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An autumnal bloom of the diatom *Melosira granulata* in a shallow eutrophic lake: physical and chemical constraints on its population dynamics

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With 9 figures in the text

Abstract

Temporal changes in population densities of algae and concentrations of chlorophyll-a, particulate organic carbon, and both soluble inorganic and particulate organic fractions of Si, N and P, were surveyed in summer and autumn 1991 in the south basin of Lake Biwa, Japan, at three stations different in the nutritional status. Phytoplankton community during the survey period was characterized by overwhelming dominance by a diatom (*Melosira* (syn. *Aulacoseira*) *granulata* (Ehrenb.) Ralfs), which was presumably brought about by exceptionally windy weather in this year. Diatom population density and concentrations of biogenic silica and chlorophyll-a were higher in the more eutrophied stations. It seemed unlikely that the diatom population growth was limited by the supply of silicate, except in a short period in October at the station of median nutritional status. Rather, an observation that diatoms tended to decrease in August when dissolved inorganic nitrogen was commonly depleted suggested the diatom population size to have been determined principally by the nitrogen availability. A comparison of relative turnover periods among soluble inorganic N, P and Si supported further that the growth of phytoplankton as a whole was limited by nitrogen supply during August and the first half of September, and by phosphorus supply in the other period. Some potential factors are discussed which would determine the availability of nutrients during the successional passage from summer to autumn in this basin.

Introduction

The spatial and temporal distribution of silicate in lake water is determined by the dynamic balance between the internal precipitation and dissolution processes. In many lentic waters, the most effective and predominant removal process of dissolved monosilicate (designated $Si(OH)_4$ in the following) is the extraction by planktonic and sessile silicon-secreting autotrophs such as

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diatoms and silicoflagellates and the subsequent settlement of their biomass to sediment (Calvert 1983), although inorganic adsorption and coprecipitation with terrigenous clay particles may also contribute to some extent in highly turbid waters (Mayer & Gloss 1980). Since the population of silicon-secreting algae shows a clear seasonality in temperate lakes, the $Si(OH)_4$ concentration also has seasonality with a minimum, as a rule, just after the cessation of the spring diatom growth (Paasche 1980). The spring bloom in many lakes ever studied ceased with a few μM of free $Si(OH)_4$ left behind in lake water, which may suggest that this concentration range represents a threshold for the growth of indigenous diatom populations (Lund 1964, Conway et al. 1977, Sommer 1993). The silicate incorporated into diatoms' frustules as amorphous polymer can be redissolved after the death of diatoms. However, redissolution of diatoms' frustules has been recognized to be a slow, probably non-enzymatic process (Golterman 1975, chapter 8). Although no consistent value has been obtained yet as to any sort of rate constants for in-situ dissolution processes, it seems a rather common observation that the rate is so slow as for the major part of regeneration of $Si(OH)_4$ to proceed after deposition to lake sediment (Bailey-Watts 1976, Parker et al. 1977 a). In deep stratified lakes, the regnerated $Si(OH)_4$ tends to accumulate in the deepest water layer and thus remains unavailable for primary producers until the onset of autumnal overturn (Parker et al. 1977 b). Thus, the inorganic redissolution of diatom frustules and, in deep lakes, the vertical mixing of lake water seem to be the most likely rate-limiting steps in the internal silicate cycle.

One of the problems of interest in concern of the actual turnover rates of the silicate cycle is in what manner the population size and the growth rate of diatoms are determined by environmental factors. Although the cessation of seasonal diatom blooms has been often observed in association with apparent depletion of $Si(OH)_4$ from euphotic zone, there is few direct evidence for the silicate as a growth-limiting factor of natural diatom population (Paasche 1980). As the spatial and temporal distribution of $Si(OH)_4$ within a lake is tightly coupled with those of other nutrients, it is usually difficult to discriminate the limiting effect of $Si(OH)_4$ alone from those of nitrogen and phosphorus upon algal communities based solely on observations of temporal changes in the ambient nutrient concentrations. Even some evidence are found in literature which show the factors other than $Si(OH)_4$ supply, such as light (Golterman 1975, chapter 7), turbulence (Talling 1969) and phosphorus supply (Eriksson & Forsberg 1992), to operate as a growth-limiting factor of natural diatom populations. These evidences are important in the geochemical perspective because they mean that those factors whose behaviors are more or less independent of that of silicate determine the removal rate of $Si(OH)_4$ and thus its absolute concentration remaining in lake water. Which factor is actually critical may, however, vary depending on the hydrology of individual lakes.

While the deposition of diatom frustules and the confinement of regenerated $Si(OH)_4$ within the deepest hypolimnetic layer may lead to actual silicate deficiency in the epilimnetic phytoplankton of deep stratified lakes, silicate recycling in shallow non-stratified lakes does not appear as susceptible to such retarding effects.

The present authors report here a case study on the population dynamics of diatoms and associated changes in the silicate distribution in a shallow eutrophic basin where the algal succession pattern seems to depend upon factors other than silicate supply. The study site, the south basin of Lake Biwa, Japan, is a shallow (mean depth, 3.3 m) but relatively large (57 km^2) basin where wind-generated turbulence almost always inhibits stable vertical stratification. Diatoms together with some green algae constitute the indigenous algal community of this basin. If conditions are favorable, diatoms predominate in the planktonic flora from spring through late autumn, which implies the persistence of effective internal recycling of silicate in this basin. The diatom community is usually dominated by *Asterionella formosa* (and in some years *Fragilaria crotonensis*) in spring, and by *Melosira* spp. in summer and autumn. However, it has become a usual observation of recent years that the dominancy of the indigenous community is interrupted by an episodic cyanobacterial bloom in late summer. The fact that the cyanobacterial bloom often commences with an occurrence of nitrogen-fixing *Anabaena* app. indicates that this event is induced by nitrogen deficiency with a relatively abundant supply of phosphorus (Tezuka 1988). Thus, we suspect whether the growth of indigenous populations including diatoms as well as the efficiency of the biological silicate turnover in this basin may be limited by the nitrogen availability to primary producers, especially in late summer.

To elucidate the effects of such an interaction between biogeochemical pathways of nutrient elements, the authors carried out a comprehensive survey on the dynamics of nutrient elements and algal community in the south basin during summer and autumn 1991. For comparison, the survey was conducted at three regions of different nutritional status (mesotrophic, eutrophic, hypertrophic) within this basin. The results will be described and discussed in two separate papers. This paper mainly deals with the temporal changes in diatom population, nutrient concentrations, and elemental composition of plankton biomass and tries to clarify what factor(s) actually determined the diatom population dynamics. Our second paper (Miyajima et al., in prep.) will include general review and discussion about the relationships of diatom community dynamics with distribution of silicate ever studied in Lake Biwa, with some additional data on the nutrient regeneration processes. Observations on the population dynamics of non-diatom algae are not extensively discussed in these papers and the reader is referred for this point to Nakanishi et al. (1992) and Nakano et al. (in press).

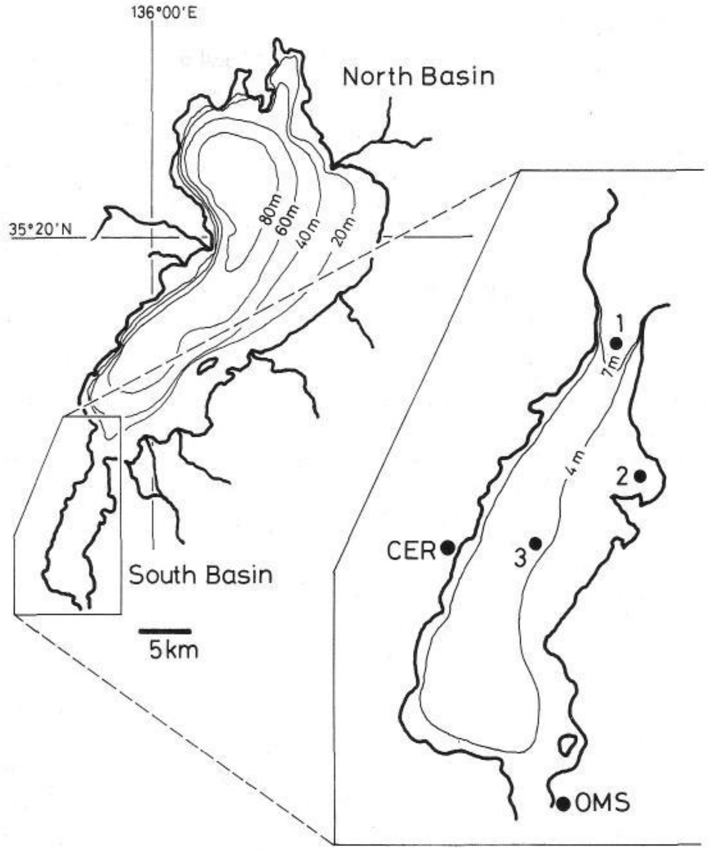

Fig. 1. Location of sampling stations in the south basin of Lake Biwa. CER: Center for Ecological Research; OMS: Otsu Meteorological Station.

Material and methods

Study site

Three sampling points of different nutritional status were selected within the south basin of Lake Biwa (Fig. 1). At Station 1 located at the strait connecting the north and the south basins (depth, ca. 8 m), the water quality is strongly affected by inflow water from the mesotrophic north basin (624 km^2, mean depth 44 m) to the south one, and a weak thermal stratification is observed during spring and summer. The inflow water brought through the strait is said to flow along the west shoreline southwards with gradual eutrophication by mixing with domestic and agricultural wastes rich in N and P. Station 2, a hypertrophic site, is located in Akanoi Bay (depth, ca. 2 m) in the northeast district of the south basin. Lake water exchange with the other part of the south basin is partially inhibited by artificial barriers placed at the mouth of the bay, and an extensive loading of agricultural waste has rendered the bay the most eutrophied region in Lake Biwa. Station 3, located at the center of the south basin, is a station typical to this basin characterized by eutrophy, shallowness (ca. 4 m), and moderate turbidity caused by wind-driven turbulence. Thermal stratification is scarcely formed at Stations 2 and 3.

Sampling processes

Sampling was conducted between 0930 and 1100 (local time) once a week from 23 July through 30 October 1991. Water samples (5 litre for each site) were collected with a 3 l Van Dorn sampler from a depth of 0.5 m below the surface. At Station 1, vertical sampling was also done with 1 m intervals biweekly. Water temperature, pH, and transparency were determined on shipboard with a thermistor thermometer (Toho Dentan, model RB-2), a portable pH electrode (Yokogawa, type PH82), and a Secchi disk of 20 cm diameter, respectively. 250 and 50 ml portions of each water sample were fixed on board with acid Lugol's solution for phytoplankton counting and with glutaraldehyde solution for bacterio- and picophytoplankton counting, respectively. The remainder was packed in a polypropylene bottle and transported to the laboratory with ice for further processing.

Two 300 – 500 ml portions of each sample were filtered through polytetrafluoroethylene (PTFE) filters of 1 μm-mesh (ADVANTEC, type T100A, prewetted with acetone and rinsed with deionized-distilled water) to separate soluble and particulate fractions. One of the two filters was used later for determination of total particulate Si, P, Al and Ti contents and the other for determination of alkali-soluble (biogenic) particulate Si and P. The filtrate was used for nutrient analyses. The filters and the filtrates were packed within polythene sacks and polypropylene bottles, respectively, and stored at -20 °C until further treatments.

Another 400 – 2000 ml portion of each sample was filtered through a glassfiber filter (Whatman, type GF/F, pre-ignited at 450 °C for 2 h) and then the filter was dried at 60 °C for 2 days for later use for determination of particulate organic matter. Another 80 – 200 ml portion of each sample was filtered with a 2 μm-mesh Nuclepore membrane filter, and the resulting filtrate was filtered again with a 0.2 μm-mesh Nuclepore membrane. These filters were used for analyses of chlorophyll contents in $> 2\,\mu$m and 0.2 – 2 μm fractions of particulate matter, respectively. The glassfiber and Nuclepore filters were enveloped with pieces of aluminum foil and stored at -20 °C until further treatments.

Any filters used above were not washed so rigorously before use, except for several times of cleaning with deionized-distilled water. Instead, we carried out blank correction with three or more pieces of unused filters in every sort of analyses. Contamination from filters was proved to be negligible in any case.

Counting of phytoplankton

Phytoplankton cells in the samples fixed with acid Lugol's solution were allowed overnight to settle, concentrated 400 to 2000-folds by discarding supernatants, and counted by use of a haemocytometer under a microscope (NAKANISHI et al. 1992). Counting of bacteria and picocyanobacteria were done by an epifluorescent microscopy with or without acridine orange staining (NAKANO et al., in press). However, data of phytoplankton other than diatoms as well as those of bacteria and picocyanobacteria are reported in the above mentioned literature and not thoroughly described here.

Analyses of soluble nutrients

Concentrations of NH_4^+, NO_2^-, and NO_3^- were determined after methods of BOWER & HOLM-HANSEN (1980), BENDSCHNEIDER & ROBINSON (1952), and SCHEINER (1974), respectively. Dissolved inorganic nitrogen (DIN) is defined here as $NH_4^+ + NO_2^- +$

NO_3^-. Soluble reactive phosphorus (SRP) was determined by the molybdate method (Murphy & Riley 1962). Soluble reactive silicon (SRSi or $Si(OH)_4$) was determined by the molybdenum yellow method though reduction into heteropolyblue was also adopted when silicate concentration was extremely low. Before the analysis of SRSi, water samples were left at room temperature for two days in order to preclude interfering effects of freezing (Burton, Leatherland & Liss 1970). By this tretment, filterable colloidal (nonreactive) silicate if already present in original samples might have been converted into molybdate-reactive forms and thus given a positive error in SRSi determination. But we neglect here the possible existence of colloidal silicate based on that it is unstable and readily dissociate into monomers under natural conditions (Aston 1983).

Analyses of particulate matter

Particulate matter trapped on 2 and 0.2 μm-meshed Nuclepore membranes was subjected to overnight extraction of photosynthetic pigments with 15 ml of 90 % (v : v) aqueous acetone. Concentrations of chlorophyll-a and phaeopigment were measured with a fluorometric spectrophotometer. However, we report in this paper the pigment contents of $>2\,\mu m$ fraction alone because most diatom biomass belongs to this fraction. The ratio of the $0.2-2\,\mu m$ fraction to the total chlorophyll-a tended to take the higher values where diatoms were the less abundant, though scarcely exceeded one third.

Total particulate organic carbon (POC) and nitrogen (PON) contained in the sestonic samples trapped on glassfiber filters were analyzed with a CHN analyzer (Yanaco, model MT-3).

Total particulate Si (TPSi), P (TPP), Al, and Ti were determined on the sestonic samples trapped on PTFE filters after the microwave acid digestion method (Suzuki & Sensui 1991) described below. One of the two PTFE filters for each original sample is transferred into a PTFE crucible with care for the filter not to be dried up (if the filter dried, digestive reagents do not penetrate enough into the filter). 1.0 ml of conc. HNO_3 and 0.3 ml of conc. HF are then added with the filter allowed to be wetted well with them. The crucible is closed with a PTFE cap, placed within a pressure-resistant, microwave-transparent bomb with a tight screw cap, heated in a microwave oven at 600 W for 150 seconds during which the sample is digested, and then cooled in a cold water bath for 30 minutes. After taking out the crucible from the bomb, 15.0 ml of deionized-distilled water is added to the crucible. The PTFE filter was washed well within the crucible with a PTFE forceps and then discarded. A portion (ca. 8 ml) of the resultant solution in the crucible is transferred to a screw-capped 10 ml polysulfone tube and stored at −10 °C. Biogenic particulate Si (BPSi) and P (BPP) were determined after the alkali-digestion method. Each sestonic sample trapped on another PTFE filter is placed in a screw-capped 10 ml polysulfone centrifugation tube containing 8.0 ml of 5 % (w : v) Na_2CO_3. The tube is kept in a water bath at 80 °C with occasional shaking by hands for 6 hours during which organically bound silicate and phosphate as well as amorphous silicate polymers such as diatom frustules are converted into soluble forms. After cooling, the PTFE filter is washed within the tube with a polypropylene pick and then discarded. The resultant solution is subjected to centrifugation (3000 rpm, 10 minutes) to remove alkali-resistant particles. The supernatant is transferred to another polysulfone tube and stored at −10 °C. Concentrations of Si, Al, P and transition metals in the acid- or alkali-digested solutions were determined by the inductively coupled plasma atomic emission spectrometry.

It is noteworthy that although the alkali (Na_2CO_3 or NaOH) digestion method has been widely used for estimating biogenic silica in water samples (Conway et al. 1977, TRÉGUER et al. 1991, CORNWELL & BANAHAN 1992), its application to the estimation of organically bound phosphorus seems to have been largely restricted so far in the realm of chemical sedimentology (e.g. PETTERSSON et al. 1988). However, the phosphorus inorganically bound to particulate matter (alkali-insoluble fraction) presumably derived from resuspension of sediment sometimes constitutes a significant portion of total particulate phosphorus standing stock of the water column, especially in shallow turbid regions such as Station 3. Thus, we adopted in this paper the alkali-soluble particulate phosphorus as the biomass fraction. The ratio of alkali-insoluble fraction to alkali-soluble one often exceeded unity at Stations 1 and 3, though scarcely exceeded 4.

Results

Physical conditions

The seasonal change in water temperature did not differ significantly among stations. During July and August, water temperature remained between 26 and 28 °C, and linearly lowered thereafter from 28 °C on 3 September to 18 °C on 30 October. The pH value ranged 8 to 9 with relatively high values in August at all the three stations and relatively low values in October at Stations 1 and 2. Transparency was almost always the highest at Station 1 (3 – 6 m) and the lowest at Station 2 (1 – 1.5 m), which supposedly reflected the differences in both the absolute water depth and the degree of eutrophication among stations. The temporal variation in the transparency was negatively correlated with chlorophyll-a concentration. As discussed later, the monthly averaged wind speeds from July to October 1991 ($1.2 - 1.7\ \mathrm{m\,s^{-1}}$) were considerably higher than those in the average year ($0.9 - 1.1\ \mathrm{m\,s^{-1}}$).

Silicate and diatoms

The temporal changes in concentration of soluble reactive silicate (SRSi), total (acid-soluble) particulate silicon (TPSi), and biogenic (alkali-soluble) particulate silicon (BPSi) are compared with those of densities of total diatoms and *Melosira granulata*, the most dominant species, in Fig. 2. Decrease in SRSi concentration at the beginning of August observed at Stations 2 and 3 as well as that in September and the second half of October observed at all the stations seemed to be ascribed to concomitant outgrowth of diatom population. However, if we adopt here the apparent growth-limiting concentration of 8 μM SRSi proposed by LUND (1950) or 6.5 μM proposed by PARKER et al. (1977 b), the cessation of growth period of diatom population is thought to have been caused by silicate deficiency only in the cases of those observed at Stations 2 and 3 at the end of October. Interstational variation of SRSi concentration did not necessarily reflect that of nutritional status though relatively high values of $> 50\ \mu$M were occasionally recorded at the most eutrophied Station 2. Nevertheless, the density of diatoms was almost always much higher in the more eutrophied station. Temporal changes in BPSi concentration corre-

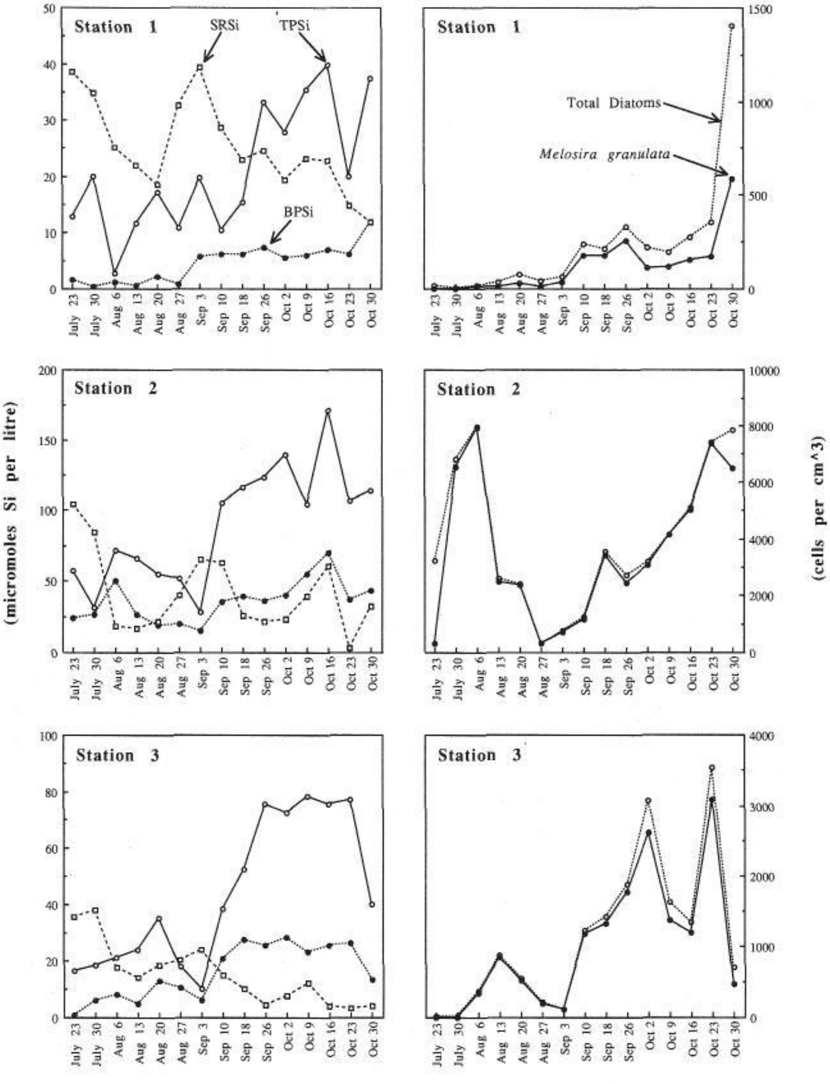

Fig. 2. Temporal changes in (left) the concentrations (in mmol m^{-3}) of total (HF-soluble) particulate silicon (TPSi, open circle), biogenic (alkali-soluble) particulate silicon (BPSi, solid circle) and soluble reactive silicate (SRSi, open square) as well as in (right) the densities (in cell counts cm^{-3}) of total diatoms (open circle) and *Melosira granulata* (solid circle) at respective stations during the survey period.

sponded well with population dynamics of diatoms, while those of non-biogenic particulate silicon (TPSi minus BPSi) seemed to be independent of biological activities. The diatom community was usually dominated by *Melosira granulata*, except for on 23 July at Station 2 where *Cyclotella* spp. dominated and on 30 October at Station 1 where *Fragilaria crotonensis* dominated. Ex-

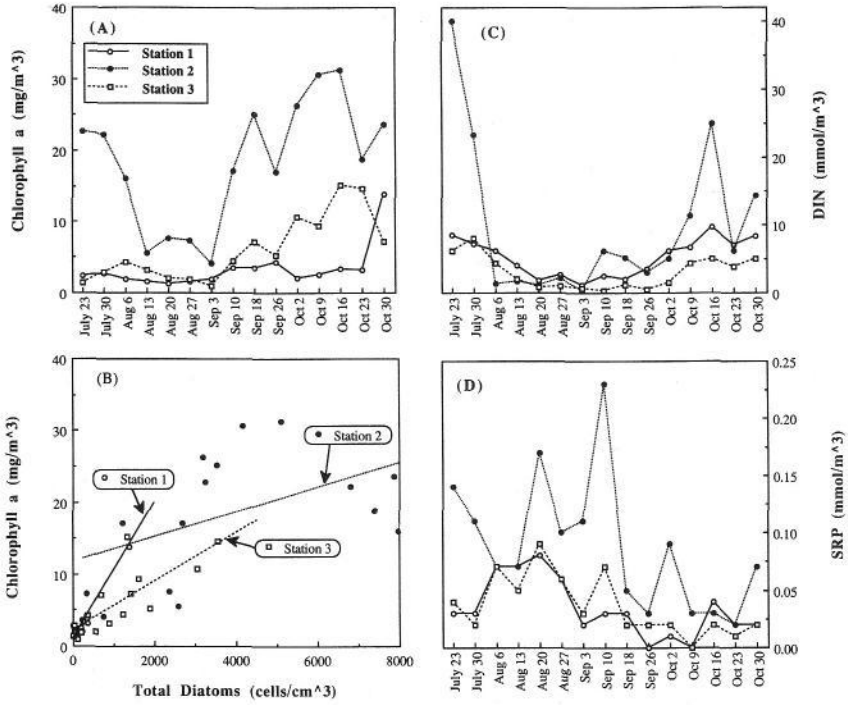

Fig. 3. Temporal changes in concentration (in $\mathrm{mg\,m^{-3}}$) of chlorophyll-a contained in $>2\,\mu\mathrm{m}$ particulate fraction (A), and in the concentrations (in $\mathrm{mmol\,m^{-3}}$) of dissolved inorganic nitrogen (DIN, C) and soluble reactive phosphate (SRP, D). Concentration of chlorophyll-a is also plotted against total diatom density in (B) where the positive correlation is statistically significant ($p > 0.99$) at Station 1 and 3. Symbols of open circle, solid circle and open square represent the data at Stations 1, 2 and 3, respectively.

tremely sparce diatom population at Station 1 during July and August comprised of *Cyclotella* spp. and *Stephanodiscus carconensis.* The dominance of *F. crotonensis* in late autumn might have been induced by phosphorus deficiency (see below) because this species has nutritional requirement of higher N/P and Si/P ratios than other diatoms (KILHAM & KILHAM 1984).

Chlorophyll and nutrients

Concentration of chlorophyll-a (Fig. 3 (A)) showed similar temporal patterns and similar interstational difference to the density of diatoms (Fig. 2), though the gradient of the best-fit line between these two variables showed difference among stations (Fig. 3 (B)). The correlation was less obvious at Station 2 ($p < 0.95$) than at the other stations, presumably reflecting the fact that at Station 2 *Oscillatoria* spp. sometimes represented a significant fraction of phytobiomass in which diatoms were dominating otherwise. *Anabaena affinis, Microcystis aeruginosa* and *M. wesenbergii,* which form a bloom in this season of usual years replacing indigenous species, were barely observed in the year of 1991 (Nakanishi et al. 1992). Chlorophyll concentration reached minimum at each station during late August or early September. In other years in which a conspicuous cyanobacterial bloom occurred, the minimum values have been commonly observed just before the onset of the bloom (Tezuka 1985, 1988; Nakanishi et al. 1990). Considering that the bloom often started with massive proliferation of nitrogen-fixing *Anabaena affinis*, it appears natural to hypothesize that the chlorophyll minimum in late summer be induced by nitrogen deficiency. In fact, dissolved inorganic nitrogen (DIN) seemed to be depleted at each station when chlorophyll concentration reached minimum, in contrast to soluble reactive phosphate (SRP) whose concentration was somewhat higher in late summer than in July and October (Fig. 3 (C, D)). Both DIN and SRP concentrations were generally higher at the most eutrophied Station 2 though no consistent difference was observed between Stations 1 and 3.

Elemental composition of seston

As the temporal and interstational variations of concentration of POC (Fig. 4 (A)) have a good agreement with those of chlorophyll concentration (positive correlation with $p > 0.90$ at Station 1, $p > 0.99$ at Stations 2 and 3), algal biomass is thought to have represented the major fraction of particulate organic matter present in lake water. The sort of limiting nutrient and the degree of nutrient limitation for phytoplankton are reflected in the elemental composition of algal biomass, because the growth rate of algae depends on the internal concentration of nutrient elements within algal cells which, in turn, depends on the degree of limitation of respective nutrients (Hecky & Kilham 1988). Cellular content of N or P per unit dry weight usually falls in a narrow range irrespective of algal taxonomy if the algae under consideration are grown at a defined degree of N or P limitation normalized as relative growth rate to the optimal one (Healey 1978). Based on this empirical regularity, Healey & Hendzel (1980) introduced some criteria for the degree of nutrient deficiency based on elemental ratios such as C/N and C/P of algal biomass in natural assemblage. The carbon content of algal cells is assumed by them to be half of dry weight, which may not necessarily be valid when the algal community is dominated by silicified algae such as diatoms. Applying their criteria to the POC/BPP ratios of our data, we find that phytoplankton communities of all the three stations were in the state of "extreme P deficiency" during the first half of August (Fig. 4 (B)) though in the other periods many plots of Stations 1 and 3 remained in the range of "moderate P deficiency" with those of Station 2 mostly being in the realm of "no deficiency". Although the POC/PON ratio varied somewhat irregularly compared to the POC/BPP ratio (data not shown), in general the plots of Stations 1 and 3 for August and Sep-

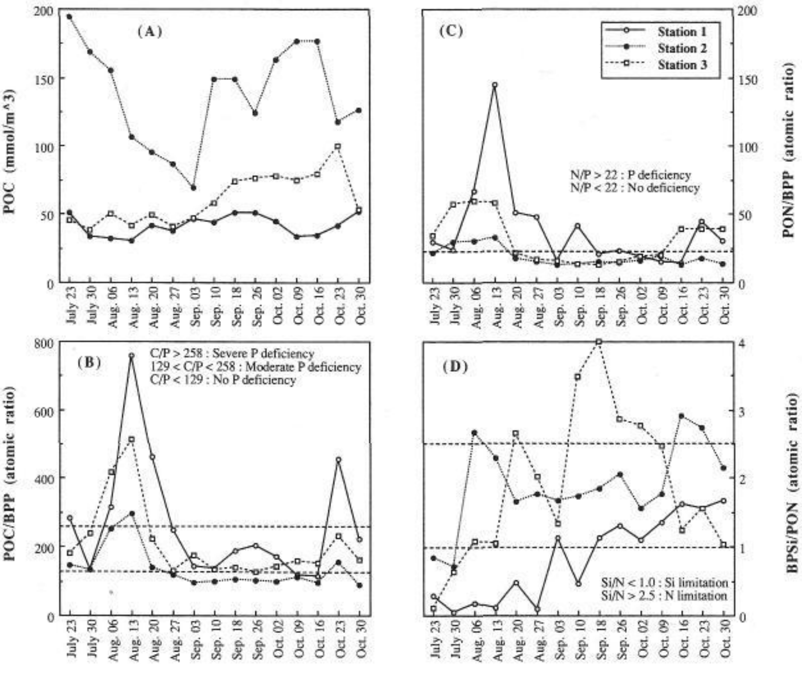

Fig. 4. Temporal changes in the concentration (in mmol m^{-3}) of particulate organic carbon (POC, A), and in the atomic ratios of C : P (B), N:P (C) and Si : N (D) in the particulate organic fraction. Criteria for nutrient deficiency on C : P and N:P ratios are according to HEALEY & HENDZEL (1980) and those on Si : N ratio to HARRISON et al. (1977). Symbols are the same as in Fig. 3.

tember suggested "moderate N deficiency" whereas "no deficiency" was indicated for the other period. At Station 2, N deficiency was scarcely indicated. The PON/BPP ratio, for which the criterion of HEALEY & HENDZEL (1980) may have more validity than for C-based ratios when applied to diatom-dominated community, indicated P deficiency for the periods of July, the first half of August, and the second half of October, and no (or N or Si) deficiency for the rest of the survey period at Stations 2 and 3 (Fig. 4 (C)). At Station 1, more prolonged prevalence of P deficiency was suggested.

Cellular silica content as well as elemental ratios such as Si/C and Si/N of diatoms also depends on the limiting nutrient and degree of nutrient limitation, though the mode of dependence may vary by species. After comparing various biochemical indicators, HARRISON et al. (1977) found that cellular Si/N ratio was the most sensitive to nutrient limitation, being >2.5 and <1.0 under nitrogen and silicon limitation, respectively, for three different species of marine colonial centric diatoms. The majority of the sestonic BPSi/PON ratio found in this survey (Fig. 4 (D)) fell in the range between 1.0 and 3.0 except for

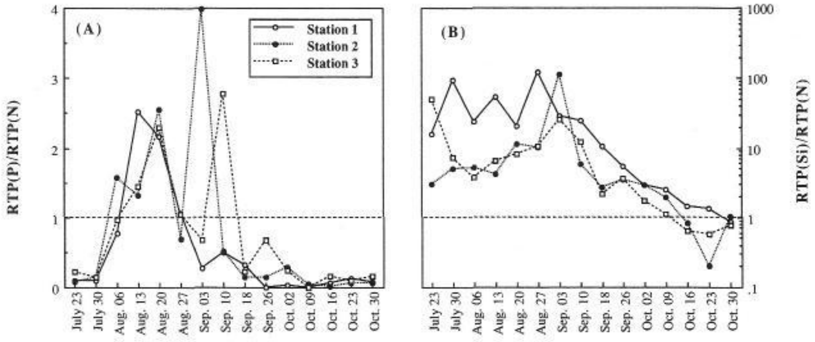

Fig. 5. Temporal changes in the ratios of relative turnover period of dissolved inorganic fraction (see text) between P and N (A) and Si and N (B). Symbols are the same as in Fig. 3.

some data at Stations 1 and 3 in which the diatom density was extremely low. As the natural seston samples inevitably contained planktonic organisms other than diatoms, the ratio for diatoms alone must have been higher than the values in Fig. 4 (D). These results, unfortunately, cannot be compared directly with those of Harrison et al. (1977) because of difference in species.

Relative turnover period of nutrients

The ratio of the concentration of a nutrient element present as dissolved inorganic forms to the concentration of the same element present as biomass is expected to be proportional to the turnover period of the dissolved nutrient, suppose that the elemental composition of algal biomass does not abruptly vary during the growth. This ratio, called here relative turnover period (RTP), of different nutrient elements taken at a single site and date can be compared and used for inferring which nutrient is the most likely to limit algal growth at the site and date. That is, an element which has the shorter RTP is the more likely to be limiting. The ratio of RTP for phosphorus to that for nitrogen was always smaller than unity during July, the second half of September, and October (Fig. 5 (A)), which suggests limitation of P rather than N in these periods. The ratio often exceeded unity between 6 August and 10 September, indicating that N rather than P tended to be limiting. The RTP ratio of silicon to nitrogen (Fig. 5 (B)) was always larger than unity except during the second half of October. The RTP of Si was always more than 3 times as long as that of P (data not shown). Binding all the above data, we can suppose that nutrients should have been likely to be limiting for algal community in such orders as: P>N>Si for July, the second half of September and the first half of October; N>P>Si for August and the first half of September; and P>Si>N for the second half of October.

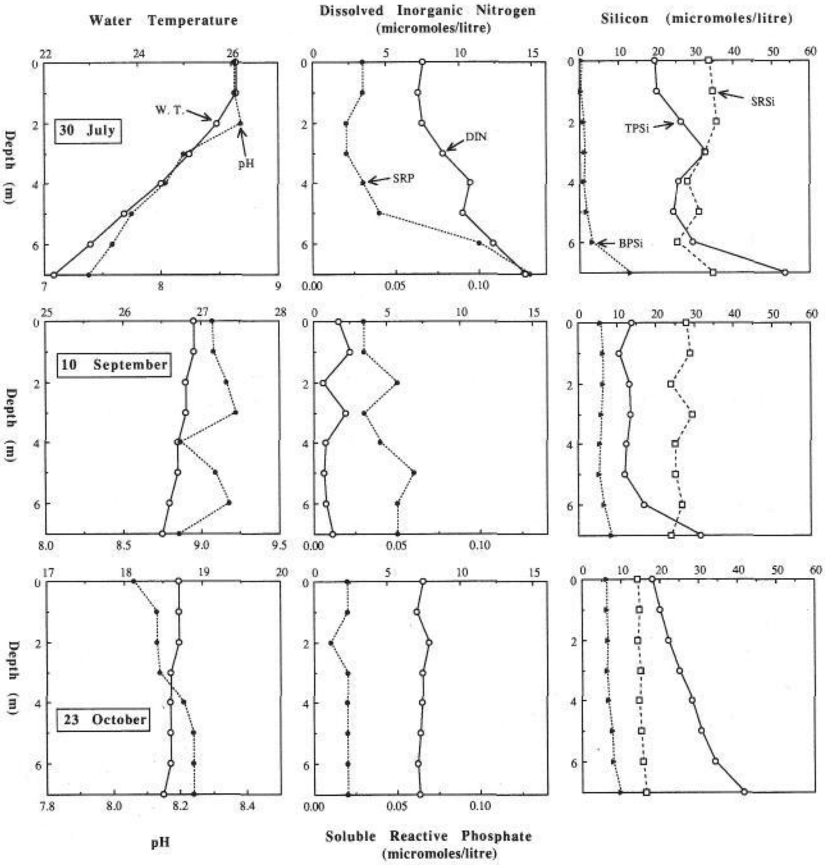

Fig. 6. Vertical distribution of some physical and chemical parameters at Station 1 on 30 July (upper row), 10 September (middle row) and 23 October (lower row). Left column: water temperature (open circle) and pH (solid one). Central column: concentrations (in μM) of DIN (open circle) and SRP (solid one). Right column: concentrations (in μM) of TPSi (open circle), BPSi (solid triangle) and SRSi (open square).

Inflow water from the north basin

Although seasonal changes in either the water quality or the flow rate of the inflow water from the north basin was not determined directly, some speculation is possible based on the data of physico-chemical factors observed at Station 1 where the water quality is affected directly by the epilimnetic water of the north basin. The quality of the epilimnetic water of the north basin, and thus the quality of the inflow water to the south basin, is affected by the degree of vertical water mixing in the north basin because the hypolimnetic water is usually much richer in nutrients (especially nitrate) than the epilimnetic one. At the beginning of this survey period (30 July), the thermocline was so

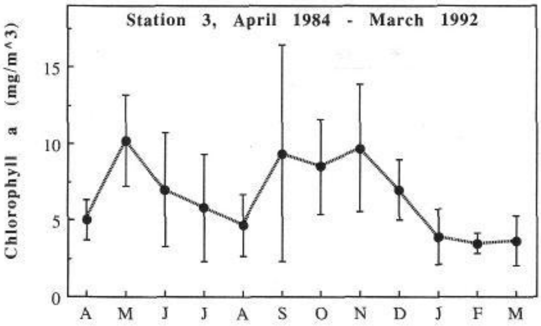

Fig. 7. Monthly trends in the chlorophyll-a concentration ($mg\,m^{-3}$, solid circle) in the surface water at Station 3, averaged over the last 8 years (April 1984 through March 1992) with standard deviations (vertical bars). Drawn from data file of the regular limnological survey conducted by the Center for Ecological Research (formerly Otsu Hydrobiological Station), Kyoto University.

shallow that even at Station 1 the vertical stratification was evident (Fig. 6). Thus, the hypolimnetic water rich in DIN and SRP (Fig. 6) could have invaded readily into the south basin once the hydraulic balance had favored the southward flow. Around the middle of the survey period (10 September), the thermocline had moved down and disappeared at Station 1 where DIN was mostly depleted from the entire water column (Fig. 6). TEZUKA (1985) ascribed the DIN depletion from the epilimnetic water of the north basin to the incorporation by primary producers followed by sedimentation of their biomass into the hypolimnion. Concomitant increase in DIN in the hypolimnetic water due to the decomposition of settling biomass observed by MIYAJIMA (1992) supports this idea. At the end of the survey period (23 October), DIN concentration in the epilimnetic water increased again (Fig. 6) presumably due to the progression of vertical mixing in the north basin which drew up nitrate accumulated in the hypolimnion. As the hypolimnetic water usually contained very little phosphate, the SRP concentration on 23 October remained low.

Discussion

Although the main point to be discussed in this paper is which factor governs the population dynamics of diatoms in the south basin of Lake Biwa, it is valuable to mention briefly the seasonal dynamics of phytoplankton as a whole in this lake. The whole algal biomass, represented by chlorophyll-a concentration, has seasonality characterized, as a trend in the last 8 years, by waxes in early summer and autumn (Fig. 7). Although the indigenous planktonic flora of this basin comprises mainly of diatoms and green algae, the algal communities at the maxima in May and September are often dominated by episodic blooms of a mixotrophic flagellate (*Uroglena americana*) and cyano-

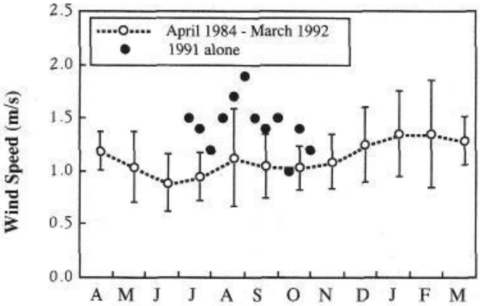

Fig. 8. Monthly mean wind speeds averaged over last 8 years (April 1984 through March 1992, open circle) with standard deviations (vertical bars), and mean wind speed in every 10 days from July to October 1991 (solid circle). Estimated at Otsu Meteorological Station (OMS, Fig. 1) and published by Hikone Meteorological Observatory, Shiga Pref., Japan.

phytes (*Anabaena* spp. and *Microcystis aeruginosa*), respectively. In spite of relatively high ambient nutrient concentrations, the algal biomass remains depressed in winter presumably due to low temperature and/or insolation. The decline of phytobiomass observed in mid summer, where the temperature or light limitation is unlikely, is presumably caused by nutrient deficiency and/or grazing pressure. Seasonal dynamics of chlorophyll-a in our study at Station 3 (Fig. 3) showed some differences from that of the average year. That is, the September maximum due to the cyanobacterial bloom was absent and the November peak due to diatoms shifted to October. At Station 1 where the algal flora is strongly affected by that of the north basin, the seasonal pattern was distinct from those observed at the other stations. The chlorophyll concentration (per unit volume) in the north basin is usually much lower than that in the south basin (NAKANISHI 1984).

The indigenous algal community of the south basin comprises of green algae including *Staurastrum dorsidentiferum, Closterium aciculare, Pediastrum biwae,* and others in addition to diatoms such as *Asterionella formosa, Fragilaria crotonensis, Melosira* spp. and other small centric species. The relative abundance of particular species varies drastically year by year, and the mechanisms responsible to the yearly variation are hitherto barely understood. One of the distinctive characteristics in the algal flora in 1991 is the prominent dominance (in biomass) of *Melosira granulata.* This phenomenon may be ascribed to the abnormally windy weather observed over the survey period (Fig. 8), because *Melosira* spp., which have large specific gravity compared with other algae, prefer relatively high turbulence of lake water in order to decrease their loss rate due to sinking (LUND 1954, TALLING 1969, PETROVA 1986). The planktonic flora of the north basin in summer, on the other hand, is principally dominated by desmids with relative paucity of diatoms despite non-limiting concentration of dissolved silicate (see Fig. 2, Station 1). *Melosira* spp. increase their abundance gradually there with the vertical stratification being progressively destructed in autumn, and among them *Melosira solida* eventually dominates during winter holomixis until being replaced at the onset of vernal stratification by pennate diatoms such as *A. formosa* and *F. crotonensis* (Nakanishi 1984) which are less susceptible to gravitational sinking than *Melosira* (Reynolds 1989). Thus, the phenology of diatom species in the north basin with their paucity observed at Station 1 in summer (Fig. 2) seems to be generally explained by the turbulence-dependent growth of diatoms.

The effect of wind-driven turbulence, however, cannot explain the temporal changes in diatom density and chlorophyll concentration observed during this survey, both of which reached minimum during August or September (Figs. 2 and 3) where mean wind speed remained high (Fig. 8). Since conspicuous proliferation of *M. granulata* has been recorded both in early August and late October (Fig. 2), changes in temperature and/or irradiance do not seem responsible either. Thus, the diatom population dynamics in this period is thought to have been controlled primarily by chemical conditions. We have examined nutritional conditions during the survey period from three standpoints: ambient concentration of dissolved nutrients, elemental composition of seston, and relative turnover period of nutrients. The results can be summarized as that in August and early September where the diatom population was the most severely depressed, nitrogen deficiency seemed to prevail, whereas phosphorus was more likely to be limiting during the rest of the survey period. In addition, silicate supply seemed to have become progressively restrictive towards the end of the survey period. From the view of population dynamics, the behavior of nitrogen is thus thought as the most critical determinant in this season of a year, though the cessation of autumnal diatom bloom, usually observed in November (Fig. 9), may be ascribed to silicate deficiency. The zooplankton grazing is another possible explanation for the decline of diatom population. However, the regeneration of nitrogen concomitant with the decline of algal population, which often associates with active grazing (Sterner 1989), was lacked in this case (Fig. 3), suggesting the grazing effect to have been less important. Actually, large colonial diatoms such as *Melosira* are known to be poorly ingestible to indigenous crustacean zooplankters in Lake Biwa (Kawabata 1987). The fact that a bloom of nitrogen-fixing cyanobacteria often occurs in this season of recent years also suggests nitrogen deficiency. In the years where the cyanobacterial bloom occurred conspicuously, the population of *Melosira* spp. declined concomitantly with the outgrowth of *Anabaena* spp. and was depressed during the bloom presumably due to both nitrogen deficiency and competition for light. After the bloom was destructed, *Melosira* started to grow towards November (Fig. 9 (B)). In the years without a conspicuous *Anabaena* bloom (Fig. 9 (A)), the November peak of *Melosira* popula-

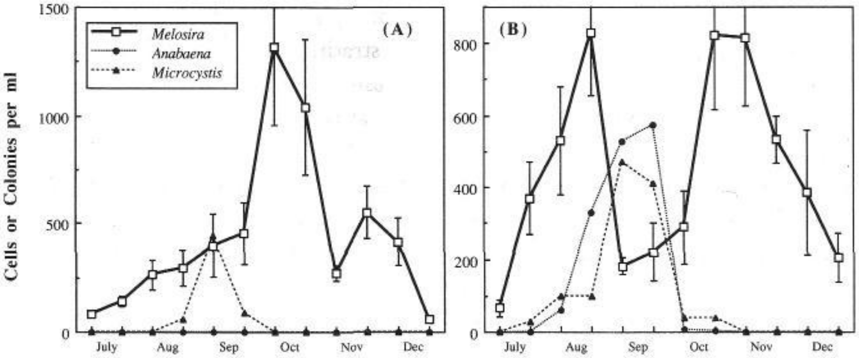

Fig. 9. Population dynamics of *Melosira* spp. (cells, open square), *Anabaena* spp. (filamentous colonies, solid circle), and *Microcystis aeruginosa* (colonies × 10, solid triangle) at a station near Station 3 during the last twelve years (1978 – 89). (A) Average of 5 years (1980, 82, 84, 88, 89) where an *Anabaena* bloom was not recorded. (B) Average of other 5 years (1978, 81, 83, 85, 87) where conspicuous blooms of both *Anabaena* (> 200 colinies/ml) and *Microcystis* (> 10 colonies/ml) were recorded. Data of 1979 and 1986 where the *Anabaena* bloom alone was recorded are omitted. Vertical bars for *Merosira* plots represent standard deviations × 0.25. *Melosira* spp. include *M. granulata* (the majority), *M. granulata* var. *angustissima*, *M. italica*, *M. italica* var. *tenuissima*, *M. distans*, *M. solida*, *M. varians*, and *M. japonica*. *Anabaena* spp. include *A. affinis*, *A. macrospora*, and some unidentified species. Drawn from Shiga Pref. Inst. Pub. Hlth. Environ. Sci. (1984, 85, 86, 91).

tion shifted to October, like the case of 1991. These autumnal proliferations of *Melosira* are supposedly triggered by replenishment with DIN due to nitrate-rich inflow water from the north basin in this season.

The mechanisms whereby the nitrogen economy in this basin is determined are barely understood at present, but a few factors as follows seem to be important among others. First, the quality of the epilimnetic water of the north basin which flows into the south basin tends to be depleted of DIN in late summer (Fig. 6), which seems one of the causes of N deficiency in the south basin in the same season (TEZUKA 1985). Second, some observation suggests that the efficiency of internal recycling of nitrogen through the mineralization of PON within the south basin may be reduced in summer while silicate is persistently regenerated with high efficiencies (MIYAJIMA et al., in prep.). This may be accounted for by some biological constraints. Benthic invertebrates' feeding of PON can immobilize some nitrogen but not silicate within their biomass and eventually take it out from the basin on the hatch of chironomids. Further, a significant fraction of nitrogen mineralized at the sediment surface can be lost through denitrification in anaerobic microsites whose formation is enhanced by high oxygen consumption rate in summer. Thus, the south basin seems to have an inherent tendency towards depletion of DIN. In addition, the nitrogen economy in this basin can be modified indirectly through interactions with the phosphorus cycle which is highly susceptible to human activities. For example, recent extensive loading of domestic and agricultural wastes rich in phosphate to the north basin may have stimulated primary productivity and caused depletion of DIN from the epilimnetic water that inflows to the south basin. Further, a portion of the loaded phosphate should have been, either directly or through biogeochemical pathways, trapped eventually within the oxidized layer of sediment. The trapped phosphate can be recovered into soluble form as progressive reduction of surficial sediment in warmer seasons (JENSEN & ANDERSEN 1992), which may act as an internal phosphorus source during the bloom of nitrogen-fixers (TEZUKA 1988). Thus, the behavior of benthic biota is expected to play a particularly important role in nutrient dynamics through which exerting a crucial effects on the standing stock, the growth rate, and the species composition of the phytoplanktonic community.

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