Some properties of phytoplankton dynamics in a shallow hypereutrophic lake, Lake Teganuma, in central Japan

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Abstract

Phytoplankton dynamics in a shallow hypereutrophic lake, Lake Teganuma, about 40 km NE of Tokyo, were studied over 4 years from June 1972 to November 1975. Properties of phytoplankton dynamics in such environment differed in several respects from deep eutrophic lakes. Water bloom appeard twice a year, summer and winter. Dominant species were blue-green algae such as *Microcystis*, *Oscillatoria*, *Anabaena* during the summer, and *Chlamydomonas*, *Euglena* in Winter. Chlorophyll *a* content was in a range of 140–680 mg/m^2. Light saturated photosynthetic rates were almost above 10 mg O_2/mg chl. *a* /hr (with maximum value of 24.5 mg O_2/mg chl. *a* /hr) throughout the year. Average rate of daily gross photosynthetic production of 34.8 g O_2 (13.1 g C) $/m^2$/day recorded in the present study. This value was an upper limit of values reported in natural waters, and it was quite cloes to a value of 36.4 g O_2/m^2/day which has been observed in outdoor mass cultures of *Chorella*. Mean annual gross production over 3 years was estimated as 4,190 g O_2 (1,571 g C) $/m^2$/year and this value was to be the highest so far encounterd in natural waters. Photosynthetic efficiency of radiation energy by phytoplankton was 3.28% for PHAR and this value may also be the highest in natural waters.

Introduction

During the last decade, the word "eutrophication" has usually been used in the sense of the artificial and undesirable addition of nutrients to water. In such waters, nuisance growth of phytoplankton has been frequently observed and it has brought a serious algal trouble. As has been discussed by Vollenweider (1968) the eutrophication may stimulate the biological prodoction at the early stage of a long–term enrichment process, but with the advance of the process, highly enriched water may have brought undesirable cricumstance for living organisms. Excessive nutrients in the later stage of eutrophication may lead to the process of etrophication to that of destrophication. The biological events occurring under the pressure of such environment are of great interest from ecophysiological view point. The present researches were undertaken to make clear the physico–chemical nature of so–called hypereutrophic lake (Wetzel, 1975) and the biological responses, especially phytoplankton dynamics, in that environment.

Methods

Field researches were made at Lake Teganuma, which is located in central Japan, about 40 km northeast of Tokyo. The elevation is approximately 3 m. The lake has a surface area of 12 km^2 and a volume of 4×10^6 m^3 with a maximum depth of 2.9 m. The lake divided into two basins, the western basin and the eastern basin, and connected with River Tone by an aqueduct at the eastern end. The lake received minor drainage from two steams, River Ōhori and River Ōtsu at the western basin.

Several researches have been made on this lake. Nakano (1911) and Hogetsu (1948) surveyed the distribution of aquatic macrophytes. According to their reports, about 35 years ago massive invasion of hydrophytes and helophytes into the lake center had been observed. About 25 years ago Ichimura (1958) measured 9–55mg O_2/mg chl./day of phytoplankton photosynthesis, wihch were comparable to those of mesotrophic lakes.

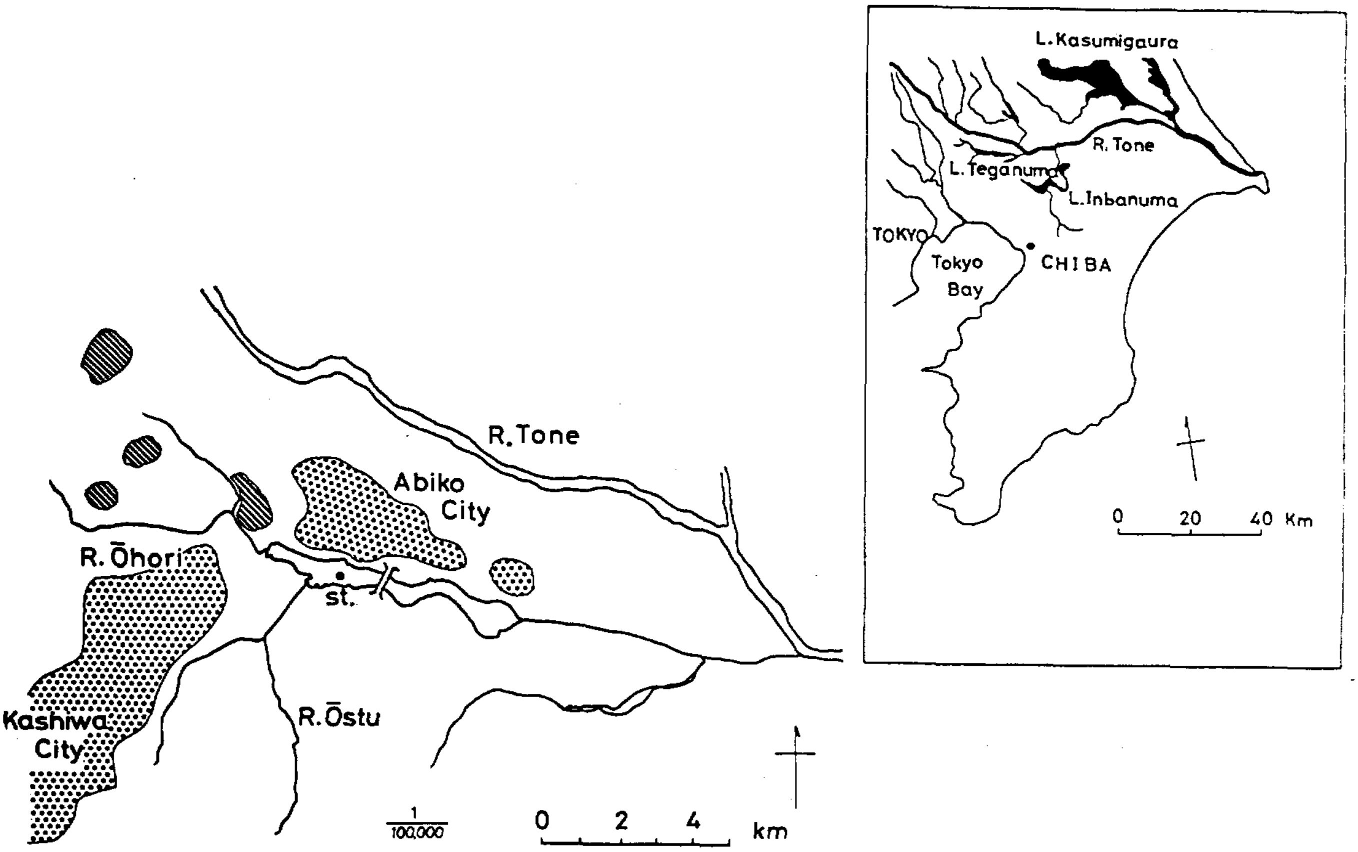

Figure 1: Map of the basin of Lake Teganuma showing the major geological region and the position of regular sampling station. The main inflows are also shown together with surrounding residential (⁙) and manufacturing (▨) quarters.

During the last decade, surrounding area of this lake has been extensively exploited and environmental disturbance associated with rapid expansion of population has occurred. The population increased from about 234 thousand in 1961 to about 575 thousand in 1975. The watershed is heavily populated, urbanization and industrialization being especially advanced it the western harf (Fig.1). Large amount of nutrients coming from domestic sewage and industrial drainage have accelerated the eutropication of this lake, and the frequent development of dense bloom of blue-green algae has resulted in remarkable reduction of transparency. At present, macrophytes have completely vanished from this lake.

After a preliminary survey, a station was selected at the center of western basin of lake for regular sampling. Samplings were made at monthly or sometimes bi-weekly intervals, over 4 years from June 1972 to November 1975. Waters were taken from various depths with a siphon between 09 : 00 and 10 : 00. Water temperature was measured by means of a thermister-thermometer (Tohodentan, ET-3). At aliquot of each water sample was immediately fixed for measuring dissoloved oxygen and was determined by the Winker method. A portion of sampled water was used for determination of phytoplankton biomass and nutrients. Analysis was in most cases completed within 4 hrs after sampling. For the determination of chlorophylls and particulate organic matter, water samples were filtered through Whatman grass fiber filters (GF/C) precombusted at 500 °C for 2 hrs and the residues retained on the filters were used as materials. Chlorophyll *a* and pheopigments were measured spectrophotometrically following the procedure of SCOR-UNESCO (1966) and Lorenzen (1967) . Particulate organic carbon and nitrogen were determined by a carbon-nitrogen analyzer (Yanagimoto, CHN-corder, MT-2) . Phycocyanin index (P.I.) was used for assessing the presence of blue-green alage in water. For this purpose, a certain volume of water sample was filterd through a glass fiber filter and light absorbance was measured for filtered wet filter at 620 nm, 650 nm and 675 nm using the double beam type spectrophotometer (Hitachi, UV-200) . The index was calculated by

$$\mathrm{P.I.} = (D_{620} - D_{650}) / (D_{675} - D_{650})$$

where D_{620} is optical density of phycocyanin at 620 nm, D_{675} is that of chlorophyll *a* at 675 nm, and D_{650} is reference.

Analysis of nutrients was made for the filtered waters which were diluted with distilled water depending on the concentrations of nutrients. Nutrients measured were NH_3-N, NO_2-N, NO_3-N and PO_4-P. Ammonia-nitrogen was measured by the indophenol method (Sagi, 1966) , and nitrate-nitrogen was determined by the modified cadomium-copper method. Final concentration of NO_3-N was determined by substracting the value of nitrite from that of nitrate which gives the sum of nitrite and nitrate.

Phosphate-phosphorus was measured by the procedure recommended by Murphy and Riley (1962).

Photosynthesis of phytoplankton was measured by the ordinary dark and light bottel method using the Winkler technique. In the laboratory experiment, the samples in glass bottles were incubated in a water bath at a constant temperature under various light intensities. *In situ* measurements of photosynthesis were made at monthly or bi-weekly intervals at the center of the lake. The water samples were collected from various depths and the *in situ* incubation lasted for 4 hours in the daytime.

Results

〈1〉 *Physico-chemical properties of hypereutrophic water*

The light penetrating into the water column diminished rapidly with the increase of depth and reached 1% of the surface light intensity at the depths 0.5-1 m throughout the year. If the light intensity at the daily compensation depth is assumed to be 1% of the surface illumination, it is inferred that the euphotic zone is at a depth of about 1 m over the study period and decreased to 0.5 m during the summer phytoplankton bloom, except for one spell in May when the species composition of phytoplankton population was altering.

Seasonal changes in the temperature of the surface and bottom waters are shown in Fig. 2-A. Because of shallow basin the thermal difference between the surface and bottom was very minor, since the lake surface is usually exposed to the wind prevailing in the afternoon. The temperature began to increase in April and reached a maximum of 30 °C in August every year, then decreased to below 10 °C in December.

Seasonal variations of oxygen concontration in water are shown in Fig. 2-B. The highest value of oxygen saturation occurred in summer from July to September and it reaced 200% both in 1973 and 1975, and 280% in 1974. Oxygen was much lower during the winter from December to February. During the summer of the study period in

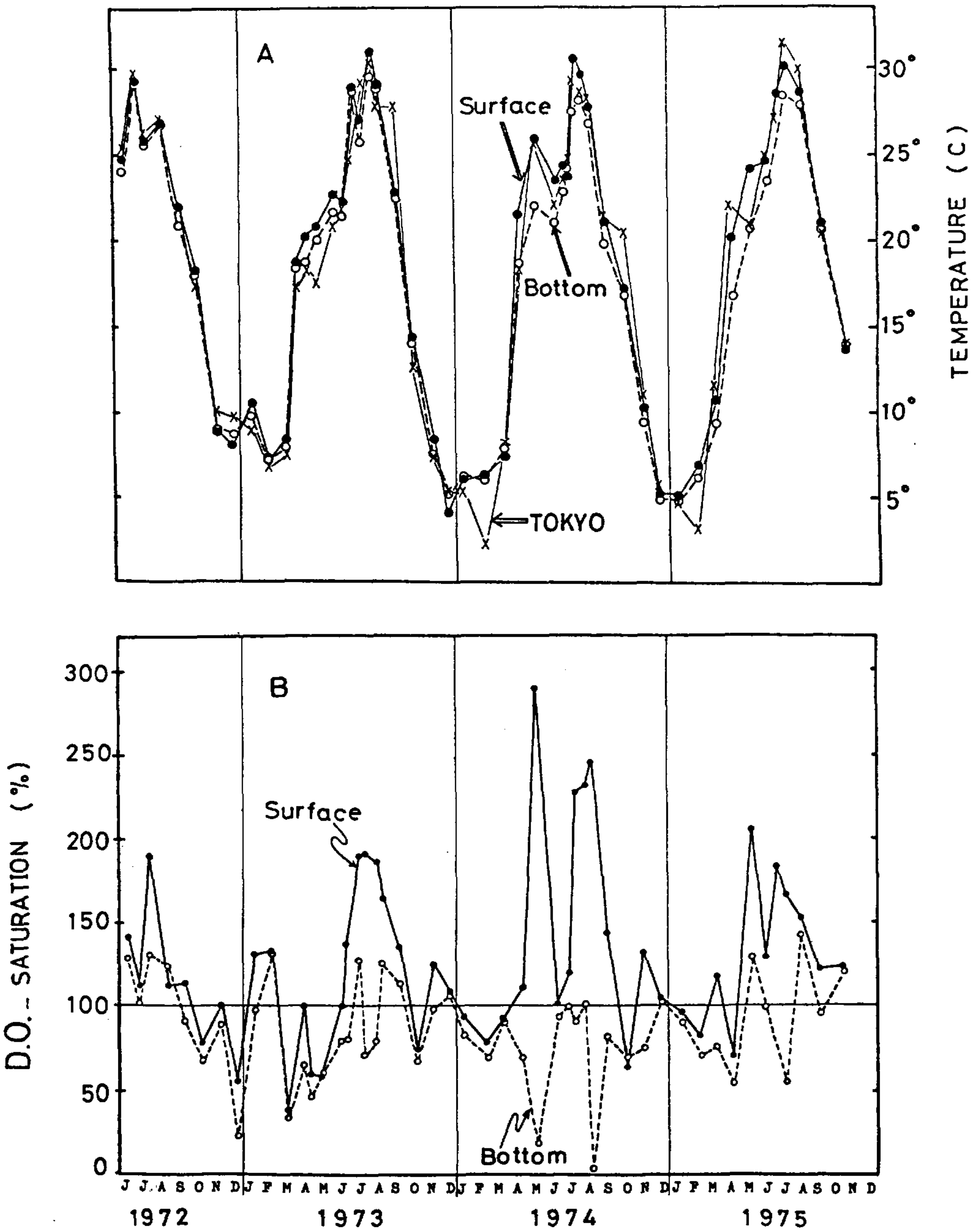

Figure 2: Seasonal changes in temperature of the surface and bottom waters and of Tokyo (A), and oxygen content (B) measured at 10:00 during the period from June 1972 to November 1975.

1974 twice the oxygen content below physiologically critical level of 1mg/l in the bottom water.

Seasonal changes in NH_3-N, NO_2-N, NO_3-N and PO_4-P concentrations are shown

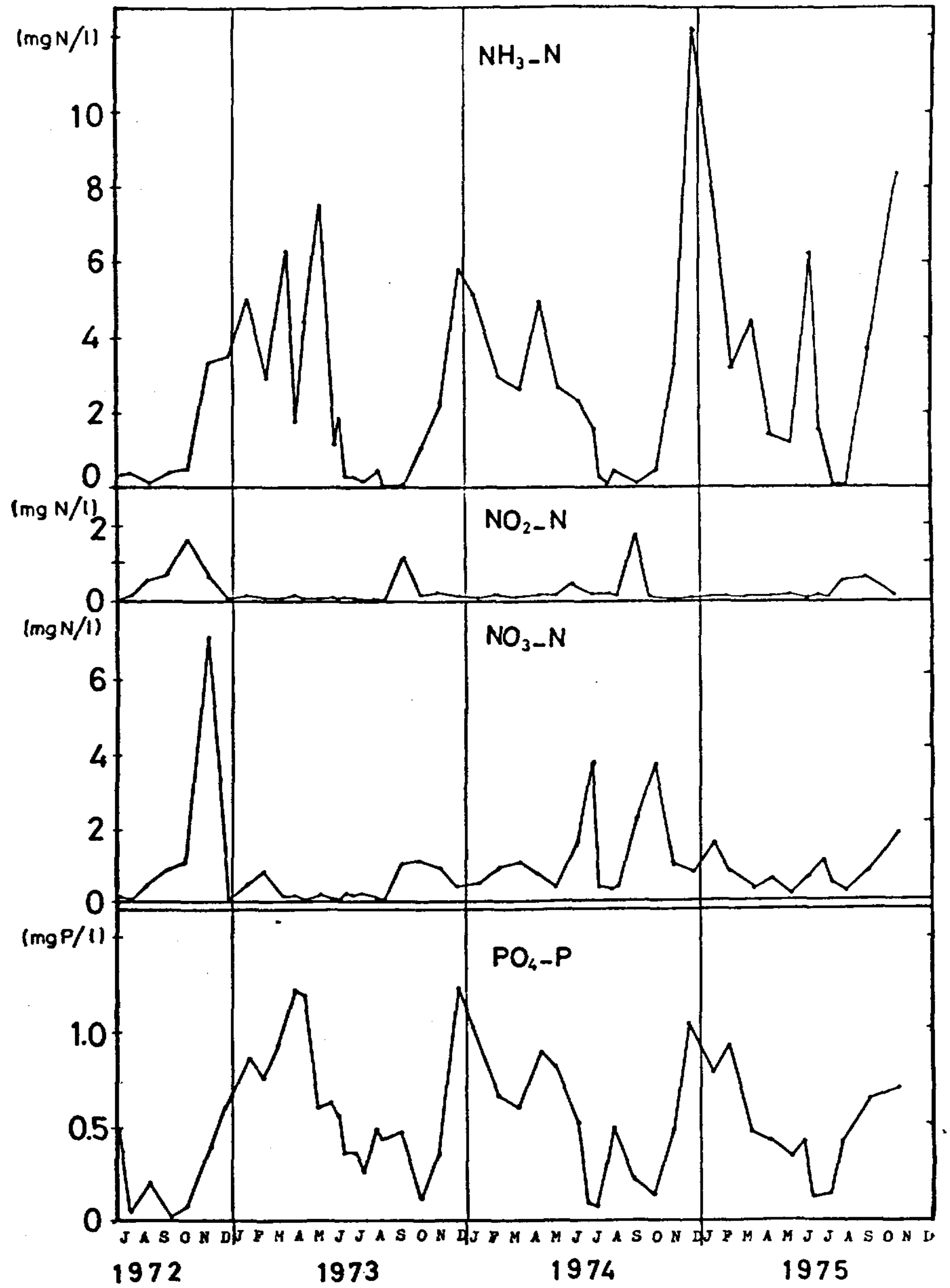

Figure 3: Seasonal changes in the concentrations (mg/1) of NH_3–N, NO_2–N, NO_3–N and PO_4–P in the surface water.

in Fig. 3. The characteristic of annual changes in inorganic nitrogen in this lake were represented by a noticeable change in ammonia-nitrogen. There was usually a rapid decline from 5–8mg NH_3-N/1 in late spring to a minimum of 0.2–0.5mg NH_3-N/1 in summer. The highest values of 6–12mg NH_3-N/1 were measured during the winter. Corresponding highest values of nitrate-nitrogen were 7mg NO_3-N/1 in 1972 and 3.5mg NO_3-N/1 in 1974, respectively. Phosphate-phosphorus varied remarkably from

0.1–1.2mg PO_4-P/1 in a year. The concontration of PO_4-P/1 was highest in winter and it decreased rapidly during the spring phytoplankton outburst and reached about 0.1mg PO_4-P/1 during the period of summer phytoplankton bloom. Immediately after the summer bloom, PO_4-P began to increase and reached winter maximum of about 1mg PO_4-P/1. It should be stressed that an extraordinary high concentration of NH_3-N, NO_3-N and PO_4-P persisted throughout the year and even the lower concentration measured at the period of dense bloom was comparable to those found in ordinary eutrophic lakes.

〈2〉 *Species composition of phytoplankton population*

Seasonal changes in species composition of phytoplankton population are illusrated in Fig. 4, where individual number of species is indicated by relative frequency. Main families observed belonged to Cyanophyceae, Bacillariophycae, Euglenophyceae and Chlorophyceae. Component genera altered regularly in their occupation

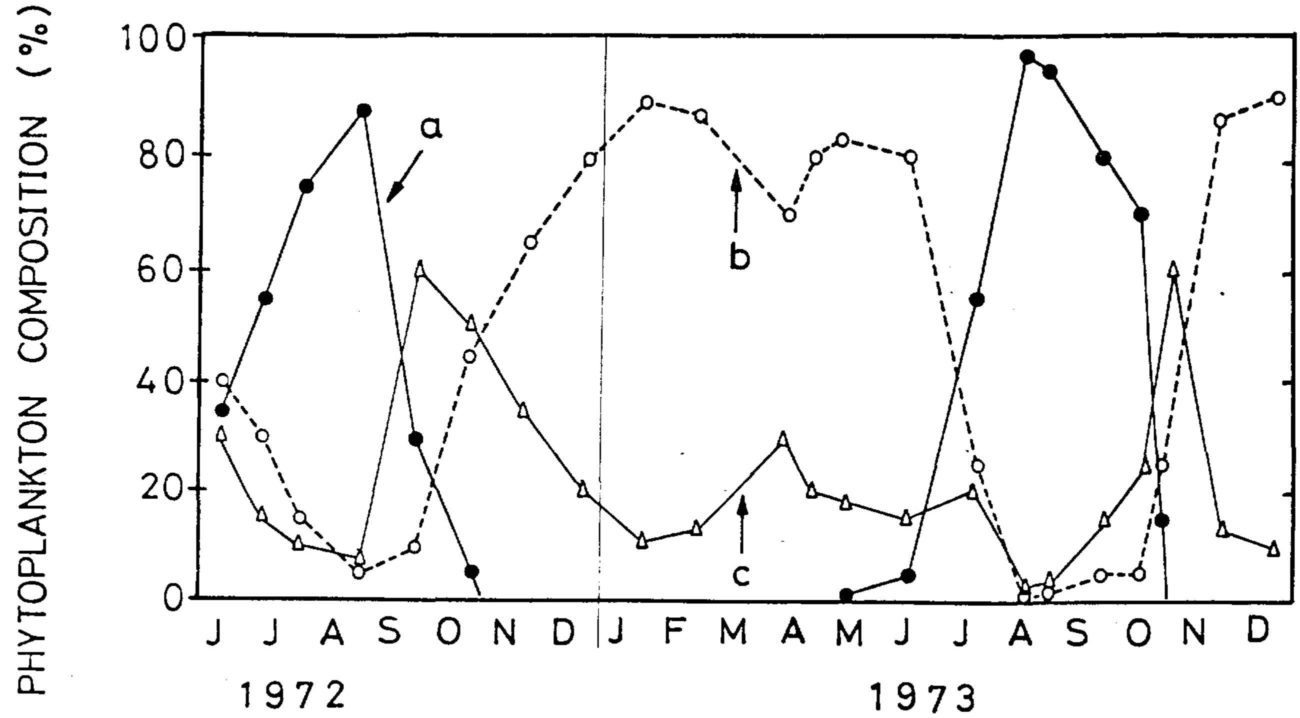

Figure 4: Seasonal changes in the relative abundance of four algal groups measured in terms of individual number. a: Cyanophyceae, b: Euglenophyceae and Chlorophyceae, c: Bacillariophyceae

with the progress of season. Blue-green algae prevailed during the summer bloom but their position was replaced by diatoms in autumn.

Cell numbers of Euglenoid were relatively few,thereby the monospecific phytoplankton assemblage was frequently encounterd in successive months. This situation was indicated by a shift order on species as seen in Fig. 5. Species of the summer bloom were *Microcystis aeruginosa*, *Oscillatoria tenuis*, *O. raeborskii*, *Anabaena spiroides*, and *Spirulina maxima*. A sequence diagram of alternation of species is as follows; *Microcystis* (early summer) —— *Oscillatoria*, *Spirulina* (mid summer) —— *Anabaena* (late summer) . Dominant species in late summer and autumn were diatoms such as *Cyclotella menqhiana*, *Melosira granulata*. However, a large number of blue-green algae still remained.

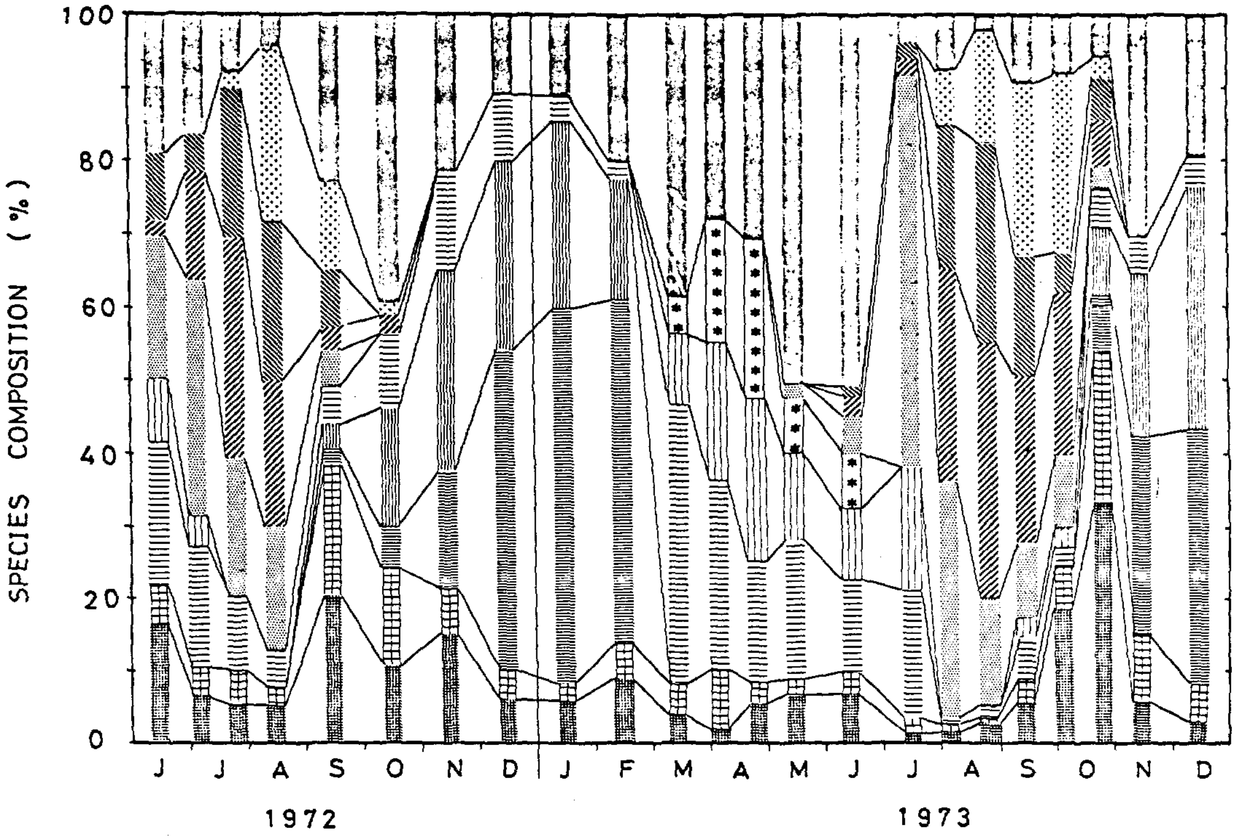

Figure 5: Seasonal changes in the relative abundance of the species measured in terms of individual number. Main species are indicated as follows: Cyanophyceae: ▒ Microcystis, ▨ Oscillatoria, ▧ Spirullina and ⁘ Anabaena; Chlorophyceae: ☰ Scenedesmus, |||| Pediastrum, ✱ Oocystis and ≣ Chlamydomonas: ‖‖ Euglena; Bacillariophyceae: ▦ Cyclotella and ⊞ Melosira; ▩ Others.

It is noticeable that a dense algal bloom comparable to summer bloom was formed in winter. Dominant species during the winter bloom were *Euglena geniculata*, *Chlamydomonas*, spp., and serveral species of Dinoflagellates. These algae have been well known as a shade form. In spring, phytoplankton was the lowest in biomass but a considerable number of species was observed. They were mostly green algae such as *Pediastrum*, *Oöcystis*, and *Scenedesmus* etc. Blue-green algae which most frequently formed water bloom in this lake were *Microcystis aeruginosa*, *Oscillatoria rubescens* and *Anabaena flosaquae*. Especially, *Oscillatoria rubescens* is known as an indicator of the onset of polyeutrophic lake (Vollenweider, 1968).

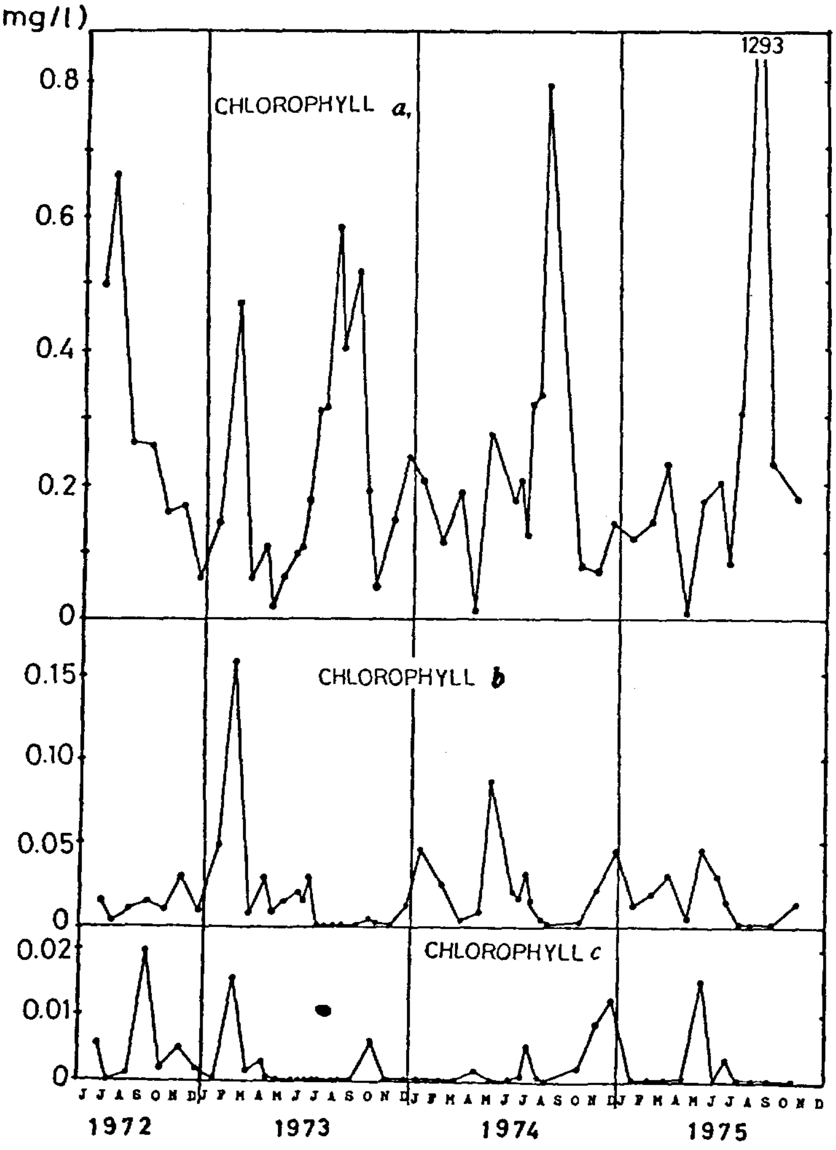

Figure 6: Seasonal changes in the concentrations (mg/l) of chlorophyll *a*, *b* and *c* measured by the method of SCOR-UNESCO (1966).

〈3〉 *Phytoplankton dynamics*

〈3, 1〉 *Standing crop of phytoplankton* : The standing crop of phytoplankton measured by chlorophyll *a*, *b* and *c* is shown in Fig. 6, where each value is the average of the whole water column. The high concentrations of 0.6–1.0mg/l were measured for chorophyll *a* at the beginning of the summer outburst and subsequently dropped rapidly to low value of 0.05mg/l in October. In November, chlorophyll *a* began to increase again and reached a level as high as 0.3mg/l in December and January. This value was comparable to those reported in ordinaly eutrophic lake at the time of outburst in late spring. Considerably lower values less than 0.01mg/l were measured in March when the alternation of algal species occurred in plankton population.

Seasonal changes of chlorophyll *b* and *c* corresponded with that of species composition. Chlorophyll *b* was most abundant in winter and early summer, when green algae and euglenoid algae were vigorously growing. Large values of chlorophyll *c*

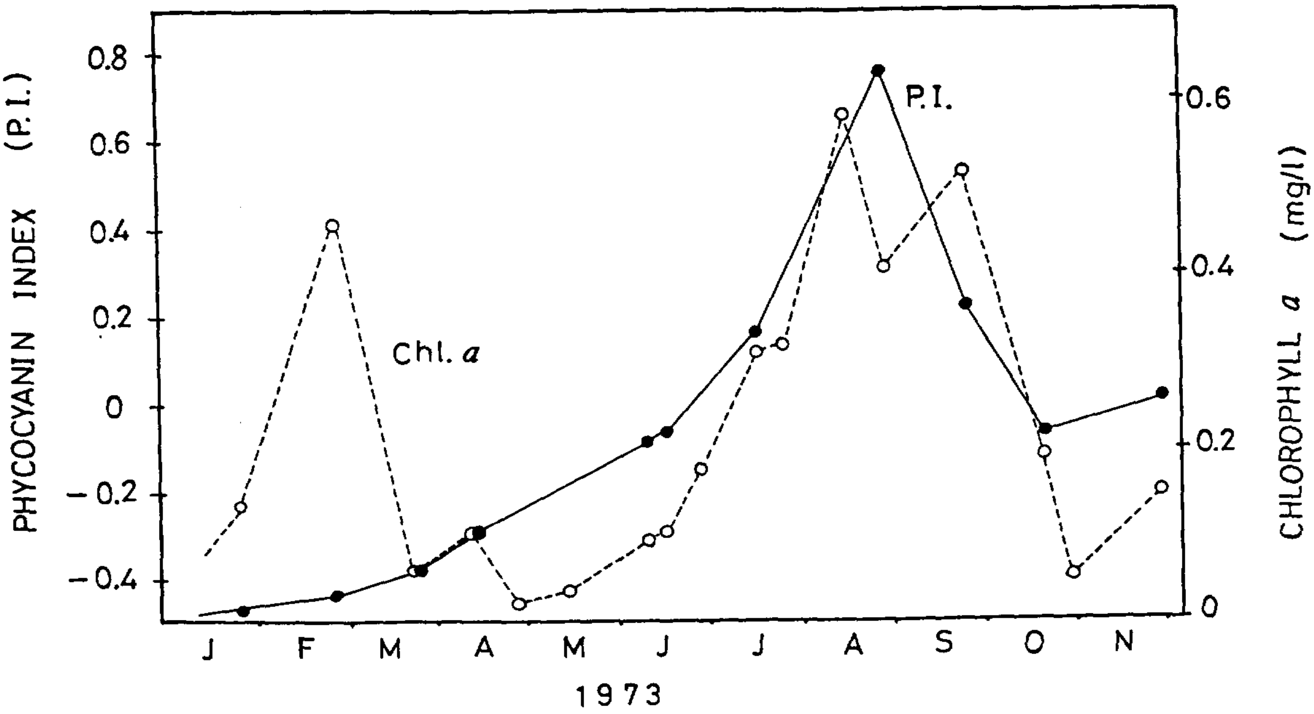

Figure 7: Seasonal changes in index of phycocyanin contents and chlorophyll *a* concentration in the surface water.

were measured in autumn, when diatoms prevailed in the lake.

Seasonal changes of phycocyanin index (P.I.) in the surface water are illusrated in Fig. 7, together with the changes of chlorophyll *a* concentration. The high values of 0.4–0.8 were obtained during the summer bloom and the low values of −0.2– −0.4 in winter. Dominant species were *Oscillatoria* in summer, and *Euglena* and *Chlamydomonas* in winter. The values of P.I. for unialgal cultures were −0.77 in *Chlorella*, −0.68 in *Scenedesmus*, +0.68 in *Microcystis* and +1.71 in *Oscillatoria*. Therefore, the P.I. values in summer accorded fairly well those obtained in monospecies of blue-green algae and those in winter were of the same order to those in green algal cultures. From these results, pigment compositions in the water may be used as an index for

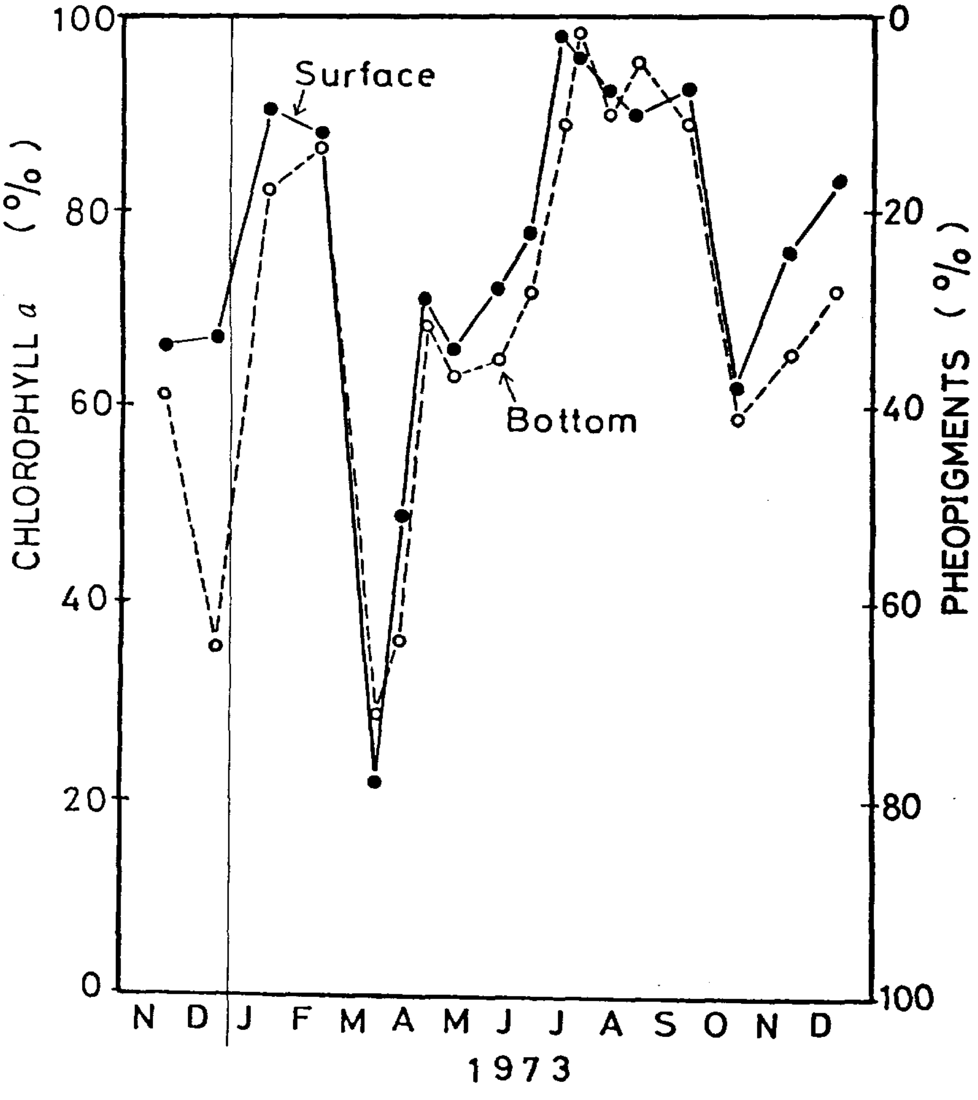

Figure 8: Seasonal changes in the percentage of chlorophyll *a* and pheopigments, the total amount of chlorophylls (Chl. *a* + pheopigments), in the surface and bottom waters.

species diversity of phytoplankton assemblage.

Concentration of chlorophyll *a* is sometimes overestimated by the SCOR-UNESCO method due to association of degraded chlorophylls. For this reason, the method of Lorenzen (1967) was employed to measure separately chorophyll *a* and pheopigments. Concentrations of both pigments are given in Fig.8. Chlorophyll *a* varied from 20 to 98% of the total amount of chlorophylls (chlophyll *a* + pheopigments) . Large value of chorophyll *a* was measured in dense algal bloom of summer and winter. Pheopigments wer relatively large in spring and autumn when the replacement of algal species occurred in phytoplankton population. If the amount of chlorophyll *a* measured by this method is regarded as that in living phytoplankton,

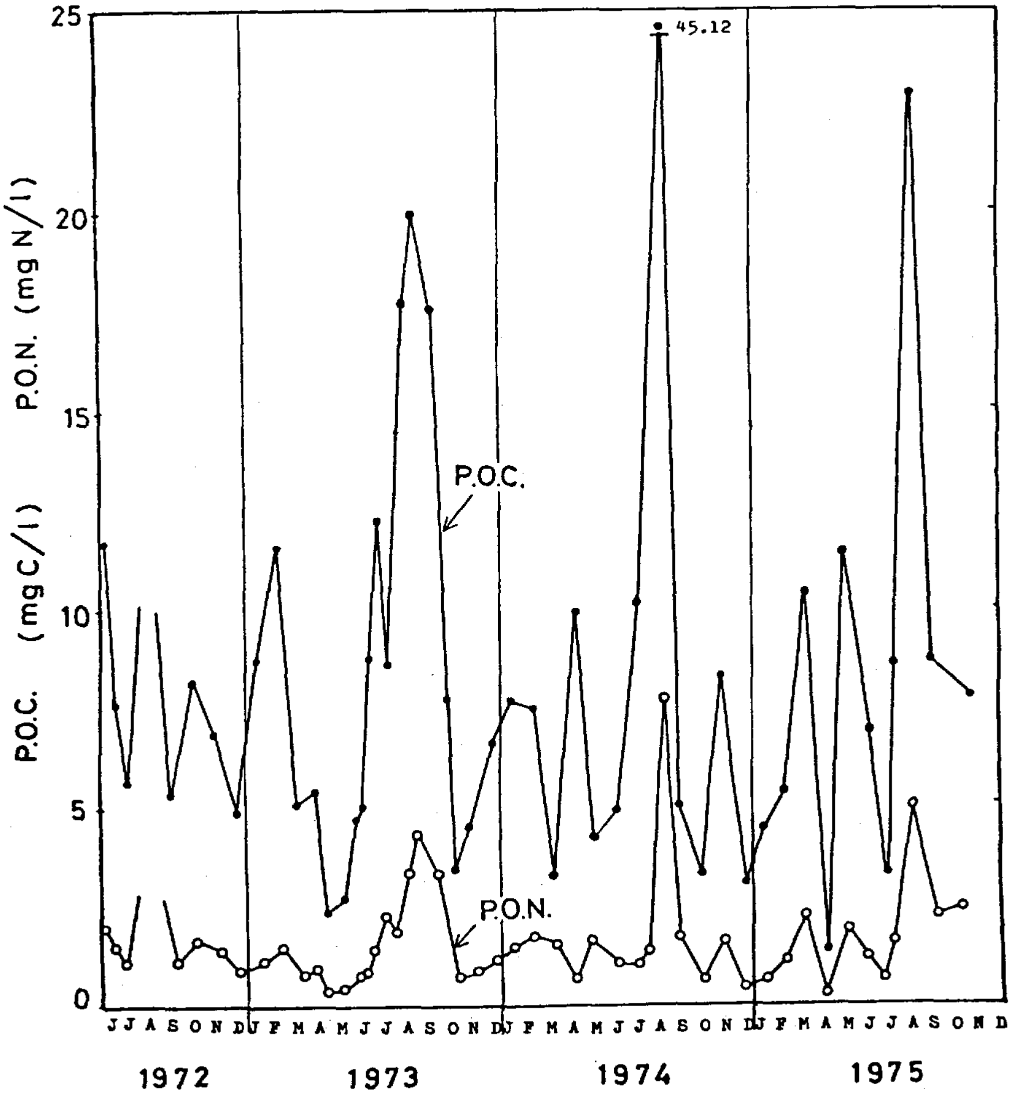

Figure 9: Seasonal changes in the concentration of particulate organic carbon (POC) and nitrogen (PON) of the surface water.

phytoplankton population in Lake Teganuma is mostly active throughout the year.

⟨3, 2⟩ *Particulate Organic matter* : As the biomass of microorganisms, particulate organic carbon (POC) and nitrogen (PON) were measured. The results are shown in Fig. 9. The amounts of POC and PON were relatively small in spring and extremely large in summer. A range of annual variation was 4–10mg/1 for POC and 0.5–3mg/1 for PON. The total content of both materials in the entire water column varied from 28 to 39.2 g/m^2 for POC and from 0.48 to 8 g/m^2 for PON. Such values were extremely high compared with those in typical eutrophic likes. The POC/PON ratio for the surface and bottom wateres fluctuated between 4 and 7, and it was almost identical to that obtained in unialgal cultures. The POC/PON ratio in unialgal cultures at log-phase was about 7 for green algae (*Chlorella*, 7.4; *Scenedesmus*, 5.1) , and 5.4 for blue-green algae (*Microcystis*, 5.9; *Oscillatoria*, 5.1) . Thus, it will be inferred that the nutrient conditions of Lake Teganuma are quite similar to that of the enriched culture medium. Furthermore, there are linear relationships between chlorophyll *a* and POC concentrations, and between chlorophyll *a* and PON concentrations with a significant correlation coefficient of 0.705 for the former and 0.681 for the latter. Thus, phytoplankton seems to be main contributor of particulate matter in this lake.

⟨3, 3⟩ *Photosynthetic properties of phytoplankton* : Light-dependency of photosynthesis is usually examined by the light-photosynthesis curve. To examine the characters of light-photosynthesis curve, water samples were taken from several depths and photosythesis was measured by the tank or the *in situ* method. The light-photosynthesis curves in Fig. 10–A were obtained by the *in situ* method on 19th July, 1973. The number of phytoplankton population consisted nearly 60% of blue-green algae (mainly *Microcystis*) and about 40% of green algae (*Scenedesmus*, *Pediastrum*) . The curve obtained in the surface water was fairly similar to that of 50 cm depth but photo-inhibition, (Talling, 1957) did not occur even at high ligh intensity of 30 klux. The photosynthetic rate was higher in the water of 50 cm depth than that of the sur-

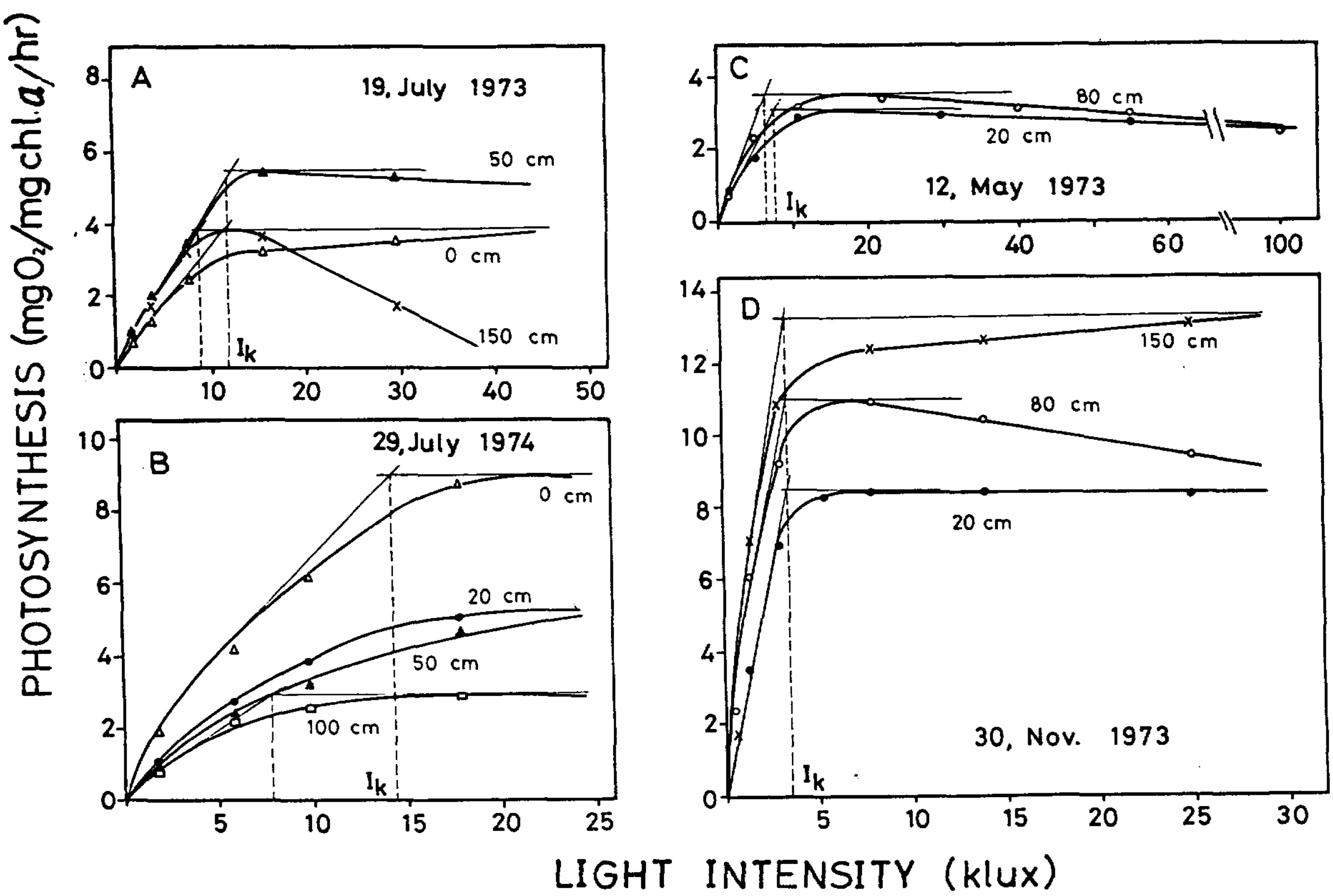

Figure 10: Light-potosynthesis curves of water samples taken from various depths. Measurements were made (A) *in situ* on 19, July, 1973, (B) in laboratory on 29, July, 1974, (C) *in situ* on 12, May, 1973 and (D) 30, November, 1973.

face water. The water from 150 cm showed a considerable photo-inhibition at a light intensity of 16 klux. Regardless of difference in light-photosynthesis curves, I_k (Talling, 1957) was almost 12 klux in every sample. Fig. 10–B shows the curves for the samples on 29th July 1974 measured by the tank method. Dominant species of phytoplankton population were blue-green algae. Photo-inhibition was not observed even at 18 klux in all samples. The value of I_K was higher than 15klux in the surface sample, while about 8 klux in the sample from 100 cm depth. Further, the photosynthetic capacity of the surface water was much higher than that of the sample taken from 100 cm depth.

Fig. 10–C and 10–D show the light-photosynthesis curves obtained by the *in situ* method in May and November 1973, respectively. Phytoplankton population in May

consisted of *Scenedesmus*, *Nitzchia*, and *Fragilaria*. The shapes of the curves were identical to each other. The photosynthetic of 3mg O_2/mg chl. *a*/hr and I_k of 5 klux were relatively low compared with thoes in summer samples.

Photo-inhibition occurred to some extent at light intensities of above 20 klux. The water samples in November were dominated *Euglena* and *Chlamydomonas*. Photosynthesis was saturated at near 5 klux and the value of I_k was about 3 klux. The light-saturated photosynthetic rate was about 10mg O_2/ mg chl. *a*/hr and photo-inhibition did not occur except for the water sample from 80 cm depth.

〈3, 4〉 *Seasonal variations of photosythetic activity* : The photosynthetic rate of phytoplankton showed a cosiderable seasonal variation. The results obtained by the *in situ* method during 1972–1975 are shown in Fig. 11 were photosynthetic rates at the surface and light saturated depth are presented. Photosynthesis began to increase in April and reached a large summer value and thereafter decreased during the summer.

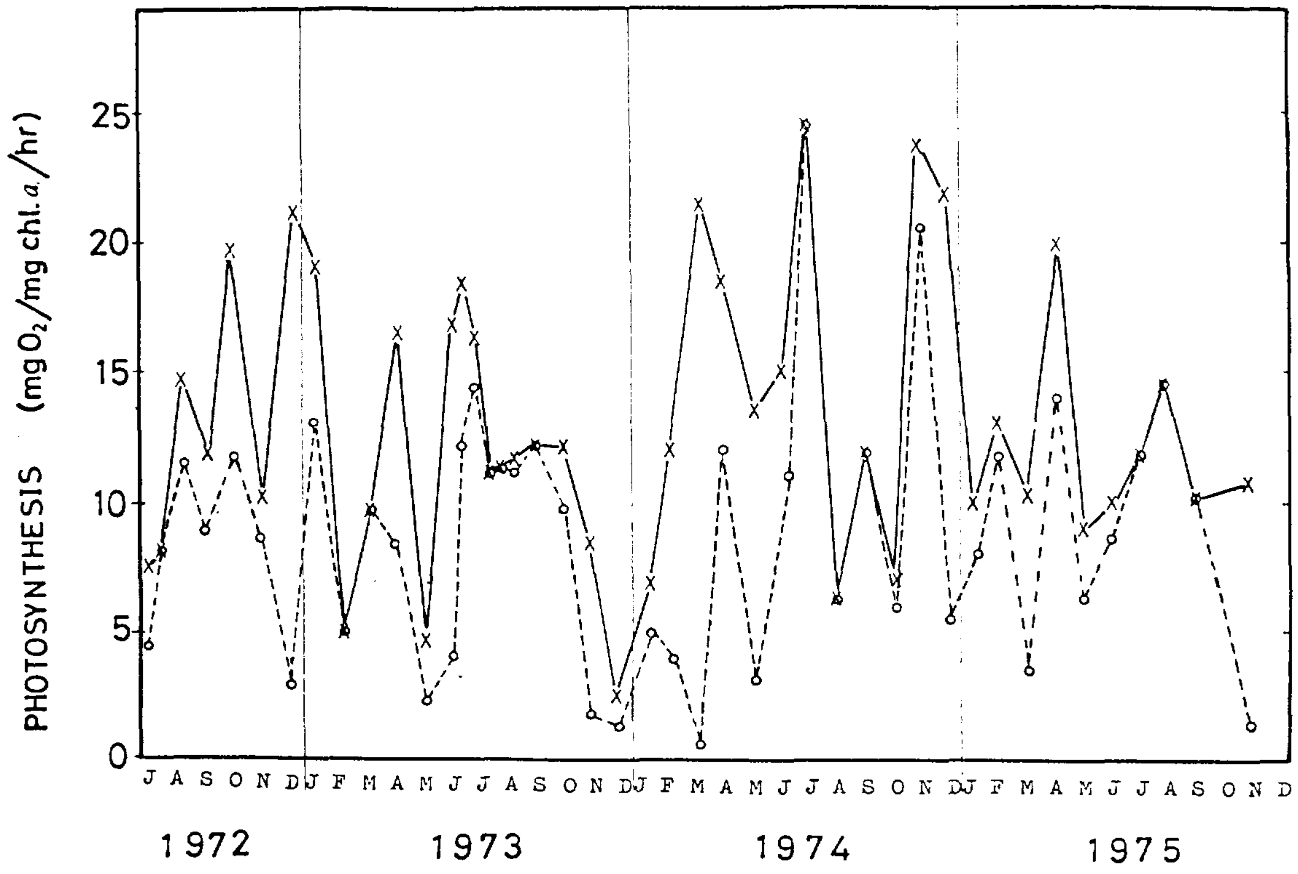

Figure 11: Seasonal changes in the *in situ* photosynthetic acivity of phytoplankton at the surface (--O--) and the layer of photosynthetic maximum (—×—).

It, however, increased in autumn again and reached a large autumn value. Especially, the intensive photosynthetic rate of 20mg O_2/mg chl. *a* /hr was measured in spring, midsummer and late autumn. The lowest rate of 2–3mg O_2/mg chl. *a* /hr was observed in March and winter. Maximum photosynthetic rate reported in eutrophic lakes are usually between 8 and 12 mg O_2/mg chl. *a* /hr. Therefore, the value of 20mg O_2/mg chl. *a* /hr was extremely large and it has never been reported in Japanese lakes.

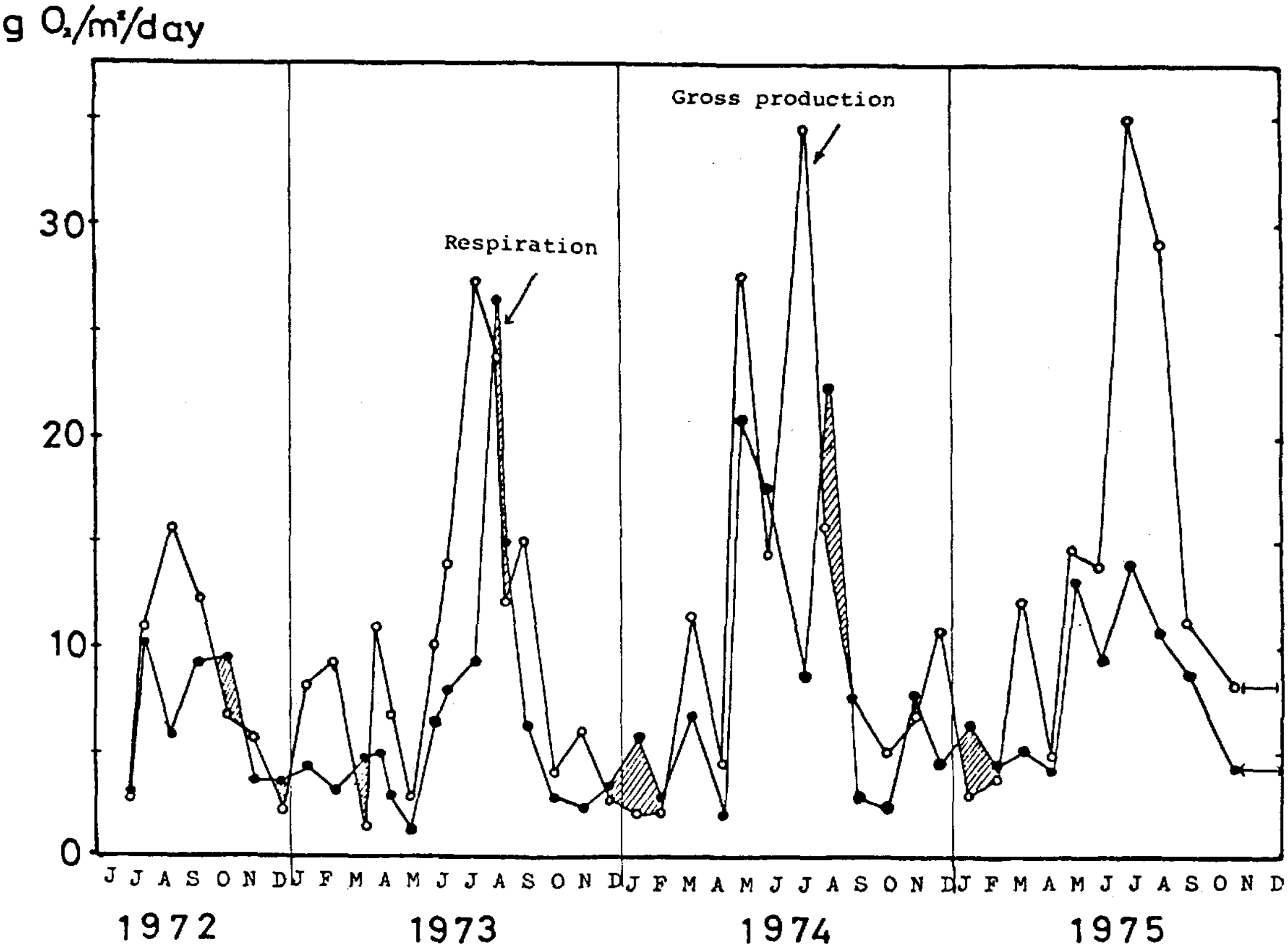

Figure 12: Seasonal changes in daily gross production (○) and respiration (●). Bias parts indicate microbial respiration exceeded daily photosynthetic production.

〈3,5〉 *Seasonal variations of primary production* : By integrating the depth-photosynthesis-respriation profiles, the total net production and respiration were calculated. Then the gross production was presented by adding the restration to the net production. Results of these calculations are shown in Fig. 12. Seasonal variation of gross production and respiration were observed with a range of 1.5–34.8 g O_2/m^2/day and with a range of 1.2–33.5 g O_2/m^2/day, respectively. Under low light and low temperature, the gross production was in general low in winter but the value of above 10.0 O_2/m^2/day was mesured in 1973 and 1974, when winter bloom appeard. The highest values of 15.0–35.0 g O_2/m^2/day were common in summer. On the other hand, rate of microbial respiration was low during the period of autumn to winter months and high values were measured in summer. Large amounts of microbial respiration exceeding the daily photosynthetic production were frequently found in winter and just after the period of dense algal bloom.

Table 1: Annual primary production, photosynthetic active radiation (PHAR) and photosynthetic efficiency of radiation estimated for 1973–1975.

YEAR	Gross production		Net production		Photosynthetic active radiation (PHAR)	Photosynthetic efficiency of radiation	
	gO_2/m^2/year (gC/m^2/year)	cal/m^2/year x10^6	gO_2/m^2/year (gC/m^2/year)	cal/m^2/year x10^6	cal/m^2/year x10^6	gross %	net %
1973	3611 (1354)	12.93	1335 (501)	4.78	436	2.97	1.10
1974	4220 (1583)	15.11	993 (373)	3.56	418	3.62	0.85
1975	4735 (1776)	16.96	2028 (761)	7.26	561	3.02	1.29
mean	4190 (1571)	15.00	1452 (545)	5.20	472	3.20	1.08

Annual rate of primary production was calculated by using the data in Fig. 12 and summerized in Table 1. Total annual radiation and photosynthetic efficiency of solar energy are also presented. Here, it was assumed that the amount of photosynthetically active radiation (PHAR: 400–700 nm) was 46% of total incident radiation on the water surface (Talling, 1960) and the energy used for photosythesis is 9.55 kcal per gram carbon. The daily incident radiation used in the present calculation was that recorded by a pyranometer placed in the campus of the University College of Meteorology near the lake.

As shown as in Table 1, mean annual net production and gross production over 3 years were estimated at 1452 g O_2 (545 g C) /m^2/year and 4190 g O_2 (1571 g C) /m^2/year, respectively. The annual efficiency of photosynthesis in terms of primary production varied from 2.97 to 3.62% with a mean of 3.2%. The daily efficiency varied from 0.37% in winter to 5.0% in summer, although some exceptional values were measured. On the other hand, the annual efficiency of the net primary production varied between 0.85% and 1.29% with a mean of 1.08%.

Discussion

Vollenweider (1968) stated that when assimilable phosphorus and nitrogen in spring exceeded 0.01mg P/1 and 0.2–0.3mg N/1 respectively, water bloom appeared in summer. Winter maxima of assimilable phosphorus and nitrogen in Lake Teganuma are currently in excess of 1.3mg P/1 and 10mg N/1. In this respect Lake Teganuma is a shallow and typical culturally polyeutrophic lake. In such an environment the phytoplankton dynamics differed in several respects from those in deep eutrophic lakes.

The dominant species of phytoplankton population in this lake in 1953 was *Melosira italica* in summer which is an indicator plant of oligo-mesotrophic lakes (Ichimura, 1958). After 20 years, blue-green algae such as *Microcystis*, *Oscillatoria*, *Anabaena* and *Spirulina* dominatid in summer, and *Chlamydomonas* and *Euglena* in winter. Rawson (1956) described these algae as indicator plants of eutrophic and/or polyeutrophic lakes.

A range of chlorophyll *a* content in eutrophic lakes is quoted by Vollenweider (1968) as 20–140mg/m^2. Talling *et al.* (1973) reported a range of 179–325mg/m^2 in the eutrophic lakes in Ethiopia, and Bindloss (1974) found an upper limit of

456mg/m^2 in Loch Leven. Further, Gelin (1975) reported that chlorophyll *a* content in the euphotic zone of eutrophic lake, Lake Vombsjön varied from 28 to 297mg/m^2 during a year. Chlorophyll *a* concentration in Lake Teganuma was in a range of 140–680mg/m^2 in almost seasons. These high values are almost identical to the theoretical maximum values of 300–800mg chl. *a* /m^2 proposed by Steeman Nielsen (1957, 1962) but fairly lower than 1 g chl. *a* /m^2 suggested by Gessner (1949).

A luxuriant bloom of blue-green algae accompanied with high oxygen saturation in water and especially a saturation of 250–290% occurred during the summer. Jonasson *et al.* (1974) observed 148% oxygen saturation in eutrophic lake, Lake Esrom in spring. Gelin (1975) also reported that in eutrophic lake, Lake Vombsjön, Sweden, the highest value of 200% saturation occurred in the summer maxima of phytoplankton abundance. In Lake Teganuma oxygen saturations exceeding 200% were common and persisted for long period.

Causal factors for high chlorophyll concentration in Lake Teganuma are due to interaction of water circulation promoted by wind and continuous internal and external nutrient supply. Since Lake Teganuma is exposed regularly to wind prevailing in the afternoon, the water is usually circulated completely and becomes homogeneous. Thus phytoplankton in the aphotic zone may come up daily to the surface layer and the whole circulation of water must give a beneficial nutrient condition for phytoplankton in utilizing available nutrient in the bottom layer.

The rate of photosynthesis at light saturation is a good index of photosynthetic activity and it is also widely used for assessment of the fertility of water. Ichimura (1968) stated that the photosynthetic rate of phytoplankton in lakes are 5–16mg O_2/mg chl. *a* /hr in mesotrophic lakes and 0.3–3mg O_2/mg chl. *a* /hr in oligotrophic lakes. Malon (1971) employed the assimilation number as a possible indicator of nutrient defficiency and considered the values of above 8mg O_2 to be eutrophic. The assimilation number in Lake Teganuma is almost above 10mg O_2/mg chl. *a* /hr (with the maximum value of 24.5mg O_2/mg chl. *a*/hr) throughout the year.

Daily gross photosynthetic production of 34.8 g O_2 (13.1 g C)/m^2 was recorded in the present study. This is one of the highest values reported in natural waters. Of the 35 lakes in Europe and North America listed by Vollenweider (1968), only five lakes showed a value of above 10.0 g O_2 (3.8 g C)/m^2/day. Melack and Kilham (1971) reported 34 g O_2/m^2/day in Lake Nakuru, Africa. Bindloss (1972) measured the highest value of 21.0 g O_2 (7.9 g C)/m^2/day in Loch Leven. The maximum net production in Lake Teganuma was quite similar to a value of 36.5 g O_2/m^2/day which has been observed in outdoor mass culture of *Chlorella* (Tamiya, 1957). Vollenweider (1968) estimated the theoretical upper limit of daily gross production to be 10–20 g O_2/m^2/day. The annual mean daily gross production of 11.0 g O_2/m^2/day measured in Lake Teganuma is higher than that of any of "polytrophic lakes" listed by Vollenweider (1968).

In Lake Teganuma, mean annual gross production over 3 years was estimated as 4,190 g O_2 (1,571 g C)/m^2/year and this value can also be considered to be the highest so far encountered in natural waters. For example, annual production in dimictic eutrophic lake, Lake Erken, was 240 g C/m^2 (Rodhe, 1958). On the other hand, annual productions in unstratified lakes are reported to be 785 g C/m^2 in Loch Leven (Bindloss, 1974), 525 g C/m^2 in Lake Vombsjön (Gelin, 1975) and 799 g C/m^2 in Lake Suwa (Sakamoto *et al.*, 1975).

Photosynthetic efficiency of PHAR by phytoplankton population is generally much lower than that of terrestrial community. Nearly all of the estimatid efficiencies in aquatic ecosystem are less than 1%. For example, the photosynthetic efficiencies of 17 lakes listed by Wetzel (1975) varied from 0.035% in oligotrophic lakes, Lake Tahoe, to 1.76% in eutrophic water, Loch Leven. Higher values are generally found in very productive waters. Beyers (1963) measured 3% in artificial microecosystem and further high value of above 3.5% were reported by Tamiya (1957) for the mass culture of *Chlorella* and 5.5% by Odum (1957) for Silver Springs. Thus the mean gross photosynthetic efficiency of 3.2% in Lake Teganuma may be the highest value among natural waters.

The photosynthetic production has undoubtedly increased in Lake Teganuma during the last decade and the lake is extremely eutrophic. Hitherto, it has been confirmed experimentally that the growth of phytoplankton is accelerated by nutrient enrichments until a certain threshold concentration but is inhibited over this concentration (Chu, 1942, 1943; Vollenweider, 1968; Iwasaki, 1969). In aquatic ecosystems, there appears to exist an equilibrium between nutrients and growth of organisms.

If the concentration of nutrients could increase further in Lake Teganuma, the biomass of phytoplankton would reach a certain high level and subsequently further growth might be strongly limited by light available in community due to the restriction of light imposed by heavy self-shading. Additionally, the growth of phytoplankton would be restricted by toxically excessive amount of nutrients.

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