What Caused the Summer Replacement of Dominant Planktonic Algae in Lake Barato?

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Abstract

Dense water blooms of blue-green algae (*Microcystis aeruginosa* and *Aphanizomenon flos-aquae*) had been observed in hypertrophic Lake Barato in the 1980s, but have not reappeared since 1990. Instead of these water blooms, diatoms (*Melosira* spp. and *Cyclotella* spp.) have dominated in summer. Orthophosphate ($\text{PO}_4\text{-P}$) had been detected throughout the year, but since 1990 has apparently become depleted during May and June. In 1991, $\text{PO}_4\text{-P}$ concentrations increased in August and/or September, as did the biomass of blue-green algae (*Anabaena spiroides* or *Phormidium* spp.). These observations suggested that diatoms adapted to higher phosphorus limitation under conditions of low water temperature and high silicate concentration. Diatoms thus continued their dominance over blue-green algae because the latter could not grow in early summer due to a lack of $\text{PO}_4\text{-P}$, most of which was taken up by the diatoms.

Key words : Blue-green algae, diatoms, dominant species, water bloom

1. Introduction

Mesocosm and *in vitro* experiments have shown that water temperature, irradiance, bicarbonate concentration, nutrient concentrations and their ratios affect the replacement of dominant planktonic algae. However, the influence of physico-chemical factors on algal replacement have seldom been reported in a natural lake. TAKAMURA *et al.* (1992) suggested that an increase in the TN : TP ratio of lake water affected algal succession (from *Microcystis aeruginosa* to *Planktothrix agardhii*).

Lake Barato is located near the western coast of central Hokkaido, Japan. It is crescent-shaped with a maximum depth of 13 m and a surface area of 4.37 km². This lake is hypertrophic due to the inflow of urban sewage from Sapporo City. A dense water bloom of blue-green algae was observed every summer during the 1980s (HINO and TADA, 1985; HINO, 1991). However, the dominant planktonic algae changed from blue-green algae to diatoms in 1990, and water blooms of *Microcystis*

aeruginosa and/or *Aphanizomenon flos-aquae* have not been observed since then.

The recent change from blue-green algae to diatoms is an interesting phenomenon from both a biological and ecological viewpoint. The aim of this study is to examine whether or not changes in nutrient conditions and water temperature have caused this shift.

2. Materials and methods

The study was carried out at two sampling sites in L. Barato (Fig. 1), whose numbering follows that given in a previous paper (HINO and AOI, 1983). Sta. 1 is not affected directly by the inflow of urban wastewater, but Sta. 3 is affected by that as well as by a temporary invasion of seawater. Other limnological characteristics of this lake have been described in previous papers (HINO and TADA, 1985; HINO, 1988a, b; 1991; 1992).

Water samples were collected from the surface layer (0–2 m) with an acrylic core tube water sampler (diameter 4.4 cm, length 2 m) once a month from April 1988 to December 1992

Fig. 1. Map of Lake Barato and the sampling stations.

(●), Sta. 1; (■), Sta. 3.

except in January and March. Water samples were filtered through Whatman GF/F filters to separate filtrates from residues on the filters.

Water temperature was measured with a thermistor thermometer attached to a YSI dissolved oxygen meter (model 58). Orthophosphate ($\text{PO}_4\text{-P}$) was measured by the method of MURPHY and RILEY (1962). Measurements of soluble total phosphorus (STP) and total phosphorus (TP) were conducted by the same method as orthophosphate after hydrolysis by the method of MENZEL and CORWIN (1965). Ammonium nitrogen was measured by the indophenol method (JAPAN METEOROLOGICAL AGENCY, 1970), and nitrate plus nitrite nitrogen by the copper-cadmium reduction method of WOOD *et al.* (1967). Total inorganic nitrogen (TIN) was expressed as a sum of nitrate, nitrite and ammonium nitrogen. Total nitrogen (TN) was measured by the same method as nitrate nitrogen after hydrolysis with alkaline potassium persulfate (SOLORZANO and SHARP, 1980). Measurements of silicate (SiO_2) were by the molybdosilicate method (APHA, 1985), while chlorophyll-*a* (chl-*a*) was measured with a Turner

fluorometer model III by the acidification method (SAJO, 1975) after extraction with methanol.

Water samples for the identification and counting of planktonic algae were fixed with formalin at a final concentration of 5%. Cells were identified and counted under a microscope using a haemocytometer. The average cell volume of each planktonic algal species was obtained by modifying the algal shape into the simplest geometric configuration and measuring more than 30 individuals of each with a micrometer; the total cell volume of each species was then calculated by multiplying the average cell volume by the cell density.

3. Results

3-1. Seasonal change in biomass of main phytoplankton species

Figure 2 shows the seasonal changes in the biomass of the main phytoplankton species at Stas. 1 and 3 from 1990 to 1992. The dominant species at Sta. 3 in 1988 and 1989 are summarized in Table 1 cited from a previous paper (HINO, 1991). Until 1989, *Microcystis aeruginosa* and/or *Aphanizomenon flos-aquae* were dominant and formed a dense water bloom from July to September. No such water bloom has been observed since 1990, and diatoms have since dominated from July to September. Dominant species were *Melosira granulata*, *Cyclotella meneghiniana* and *Cyclotella* sp. (dia. $<15\ \mu\text{m}$) in 1990, 1991 and 1992, respectively. The total cell volume of diatoms from July to September was particularly high in 1991 and 1992, reaching five times that of blue-green algae after 1991 except in June of that year when *Apha. flos-aquae* occupied 32% of the total algal volume at Sta. 1. A small amount of *Apha. flos-aquae* occurred in November 1990 at Sta. 1, and in June and July 1991 and 1992 at both stations. *Anabaena spiroides* and *Phormidium* spp. occurred at low densities in September 1991.

The seasonal changes in chlorophyll-*a* concentration are shown in Figure 3. The maximum concentrations of chlorophyll-*a* were $100\text{--}150\ \mu\text{g} \cdot \text{l}^{-1}$ in 1988 and 1989 when the blue-green algae bloomed. However, since 1990 that

Fig. 2. Seasonal changes in cell volume of the main planktonic algal species in L. Barato from 1990 to 1992.

Table 1. Seasonal changes in the first and second dominant species at Sta. 3 in L. Barato in 1988 and 1989 (Data from HINO, 1991).

(◎), First dominant species; (○), second dominant species.

	1988												1989											
	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.						
Diatoms																								
<i>Melosira granulata</i>				○	○				○	○	○							○						
<i>Melosira ambigua</i>	○										○					○	○	○						
<i>Asterionella formosa</i>	○											○												
<i>Synedra acus</i>									○	○														
Blue-green algae																								
<i>Microcystis aeruginosa</i>				○	○	○						○			○									
<i>Aphanizomenon flos-aquae</i>												○	○	○		○	○							
<i>Anabaena flos-aquae</i>												○	○	○										
<i>Oscillatoria limnetica</i>						○																		
<i>Oscillatoria</i> spp.							○																	
<i>Phormidium</i> spp.											○													
Green algae																								
<i>Actinastrum hantzschii</i>								○																
<i>Mougeotia</i> sp.												○

Fig. 3. Seasonal changes in chlorophyll-*a* concentration in L. Barato from 1988 to 1992.

Fig. 4. Seasonal changes in water temperature in L. Barato from 1988 to 1992.

concentration has increased with the change of dominant species, with values reaching $369 \mu\text{g} \cdot \text{l}^{-1}$ at Sta. 1 in November 1991 and $276 \mu\text{g} \cdot \text{l}^{-1}$ at Sta. 3 in June 1991 due to the vast propagation of diatoms.

3-2. Seasonal changes in water temperature and nutrient concentrations

Seasonal changes in water temperature are found in Figure 4, and show a slight difference between Stas. 1 and 3. The maximum annual temperatures range was $23.6\text{--}24.9^\circ\text{C}$ in 1988–1989. The maximum temperature in 1990 (24.8°C) was similar to that in previous years, even though the dominant species had changed. Thereafter the temperature decreased during summer, with the maximum falling to 22.1 and

20.2°C in 1991 and 1992, respectively.

TIN was detected mostly as nitrate-N throughout all seasons at both stations (Fig. 5). After 1990, the concentration level of TIN from July to September was similar to that before 1989. In 1988 and 1989, the range of TN concentration from July to September was $2.8\text{--}4.1 \text{ mg} \cdot \text{l}^{-1}$ and $6.1\text{--}9.7 \text{ mg} \cdot \text{l}^{-1}$ at Stas. 1 and 3, respectively. Although the range showed no increase in early 1990, it began to increase from late 1990, reaching 7.9 and $10.2 \text{ mg} \cdot \text{l}^{-1}$ at Stas. 1 and 3, respectively, by 1992.

The $\text{PO}_4\text{-P}$ concentrations in July and August were $0.003\text{--}0.009 \text{ mg} \cdot \text{l}^{-1}$ at both stations in 1988 and 1989. However, they fell quite low after 1990 ($<0.003\text{--}0.007$ and $<0.003\text{--}0.005 \text{ mg} \cdot \text{l}^{-1}$).

Fig. 5 Seasonal changes in nitrogen concentrations in L. Barato from 1988 to 1992.

l^{-1} at Sta. 1 and Sta. 3, respectively). In particular, PO_4-P was not detected in the early summer (May and June) after 1990 (Fig. 6). The STP and TP concentrations were relatively stable from year to year (Fig. 7), except for remarkably high TP concentrations from August to October 1991 at Sta. 1.

The SiO_2 concentration peaked (17.5 – 21.2 $mg \cdot l^{-1}$ at Sta. 1 and 24.0 – 26.8 $mg \cdot l^{-1}$ at Sta. 3, Fig. 8) when the algal biomass reached its annual minimum each February. The concentration decreased from April to July or August with the increase in diatom biomass. Before 1989, the minimum annual concentration was 1.7 – 2.4 $mg \cdot l^{-1}$ and 11.9 – 14.5 $mg \cdot l^{-1}$ at Stas. 1 and 3, respectively. After 1990, it maintained its old level at Sta. 1, but fell to below 10 $mg \cdot l^{-1}$ at Sta. 3.

4. Discussion

The summer water temperature as a whole was lower after 1991 than before 1990 (Fig. 4), with the difference in the maximum being about $4^\circ C$. TILMAN *et al.* (1986) observed that blue-green algae dominated in low N:P ratios (NO_3-N : PO_4-P ratios in a synthetic medium) at $24^\circ C$, but not in low N:P ratios at 10 and $17^\circ C$ in laboratory experiments using a natural

Fig. 6. Seasonal changes in orthophosphate concentration in L. Barato from 1988 to 1992.

Fig. 7. Seasonal changes in total and soluble total phosphorus concentrations in L. Barato from 1988 to 1992.

Fig. 8. Seasonal changes in silicate (SiO_2) concentration in L. Barato from 1988 to 1992.

algal assemblage. In contrast, diatoms dominated at 9 – $17^\circ C$ under a broad range of N:P ratios unless they were silicate-limited. The lowering of water temperature during the

period when blue-green algae grow may have induced the dominance of diatoms after 1991.

However, diatom dominance in the summer of 1990 cannot be explained by low water temperature alone. Nutrient conditions are also important for the dominance of planktonic algae. *Microcystis aeruginosa* requires a fairly high concentration of phosphorus for its growth (HOLM and ARMSTRONG, 1981), and is usually abundant where the phosphorus supply is at a high level. We hypothesize that a sufficient $\text{PO}_4\text{-P}$ supply is necessary to form a dense blue-green algal bloom, since much TIN remains in L. Barato in all seasons. Although marked variations in TP and STP concentrations in summer were not observed before 1989 and after 1990, the $\text{PO}_4\text{-P}$ concentration has been clearly depleted in May and June at Stas. 1 and 3 since 1990 (Figs. 6 and 7). This depletion might be due to a remarkable increase in uptake by diatoms. Therefore, after 1990, *M. aeruginosa* could not begin to grow due to a lack of phosphorus in early summer. STP (containing dissolved organic phosphorus) is also defined as a source of $\text{PO}_4\text{-P}$ supply for planktonic algae. However, HINO (1988c) reported that planktonic algae including *M. aeruginosa* and *Melosira* spp. could not directly utilize most of the dissolved organic phosphorus in L. Barato.

The biomass of *Anabaena spiroides* (Stas. 1 and 3) and *Phormidium* spp. (Sta. 3) increased in September 1991 (Fig. 2) along with an increase in $\text{PO}_4\text{-P}$ concentration (Fig. 6). This observation supports the hypothesis that the $\text{PO}_4\text{-P}$ supply was sufficient to form a blue-green algal bloom at that time. From 1991, *Apha. flos-aquae* appeared in June and July when $\text{PO}_4\text{-P}$ was undetected. This species was found in lower temperatures, and therefore found in an earlier season than *M. aeruginosa* (HINO and TADA, 1985). Since *Apha. flos-aquae* perhaps began to grow in May before a drop in the concentration of $\text{PO}_4\text{-P}$, it may have taken up sufficient $\text{PO}_4\text{-P}$ to put in a slight, temporary appearance in June and July.

Since changes in concentrations of chlorophyll-*a* and TP occurred simultaneously

(Figs. 3 and 7), algal biomass should correspond to TP concentration. While the chlorophyll-*a* concentrations in the summer increased after 1990, TP concentrations in the summer scarcely changed before 1989 and after 1990. The phosphorus content and phosphorus demand of diatoms, which were dominant after 1990, may be less than those of blue-green algae. HOLM and ARMSTRONG (1981) suggested that *Asterionella formosa* was superior to *M. aeruginosa* under phosphorus limitation, which they based on a comparison between the nutrient parameters of the two species. In a field survey, JEWSON *et al.* (1981) observed that the biomass of *Melosira italica* and *Stephanodiscus astraea* increased in Lough Neagh when soluble reactive phosphorus was below the detection limit. These facts suggest that diatoms are more adaptive to phosphorus-deficient conditions than blue-green algae. However, NEDOMA *et al.* (1993) reported that the blue-green algae, *Apha. flos-aquae* and *M. aeruginosa*, dominated during a period of phosphorus limitation.

TILMAN (1982) proposed that dominant phytoplankton species were determined by the limiting resource ratios. Subsequently, it has been generally accepted that the N:P ratio is an important determinant of the species composition of natural algal populations in lakes. TAKAMURA *et al.* (1992) reported a change in dominant algae from *M. aeruginosa* to *Planctothrix (Oscillatoria) agardhii* in Lake Kasumigaura, and suggested that such a shift was caused by an increase in the TN:TP ratio of the lake water due to an increase in TN.

By plotting the data on TN:TP ratios of 17 lakes from various geographical regions, SMITH (1983) suggested that blue-green algae dominated where the TN:TP ratio was less than 29 (by weight). However, he noted that there were many lakes dominated by non-blue-green algae despite TN:TP ratios less than 29. From July to September prior to 1989, the average TN:TP ratios at Stas. 1 and 3 in L. Barato were 21.3 and 55.3 (by weight), respectively. Thereafter, a slight increase in the TN:TP ratio was observed (Figs. 5 and 7). Since the change in dominant algae was noted at both

stations despite the considerable difference in the TN: TP ratios between them, the shift in dominant algal species cannot be explained by the change in TN: TP ratio.

The high concentration of SiO_2 in L. Barato may contribute to the dominance of diatoms. Although much SiO_2 was taken up by diatom growth, it remained relatively abundant from 1988 to 1992 (minimum concentration, $1.2 \text{ mg} \cdot \text{l}^{-1}$, Fig. 8). JEWSON *et al.* (1981) concluded that a decrease in diatom biomass is caused by a deficiency in SiO_2 rather than in $\text{PO}_4\text{-P}$. The amount of SiO_2 taken up by diatoms in L. Barato was estimated to be $10\text{--}15 \text{ mg} \cdot \text{l}^{-1}$, based either on the difference between maximum and minimum SiO_2 concentrations (Fig. 8) or on the calculation of silicate content in the maximum diatom biomass according to the method of BAILEY-WATTS *et al.* (1989). If the maximum SiO_2 concentration was below $10 \text{ mg} \cdot \text{l}^{-1}$, the diatom biomass should not have increased in the early summer since sufficient SiO_2 was lacking. The minimum SiO_2 concentration in other lakes whose maximum SiO_2 concentration was below $10 \text{ mg} \cdot \text{l}^{-1}$ was less than $0.5 \text{ mg} \cdot \text{l}^{-1}$ resulting in a decrease in the biomass of planktonic diatoms apparently due to SiO_2 limitation (CONWAY *et al.*, 1977; GIBSON, 1981; BAILEY-WATTS *et al.*, 1989). In contrast, diatoms in L. Barato maintained an abundant biomass in summer without being limited by SiO_2 .

It seems likely that $\text{PO}_4\text{-P}$ depletion by the uptake of diatoms in early summer was the main factor influencing a change in the dominant species in L. Barato, and that low water temperature and high SiO_2 concentration helped to promote this change.

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摘 要

何が茨戸湖の夏季優占浮遊藻類種を変化させたか？

茨戸湖において、1989年以前の夏季の優占種であり、例年濃密な水の華を形成していた *Microcystis aeruginosa* などのラン藻が1990年以後にはほとんど出現せず、替わって同時期にケイ藻種が優占するようになった。リン酸態リン ($\text{PO}_4\text{-P}$) 濃度は1989年以前では年間を通じて常に検出されていたが、1990年以後、5、6月には検出されなくなり、リンが欠乏していると考えられた。1991年には、8~9月に $\text{PO}_4\text{-P}$ 濃度が再び増加した直後に数種のラン藻の発生が認められた。これらのことから、ラン藻からケイ藻への優占種の移行は、夏季に優占していた *M. aeruginosa* の成長が始まるであろう5、6月にケイ藻による取り込みによって $\text{PO}_4\text{-P}$ が欠乏したため、その現存量を増加させることができず、替わってリン制限状態に強いケイ藻種が、低水温下、高いケイ酸濃度の状況下で入れ替わって好適に細胞数を増加させ、夏季まで優占したために起きたものと推定した。

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