fig. 3). This view of nutrient deficiency is consistent with the nutritional status of phytoplankton that in Lake Baikal the concentrations of particulate carbon and nitrogen bound in algal cells were lower than, whereas the concentration of particulate phosphorus was similar to, those in Lake Biwa (Genkai-Kato et al. 2002). Despite the slightly higher availability of SRP in Lake Baikal, data on transparency and phytoplankton biomass, as well as concentrations of particulate matter (Genkai-Kato et al. 2002), indicate that Lake Baikal is more oligotrophic than Lake Biwa.

The present study showed that the H/A ratio was lower in Lake Biwa (0.32–1.46) than in Lake Baikal (1.77–9.77) (see Fig. 4). This result conformed to the pattern shown by Del Giorgio and Gasol (1995) in which the ratio in lakes worldwide ranged from 0.5 to 6 and declined with eutrophication. Straile (1998) proposed that a high H/A ratio has been often observed as a result of large zooplankton biomass in the pelagic area of a large, deep lake. Interestingly the total heterotrophic biomass including zooplankton was similar between Lakes Baikal and Biwa (Fig. 4). Thus the difference in H/A ratio between the lakes should be attributable mostly to the phytoplankton communities.

The autotrophic biomass was dominated by pico- and nanophytoplankton in Lake Baikal, whereas it was dominated by microphytoplankton in Lake Biwa (Fig. 4). Pico- and nanophytoplankton generally have high growth rates as a result of their high S/V ratios, but they are vulnerable to grazing. In contrast, growth of microphytoplankton is slower, but they are often categorized as an inedible group for most herbivorous zooplankton (Urabe et al. 1996). Thus, microphytoplankton remained unconsumed in the epilimnion (Kagami et al. 2002), resulting in a lower H/A ratio in Lake Biwa. Our results indicate that the increase of autotrophic biomass with eutrophication resulted from changes in the size distribution of phytoplankton.

Yoshida et al. (2003) reported that primary production (PP) and particulate organic carbon content (POC) in the euphotic zone of Lake Baikal were $5.5\text{--}24 \mu\text{g C l}^{-1} \text{ day}^{-1}$ and $220\text{--}720 \mu\text{g C l}^{-1}$, respectively, during the same research period of the present study. The ratios of primary production to total organic biomass (P/B ratio), reflecting energy turnover rate, calculated from these values were 0.009–0.066, which were very low compared to those in Lake Biwa (0.86–1.52) (Nakanishi et al. 1992). POC containing a considerable amount of abiotic carbon might cause such low P/B ratios in Lake Baikal. However, the P/B ratios recalculated

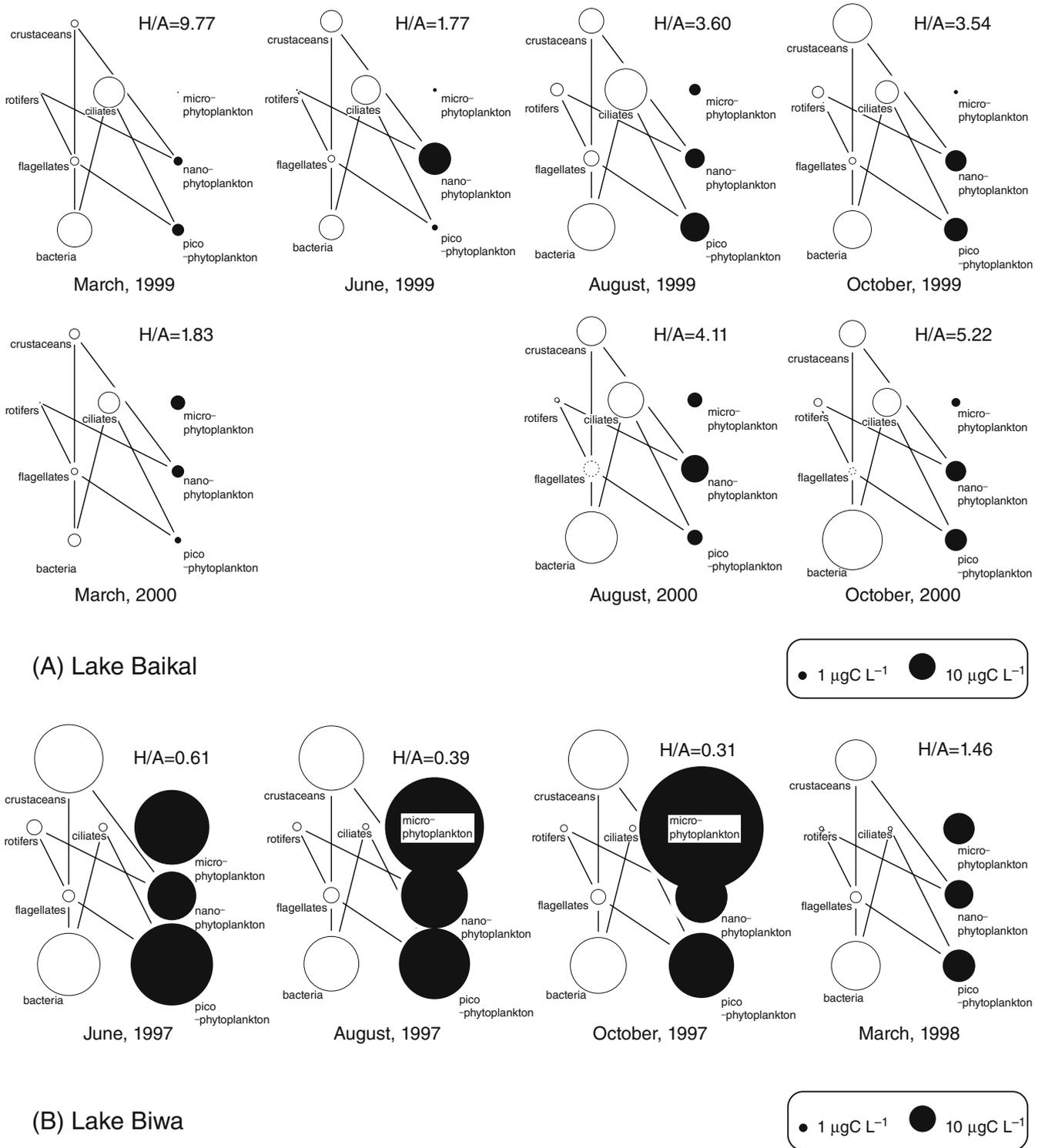


Fig. 4. Seasonal changes in biomass broken down by taxon in Lake Baikal (A) and in Lake Biwa (B). Areas of the circles indicate biomass expressed as carbon mass. Autotrophic (open circles) and heterotrophic (closed circles) biomass were used to calculate the heterotrophic to autotrophic biomass (H/A) ratios shown in the figure. Lines between

the circles show typical feeding relationships in the food web (Lampert and Sommer 1997). As biomass of flagellates in August and October 2000 are missing values, the H/A ratios in August and October 2000 were calculated using biomass of flagellates in August and October 1999, respectively

lated using only biotic carbon based on the biomass measured in the present study (0.100–0.381) were also lower than those in Lake Biwa. This difference in the ratios between the lakes implies that the turnover rate was higher in Lake Biwa than in Lake Baikal. Nevertheless, the description by P/B ratios is based on the assumption that all the primary production is available to the food web, and, therefore, turnover rate under this assumption in Lake Biwa should be overestimated because the percentage of inedible phytoplankton biomass (i.e., microphytoplankton) comprising the total autotrophic biomass often exceeded 50% in the lake. This result implies that P/B ratios do not always adequately characterize food web structure, in terms of energy flow, when inedible size-fractions of phytoplankton are abundant.

The present study showed that the H/A ratio was lower in more eutrophic lake as a consequence of an algal community change biased toward large-sized, inedible phytoplankton. Changes in the quality of the autotrophic community may influence the plankton community structure in multiple ways. Alteration of phytoplankton communities along a gradient of eutrophication has the potential to affect population dynamics of zooplankton (Semenchenko and Gorelysheva 1996), implying that the food web structure is dependent on algal communities. Moreover, food web dynamics are suggested to be stabilized under the existence of less edible phytoplankton (Kretzschmar et al. 1993; Genkai-Kato and Yamamura 1999). By comparing Lake Baikal and Lake Biwa, the present study clearly showed considerable influences of the quality of phytoplankton communities (i.e., size distribution) on lake ecosystems, through interactions between bottom-up and top-down effects on phytoplankton.

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