The Vertical Distribution of Phytoplankton Assemblages of Lake James, North Carolina in Relation to Mixing Depth and Nitrate and Phosphate Concentrations¹

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ABSTRACT. Phytoplankton, nitrate (NO₃) (mg L¹), and phosphate (PO₃³) (mg L¹) concentrations were studied in Lake James, NC, during 1997 and 1998. Depths of 2.0, 10, and 30 m were chosen for sampling to determine the vertical distribution of phytoplankton. At 2.0 and 10 m, the species diversity of Heterokontophyta was mainly represented by *Mallomonas caudata* (Ivanov); Chlorophyta by *Chlamydomonas polypyrenoideum* (Prescott); Bacillariophyta by *Melosira granulata* (Ehrenberg) Ralfs and *Asterionella formosa* (Hassall), respectively. At 30 m, the species diversity of Cryptophyta was mainly represented by *Rhodomans minuta* (Skuja); Bacillariophyta by *Cyclotella glomerata* (Bachmann), *Synedra ulna* (Nitzsch) Ehrenberg, and *Tabellaria fenestrata* (Lyngbye) Kützing; and Cyanophyta by *Chroococcus limeticus* (Lemmermann) and *Oscillatoria limnetica* (Lemmermann). The purpose of this study was to determine the vertical distribution of phytoplankton in relation to nitrate and phosphate concentrations and the mixing depth in the water column of Lake James, North Carolina, USA.

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INTRODUCTION

Aquatic ecosystems are subjected to high spatial and temporal variability. As a result, the relative abundance and species composition of planktonic organisms frequently varies in time and space. Light climate, mixing events, nutrient concentrations, and their availability relative to other elements can be important for the vertical distribution patterns of phytoplankton in the water column (Richerson and others 1970; Calijuri and others 2002; Teubner 2003).

Nitrogen and phosphorus are critically important and can be limiting to phytoplankton growth. In addition, specific rate of phosphorus and nitrogen loading may determine the number of species coexisting and their abundance in the water column (Levine and Schindler 1999).

In general, studies on phytoplankton community dynamics in deep lakes consider mixing events to be the main factor controlling the vertical distribution of species in the water column (Gaedeke and Sommer 1986; Reynolds 1987; Reynolds and others 2000; Smayda 2002).

Under stable conditions, phytoplankton growth may be limited by the scarcity of nutrients in the upper layers, but when mixing occurs, it entrains nutrient-rich water from the deeper layers and, this in turn, can result in higher primary production (Harris 1983; MacIntyre and others 1999). Hence, the extent of the mixed layer in the water column can have a strong influence on phytoplankton species composition and their abundance during thermal stratification (Viner 1985; Goldman and Jassby 1990).

Seasonal dynamics of phytoplankton have been studied intensively (Mohamed 2002; Anneville and others

2002; Tietjen and Wetzel 2003; Chang and others 2003; Murrell and Lores 2004), but studies addressing the vertical distribution of phytoplankton in relation to both nutrient concentrations and mixing depth are scarce. The goal of this study was to understand how nitrate and phosphate concentrations and mixing depth affected the vertical distribution of phytoplankton in the water column of Lake James, NC.

STUDY AREA

Lake James is a freshwater reservoir located at the latitude of 35° 44′ and longitude of 81° 55′ in North Carolina. The lake is formed by the impoundment of three-headwater streams of the Catawba River. These streams are the Catawba River, Paddy's Creek, and Linville River—each being separately dammed to form one interconnected lake (Fig. 1). The lake has a total area of 26 km², an average depth of 20 m and a maximum depth of 35 m.

MATERIALS AND METHODS

Sampling was carried out monthly at the deepest part of the lake between March 1997 and December 1998. Samples were drawn from three depths (2.0, 10, and 30 m) using a Kemmerer water sampler. Phytoplankton samples were analyzed according to Utermöhl sedimentation method (Utermöhl 1958). Enumeration and identification of phytoplankton were performed using a compound microscope equipped with water immersion lenses and a phase contrast attachment from Lugol-fixed samples.

Concentrations of nitrate (NO_3^-) and phosphate (PO_4^{3-}) were determined spectrophotometrically according to standard methods (APHA 1995). Temperature was measured using a Hydrolab® multiprobe at 1.0-m depth intervals. The mixing depth was estimated from temperature profiles. The euphotic depth was calculated as 1.7 times Secchi disk depth as reported by Scheffer (1998).

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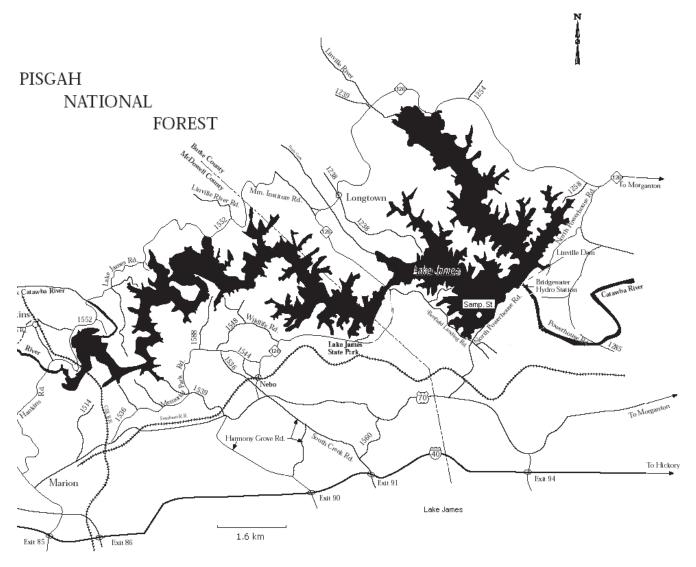


FIGURE 1. Site map of phytoplankton sampling stations (1997-1998) in Lake James, NC.

Correlation coefficients between the number of species, NO_3^- , PO_4^3 , and mixing depth were calculated. The statistical differences in species number and the overall abundance between the sampled depths and seasons were determined using an ANOVA test. The statistical analyses were performed using SAS statistical software (SAS System for Windows v6.12). The statements of significance are at $p \le 0.05$, unless otherwise stated.

RESULTS

A total of 75 phytoplankton species were identified during the study. Bacillariophyta was represented by 28, Chlorophyta by 25, Cyanophyta by 11, Heterokontophyta by 7, Cryptophyta by 3, Pyrrophyta by 2, and Euglenophyta by 1 species, respectively (Table 1).

The following species were the most abundant throughout the study period. *Mallomonas caudata* (44 cells mL⁻¹) and *Dinobryon divergens* (Imhof) (15 cells mL⁻¹) in the genera of Heterokontophyta; *Rhodomans minuta* (16 cells mL⁻¹) in Cryptophyta; *Cyclotella glomerata* (18 cells mL⁻¹), *Melosira garanulata* (15 cells mL⁻¹), *Navicula petersenii* (Hustedt) (12 cells mL⁻¹),

Table 1

Species of phytoplankton collected from
Lake James during 1997 and 1998.

CYANOPHYTA

Cyanophyceae

Choroococcales

Chroococcaceae

Chroococcus limeticus (Lemm.)

Chroococcus turgidus (Kuetz)

Chroococcus dispersus (Lemm.)

Merismopediaceae

Merismopedia elagans (Smith)

Microcystaceae

Microcystis firma (Schmidle)

Nostocales

Table 1 (Cont.)

Species of phytoplankton collected from Lake James during 1997 and 1998.

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Species of phytoplankton collected from Lake James during 1997 and 1998.

Nostocaceae

Nostoc pruniforme (Ag.)

Anabaena spiroides (Lemm.)

Oscillatoriales

Oscillatoriaceae

Lyngbya limnetica (Lemm.)

Lyngbya birgei (Smith)

Oscillatoria agardhi (Gomont)

Oscillatoria limnetica (Lemm.)

HETEROKONTOPHYTA

Chrysophyceae

Synurales

Synuraceae

Mallomonas caudata (Ivanov)

Mallomonas acaroides (Perty)

Synura uvella (Ehr.)

Chromulinales

Dinobryaceae

Dinobryon divergens (Imhoff)

Dinobryon sociale var. americanum (Bachm)

Uroglenopsis americana (Calkins)

 ${\it Uroglenopsis\ volvox\ (Ehr.)}$

PYRRHOPHYTA

Pyrrhophyceae

Gonyaulacales

Ceratiaceae

Ceratium birundinella (Müller)

Peridiniales

Peridiniaceae

Peridinium aciculiferum (Lemm.)

BACILLARIOPHYTA

Bacillariophyceae

Centrales

Attheyaceae

Attheya zachariasi (Brun)

Stephanodiscaceae

Cyclotella bodanica (Eulen)

Cyclotella ocellata (Pant)

Cyclotella glomerata (Bachm.)

Cyclotella comata (Kuetz)

C. kutzingiana (Thwaites)

Stephanodiscus asterae (Kuetz)

Melosiraceae

Melosira granulata (Ehrenberg)

M. ambigua (Grunow) O.Müll.

M. granulata var. angustissima O.Müll.

Rhizosoleniaceae

Rhizosolenia eriensis (Smith)

Rhizosolenia gracilis (Smith)

Pennales

Achnanthaceae

Achnanthes lanceolata (Breb)

Bacillariaceae

Nitzschia palea (Kuetz)

Nitzschia vermicularis (Kuetz)

Eunotiaceae

Eunotia sp.

Fragilariaceae

Asterionella formosa (Hassall)

Asterionella gracillima (Hantz.)

Fragilaria acuta (Ehr.)

Fragilaria pinnata (Ehr.)

Fragilaria crotonensis (Kitton)

Synedra ulna (Nitzsch)

Synedra acus (Grun)

Naviculaceae

Navicula petersenii (Hustedt)

Navicula monoculata (Hustedt)

Tabellariaceae

Tabellaria fenestrata (Lyngb.)

Tabellaria flocculosa (Roth)

CRYPTOPHYTA

Cryptophyceae

Cryptomonadales

Cryptomonadaceae

Cryptomonas erosa (Ehr.)

Table 1 (Cont.)

Species of phytoplankton collected from Lake James during 1997 and 1998.

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Species of phytoplankton collected from Lake James during 1997 and 1998.

Pyrenomonadales

Chroomonadaceae

Chroomonas acuta (Utermothl)

Pyrenomonadaceae

Rhodomonas minuta (Skuja)

EUGLENOPHYTA

Euglenophyceae

Euglenales

Euglenaceae

Euglena elastica (Presch)

CHLOROPHYTA

Chlorophyceae

Chlorococcales

Chlorellaceae

Ankistrodesmus fractus (Brunn)

A. convolutus (Corda)

Scenedesmaceae

Actinastrum gracillimum (Smith)

Crucigenia rectengularis (Braun)

Coelastrum microporum (Naegeli).

Coelastrum limneticum (Lemm.)

Scenedesmus alternans (Reinsc)

S. bicaudatus (Chodat)

Micractiniaceae

Golenkinia radiata (Chodat)

Oocystaceae

Errerella bornhemiensis (Conrad)

Franceia droescheri (Lemm.)

Oocystis lacustris (Chodat)

Oocystis borgei (Snow)

Hydrodictyaceae

Pediastrum boryanum (Turp)

Zygnematales

Desmidiaceae

Euastrum pectinatum (West)

Cosmarium margaritatum (Lund)

Staurastrum rotula (Norsdt.)

Staurastrum cornatum (Arch.)

Zygnemataceae

Mougeotia elagantula (Witrr)

Volvocales

Volvocaceae

Eudorina elagans (Ehr.)

Phacotaceae

Phacotus lenticularis (Stein.)

Chlamydomonadaceae

Chlamydomonas polypyrenoideum (Prescott)

C. sphagnicolo (Fritsch)

Carteria cordiformis (Diesing)

Gloeocystis gigas (Kuetz)

Tabellaria fenestrata (7 cells mL⁻¹), Synedra ulna (4 cells mL⁻¹), and Asterionella formosa (Hassall) (6 cells mL⁻¹) in Bacillariophyta; Chlamydomonas polypyrenoideum (20 cells mL⁻¹) and Coelastrum limneticum (Lemmermann) (18 cells mL⁻¹) in Chlorophyta; Oscillatoria limnetica (Lemmermann) (11 cells mL⁻¹) and Chroococcus limeticus (Lemmermann) (20 cells mL⁻¹) in Cyanophyta, respectively.

At 2.0 and 10 m, the species diversity of Hetero-kontophyta was mainly represented by *Mallomonas caudate*, Chlorophyta by *Chlamydomonas poly-pyrenoideum*, Bacillariophyta by *Melosira granulata* and *Asterionella formosa*, respectively. At 30 m, the species diversity of Cryptophyta was mainly represented by *Rhodomans minuta*; Bacillariophyta by *Cyclotella glomerata*, *Synedra ulna*, and *Tabellaria fenestrata*;

and Cyanophyta by *Chroococcus limeticus* and *Oscillatoria limnetica*, respectively.

At 2.0 and 10 m, the total number of species was high (about 65 species mL⁻¹) in spring and fall, and lower (about 55 species mL⁻¹) in summer. At 30 m, the total species number did not change significantly, oscillating about 7 species mL⁻¹ throughout the year (Fig. 2a,b). The lake was thoroughly mixed between October and March. The euphotic depth exceeded the mixing depth only during summer and was not significantly different between seasons (*p* >0.05) (Fig. 2c,d).

At 2.0 m, the species number of Heterokontophyta and Cyanophyta oscillated between 5 and 10 species mL⁻¹. Bacillariophyta species number was about 30 species mL⁻¹ and Chlorophyta species number was about 25 species mL⁻¹, respectively (Fig. 3a,b). At the

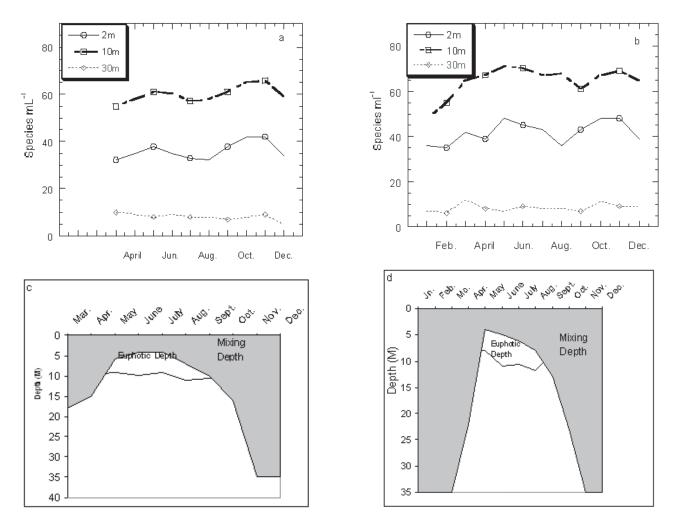


FIGURE 2. Total number of species, mixing, and euphotic depths. a) The total number of species in 1997; b) total number of species in 1998; c) mixing and euphotic depths in 1997; d) mixing and euphotic depths in 1998.

same depth, the individual number of Heterokontophyta was about 100 cells mL⁻¹ in spring and about 30 cells mL⁻¹ for the rest of the year. Chlorophyta density was about 50 cells mL⁻¹ in spring and fall and about 100 cells mL⁻¹ in summer. Bacillariophyta density was about 80 cells mL⁻¹ in spring and fall and about 20 cells mL⁻¹ in summer. Cyanophyta density was about 20 cells mL⁻¹ in spring and fall and about 145 cells mL⁻¹ in summer (Fig. 3c,d).

At 10 m, Bacillariophyta species number was about 35 species mL⁻¹ in spring and fall and about 20 species mL⁻¹ in summer. Chlorophyta species number was about 35 species mL⁻¹ in summer and about 20 species mL⁻¹ in spring and fall. Heterokontophyta species number oscillated between 2 and 5 species mL⁻¹ throughout the year. Cyanophyta species number was about 5 species mL⁻¹ in fall and spring and about 10 species mL⁻¹ in summer (Fig. 4a,b). At the same depth, Heterokontophyta density was about 120 cells mL⁻¹ in spring and about 20 cells mL⁻¹ for the rest of the year. Chlorophyta density fluctuated between 20 and 75 cells mL⁻¹ during the study. Bacillariophyta density was about 120 cells mL⁻¹ in spring and fall and about 40 cells mL⁻¹ in summer. Cyanophyta density oscillated about 30 cells

mL⁻¹ throughout the year (Fig. 4c,d).

At 30 m, the number of species all phytoplankton groups oscillated between 2 and 5 species mL⁻¹ throughout the year, except diatoms which had a diversity of about 12 species mL⁻¹ in summer and fall of 1997 and a Cyanophyta peak of 15 species mL⁻¹ in summer of 1998 (Fig. 5a,b). At the same depth, Heterokontophyta, Chlorophyta, and Cyanophyta density oscillated between 3 and 12 cells mL⁻¹ throughout the study period. Bacillariophyta density was about 8 cells mL⁻¹ in spring and about 15 cells mL⁻¹ for the rest of the year (Fig. 5c,d).

At 2.0 and 10 m, \mathbb{NO}_3^- concentration was about 0.2 mg L⁻¹ in spring and about 0.01 mg L⁻¹ for the rest of the year, except a peak of about 0.2 mg L⁻¹ in summer 1997. At 30 m, nitrate concentration was between 0.2 and 0.3 mg L⁻¹ in spring and summer and about 0.01 mg L⁻¹ in fall throughout the study period (Fig. 6a,b). At 2.0 and 10 m, \mathbb{PO}_4^{3-} concentrations were about 0.05 mg L⁻¹ in spring and fall and about 0.01 mg L⁻¹ in summer during the study. At 30 m, phosphate concentration was about 0.01 mg L⁻¹ throughout the study, except a peak of 0.03 mg L⁻¹ in winter 1998 (Fig. 6c,d).

The correlation coefficient between the total number of species and mixing depth was only significant at 10 m

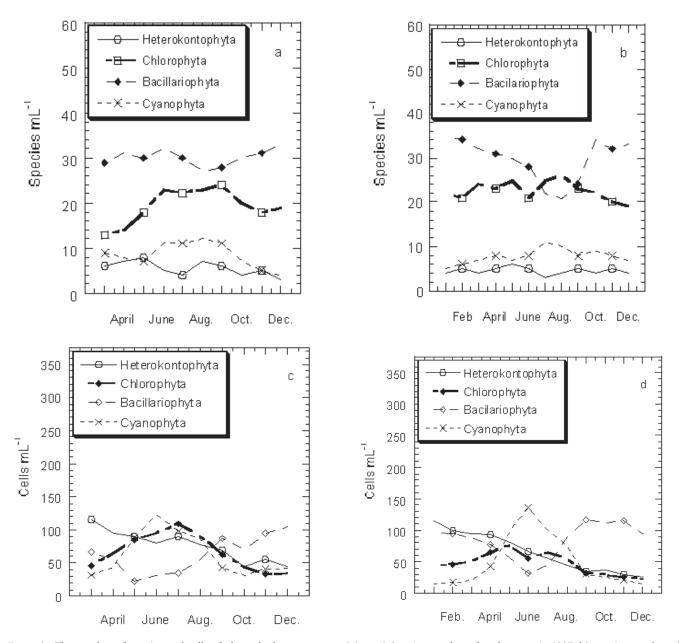


FIGURE 3. The number of species and cells of phytoplankton groups at 2.0 m. a) Species number of each group in 1997; b) species number of each group in 1998; c) cell number of each group in 1998.

(r = 0.31, p < 0.05), but not at 2.0 and 30 m (r = 0.11, p < 0.05)p > 0.05) throughout the study. Except the species number of Chlorophyta (0.38, p < 0.05), none of the other groups showed significant correlations (r < 0.3, p > 0.05) with euphotic depth. Mixing depth was significantly correlated only with the species number of Bacillariophyta (r = 0.37, p < 0.05). The total number of species, NO_3^- , and PO_4^{3-} were significantly correlated at 2.0 m (r = 0.32, p < 0.05) and 10 m (r = 0.34, p < 0.05), but not at 30 m (r = 0.19, p > 0.05). The total number of individuals, NO_3^- , and PO_4^{3-} were also significantly correlated at 2.0 m (r = 0.37, p < 0.05) and 10 m (r = 0.41, p < 0.05), but not at 30 m (r = 0.21, p > 0.05). The differences in total species number were significant between 2.0 and 30 m (F = 415, p < 0.001) as well as between 10 and 30 m (F = 357, p <0.001), but not between 2.0 and 10 m depths (F = 0.35, p > 0.05).

DISCUSSION

Bacillariophyta (28 species) and Chlorophyta (25 species) were the most dominant phytoplankton groups in Lake James. Cyanophyta (11 species), Heterokontophyta (8 species), Cryptophyta (3), Pyrrhophyta (2 species), and Euglenophyta (1 species) also contributed to phytoplankton, but they were represented by fewer species.

The total number of species was greater at 10 m than that at 2.0 and 30 m. This was probably a result of the light climate. At 2.0 m, phytoplankton were exposed to excessive amount of light particularly in summer, which is damaging to most algae (Oliver and others 2003). At 30 m, they were most likely limited by the lack of sufficient light. At 10 m, on the other hand, light intensity was probably optimum for most phytoplankton. Malinsky-Rushansky and others (2002) state that relatively

dim environments enhance phytoplankton productivity by providing habitat in which they can avoid phtoinhibition, while still having sufficient light for photosynthesis.

At 2.0 and 10 m, the total number of phytoplankton species was higher in spring and fall, but lower in summer. This pattern was probably a result of seasonal mixing, which occurs in spring and fall and moves nutrients to upper depths from deep layers (Reynolds 1984).

At 2.0 and 10 m, *Rhodomans minuta* (Cryptophyta) was abundant in early spring. This species likely took advantage of the mild temperature and high nutrient concentrations at that time of the year. Anneville and others (2002) reported that Rhodomonas minuta, which is a fast-growing small species (r-strategist), was selected by strong turbulence and high nutrient concentrations in Lake Geneva. Lake James is well mixed and the nutrient concentrations are higher in spring and fall.

At 2.0 and 10 m, Bacillariophyta was dominant in spring and summer and Chlorophyta was dominant in summer. At 30 m, Bacillariophyta was dominant in the spring and Cyanophyta was dominant in summer. The seasonal development of phytoplankton, in particular the dominance of diatoms during the spring and fall, followed the common pattern in lakes of the temperate zone (Teubner and Dokulil 2002). Munawar and Munawar (1986) reported that Bacillariophyta species were usually common during cooler or windier conditions in the North American Great Lakes. Salmaso (2000) states that increase of diatoms at the end of the winter coincides with high nutrient availability and water column turbulence. In the early spring and late fall, Lake James is well mixed and the nutrient concentrations are greater than during summer.

Cyclotella ocellata (Pant), Synedra ulna and Tabellaria fenestrata, Chroococcus limeticus and Oscillatoria limnetica were mostly present at 30 m; their densities did not change seasonally. This pattern was probably produced by the stable physical and chemical conditions at this depth compared with more dynamic conditions at 2.0 and 10 m (Melo and Huszar 2000).

Chlorophyta species number and density were higher in summer and lower in fall and spring at 2.0 and 10 m.

Oct. Dec.

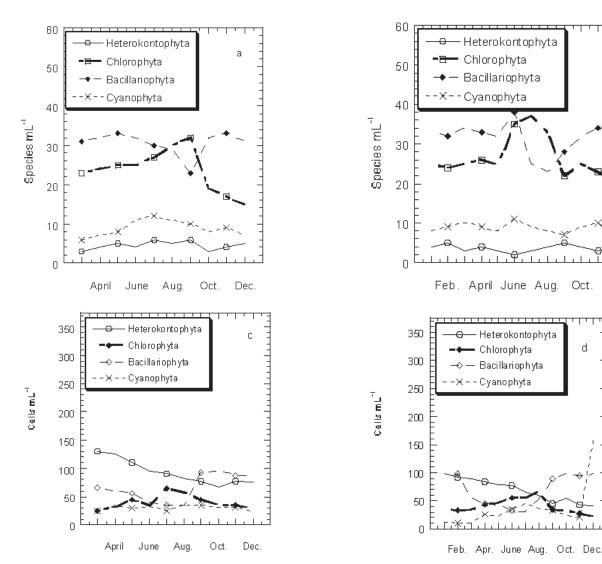


FIGURE 4. The number of species and cells of phytoplankton groups at 10 m. a) Species number of each group in 1997; b) species number of each group in 1998; c) cell number of each group in 1997; d) cell number of each group in 1998.

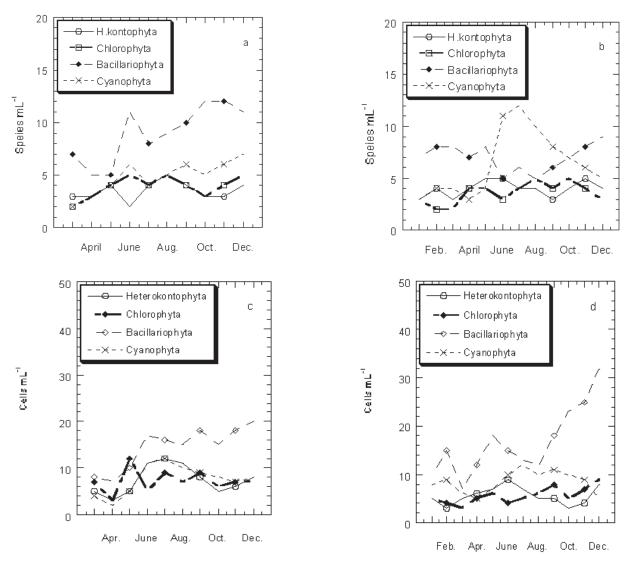


FIGURE 5. The number of species and cells of phytoplankton groups at 30 m. a) Species number of each group in 1997; b) species number of each group in 1998; c) cell number of each group in 1998.

Species of this group reached a great abundance in mid summer. Optimum light and temperature were probably the most significant factors contributing to density peaks of chlorophytes in summer (Temponeras and others 2000). Higashi and Seki (2000) found that Chlorophyta species were the dominant phytoplankton in summer in an experimental oligotrophic pond.

At 30 m, Cyanophyta was dominant during summer throughout the study period. Insufficient underwater light probably played a critical role in the selection of Cyanophyta at this depth. Brookes and Ganf (2001) state that high temperature and low light intensity favor Cyanophyta in temperate lakes. The average Secchi disk depth in Lake James is about 4.0 m and euphotic depth hardly exceeded 12 m, meaning no light at 30 m and thus phytoplankton productivity was limited by the lack of light at this depth. High temperature and insufficient light conditions could have acted synergistically to favor Cyanophyta during warm seasons at 30 m in Lake James.

Chroococcus limeticus and Oscillatoria limnetica were the most abundant Cyanophytes in summer at

30 m. Reynolds (1984) states that species of *Chrococcus* and *Oscillatoria* can survive long periods of darkness. Smith (1986) also determined that low light intensity and high temperature favored Cyanophyta in lakes.

Mallomonas caudata, Dinobryon divergens, and Chlamydomonas polypyrenoideum were the most common species that were collected from the all three depths. This could be a result of their swimming abilities as they have flagella. These species can move to the depth where they can obtain sufficient light and nutrients (Horne and Goldman 1994; Higashi and Seki 2000).

Melosira granulata and Cyclotella glomerata were also frequently collected from all three depths. Reynolds and others (1982) state that these species are able to increase under almost any given environmental condition and are common at almost all depths of deep lakes.

The correlation coefficients between the mixing depth and total number of species were significant only at 10 m (r = 0.31, p < 0.05), but not at 2.0 and 30 m during the thermal stratification. This was an expected result because during the stratification, the mixing depth was usually less than 10 m and never reached to

30 m, and 2.0 m was always within the range of mixed layer. Reynolds (1992) states that the vertical distribution of phytoplankton is fundamentally dependent on mixing properties of the lake and the occurrence of populations actively moving via flagella.

Under full isothermy, phytoplankton species were more evenly distributed in the water column but, during the stratification, about 90% of the species were collected in the upper layers. Smayda (2002) states that when the mixing is restricted to only the upper layers, despite penetration of light to the deeper layers, it imposes differentiated distribution of the phytoplankton, with fewer species and lower densities below the mixing layer.

The effects of nutrients on phytoplankton distribution has been a central theme of modern limnology (Schindler 1977; Hecky and Kilham 1988; Maberly and others 2002). N and P have commonly been observed as limiting nutrients in aquatic systems. In aerated nutrient poor lakes, over 80% of nitrogen is present as NO_3^- and phosphorus as PO_4^3 (Elser and others 1990). Keeping this in mind, the distribution of phytoplankton was analyzed with respect to the relative concentration of NO_3^- and PO_4^3 . The results suggested that the vertical

distribution of phytoplankton in Lake James was basically controlled by the relative concentrations of NO_3^- and $PO_4^{3^-}$. At 2.0 and 10 m, nutrient concentrations were more dynamic than those at 30 m and the correlation coefficients between the number of species and the number of individuals, NO_3^- and $PO_4^{3^-}$ were significant at 2.0 and 10 m, but not at 30 m.

The dominance of Chlorophyta in spring at 10 m and the dominance of Cyanophyta during summer at 30 m is consistent with the patterns seen in lakes with relatively short supply of nutrients (Hecky and Kilham 1988). Furthermore, the lower number of species and their abundance in Lake James compared with eutrophic lakes suggest that, in general, phytoplankton growth was limited by the scarcity of nutrients (Munawar and Munawar 1986; Maberly and others 2002; Teubner 2003). Another indication of nutrient limitation on phytoplankton was the relatively higher abundance of phytoplankton in spring and fall when mixes occurred compared with stagnant summer conditions.

The analyses also revealed that the temperature and light regime was also important on the seasonal patterns of phytoplankton in Lake James. Chlorophytes

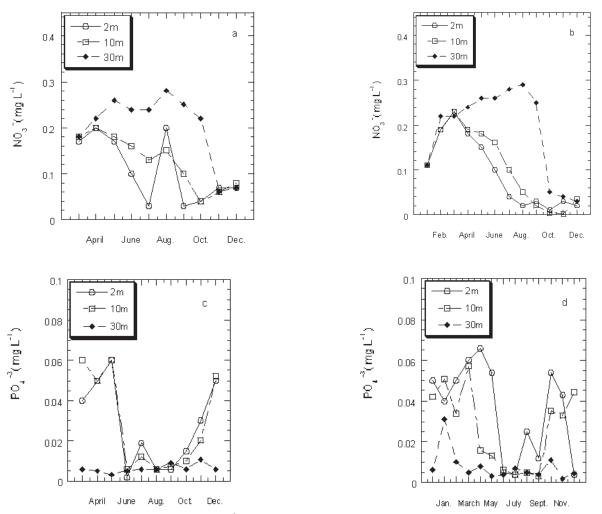


FIGURE 6. The concentration of NO_3^{-} (mg L⁻¹) and PO_3^{3-} (mg L⁻¹) at 2.0, 10, and 30 m. a) NO_3^{-} concentrations in 1997; b) NO_3^{-} concentrations in 1998; c) PO_3^{3-} concentrations in 1998.

were more abundant in spring, while diatoms were mostly abundant in winter and cyanophtes were abundant during summer. These results suggest that seasonal patterns of phytoplankton were regulated by the seasonal changes in temperature and light (Melo and Huszar 2000).

In summary, the results of this study showed that phytoplankton species numbers and their abundance were significantly different between 2.0 and 30 m and between 10 and 30 m, but not between 2.0 and 10 m during the summer stratification. Finally, the results also suggest that although the vertical distribution of phytoplankton was mostly regulated by the relative concentrations of nutrients, seasonal patterns of phytoplankton, especially in the upper layers, were mainly regulated by the temperature and light regime.

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LITERATURE CITED

- Anneville O, Ginot V, Druart JC, Angeli N. 2002. Long-term study (1974–1998) of seasonal changes in the phytoplankton in Lake Geneva: a multi-table approach. J Plankton Res 24(10):993-1008.
- APHA. 1995. Standard methods for the examination of water and wastewater. American Water Works Association, and Water Environment Federation. Washington (DC): American Public Health Association.
- Brookes JD, Ganf GG. 2001. Variations in the buoyancy response of *Microcystis aeruginosa* to nitrogen, phosphorus and light. J Plankton Res 23(12):1399–1411.
- Calijuri MC, Dos Santos AC, Jati S. 2002. Temporal changes in the phytoplankton community structure in a tropical and eutrophic reservoir (Barra Bonita, S.P.–Brazil). J Plankton Res 24 (7):617-34.
- Chang F, Zeldis HJ, Gall M, Hall J. 2003. Seasonal and spatial variation of phytoplankton assemblages, biomass and cell size from spring to summer across the northeastern New Zealand continental shelf. J Plankton Res 25(7):737-58.
- Elser JJ, Marzolf ER, Goldman CR. 1990. Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. Can J Fish Aquat Sci 47(7):468–1477.
- Gaedeke A, Sommer U. 1986. The influence of the frequency of periodic disturbances on the maintenance of phytoplankton diversity. Oecologia 71(1):25-8.
- Goldman CR, Jassby A. 1990. Spring mixing depth as a determinant of annual primary production in lakes. In: Tilzer MM, Serruya C, editors. Large Lakes: Ecological Structure and Function. New York (NY): Springer-Verlag. 356 p.
- Harris GP. 1983. Mixed layer physics and phytoplankton populations: studies in equilibrium and non-equilibrium ecology. Progress in Phycological Research 2(1):1-52.
- Hecky RE, Kilham P. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. Limnol Oceanogr 33(4):796–822.
- Higashi Y, Seki H. 2000. Ecological adaptation and acclimatization of natural freshwater phytoplankters with a nutrient gradient. Environ Poll 109(2):311-20.
- Horne AJ, Goldman CR. 1994. Limnology. New York (NY): McGraw-Hill. 576 p.
- Levine SN, Schindler DW. 1999. Influence of nitrogen to phosphorus supply ratios and physicochemical conditions on Cyanobacteria and phytoplankton species composition in the Experimental Lakes Area, Canada. Can J Fish Aquat Sci 59(3):451-66.
- Maberly SC, King L, Dent M, Jones RI, Gibson CE. 2002. Nutrient limitation of phytoplankton and periphyton growth in upland lakes. Freshw Biol 47(11):2136–52.

- MacIntyre S, Flynn KM, Jellison R, Romero JR. 1999. Boundary mixing and nutrient fluxes in Mono Lake, California. Limnology and Oceanography 44(3):512-39.
- Malinsky-Rushansky N, Berman T, Berner T, Yacobi YZ, Dubinsky Z. 2002. Physiological characteristics of picophytoplankton, isolated from Lake Kinneret: responses to light and temperature. J Plankton Res 24(11):1173-83.
- Melo S, Huszar VM. 2000. Phytoplankton in an Amazonian floodplain lake (Lago Batata, Brasil): Diel variation and species strategies. J Plankton Res 22(1):63-76.
- Mohamed Z. 2002. Allelopathic activity of Spirogyra sp.: stimulating bloom formation and toxin production by *Oscillatoria agardhii* in some irrigation canals, Egypt. J Plankton Res 24 (2):137-41.
- Munawar M, Munawar IF. 1986. The seasonality of phytoplankton in the North American Great Lakes, a comparative synthesis. Hydrobiologia 138(1):85–115.
- Murrell MC, Lores EM. 2004. Phytoplankton and zooplankton seasonal dynamics in a subtropical estuary: importance of Cyanobacteria. J Plankton Res 26(3):371-82.
- Oliver RL, Whittington J, Lorenz Z, Webster IT. 2003. The influence of vertical mixing on the photoinhibition of variable chlorophyll *a* fluorescence and its inclusion in a model of phytoplankton photosynthesis. J Plankton Res 25(9):1107-29.
- Reynolds CS. 1992. Dynamics, selection and composition of phytoplankton in relation to vertical structure in lakes. Arch Hydrobiol 35(1):13–31.
- Reynolds CS. 1987. Cyanobacterial water—blooms. Adv Botanical Res 13(1):67–143.
- Reynolds CS. 1984. The ecology of freshwater phytoplankton. New York (NY): Cambridge Univ Pr. 385 p.
- Reynolds CS, Reynolds SN, Munawar IF, Munawar M. 2000. The regulation of phytoplankton population dynamics in the world's largest lakes. Aquatic Ecosystem Health and Management 3(1):1-21.
- Reynolds CS, Thompsom JM, Ferguson AJD, Wiseman SW. 1982. Loss processes in the population dynamics of phytoplankton maintained in closed systems. J Plankton Res 4(5):561-600.
- Richerson P, Armstrong R, Goldman CR. 1970. Contemporaneous disequilibrium, a new hypothesis to explain the "Paradox of Plankton." Proceedings of National Academy of Science 67(4):1710-14.
- Salmaso N. 2000. Factors affecting the seasonality and distribution of Cyanobacteria and Chlorophytes: a case study from the large lakes south of the Alps, with special reference to Lake Garda. Hydrobiologia 438(1-3):43–63.
- SAS System for Windows, The, v6.12. SAS Institute Inc., Cary, NC, USA. Scheffer M. 1998. Ecology of Shallow Lakes. Dordrecht: Kluwer Academic Publishers.
- Schindler DW. 1977. Evolution of phosphorus limitation in lakes. Science 195(2):260–2.
- Smayda TJ. 2002. Turbulence, water mass stratification and harmful algal blooms: an alternative view and frontal zones as "pelagic seed banks." Harmful Algae 1(1):95-112.
- Smith VH. 1986. Light and nutrient effects on the relative biomass of blue-green algae in lake phytoplankton. Can J Fish Aquat Sci 43(1):143-53.
- Temponeras M, Kristiansen J, Moustaka-Gouni M. 2000. Seasonal variation in phytoplankton composition and physical-chemical features of the shallow Lake Doïrani, Macedonia, Greece. Hydrobiologia 424(1-3):9–122.
- Teubner K. 2003. Phytoplankton, pelagic community and nutrients in a deep oligotrophic alpine lake: ratios as sensitive indicators of the use of P-resources (DRP:DOP:PP and TN:TP:SRSi). Water Research 37(7):1583-92.
- Teubner K, Dokulil MT. 2002. Ecological stoichiometry of TN:TP:SRSI in freshwaters: nutrient ratios and seasonal shifts in phytoplankton assemblages. Arch Hydrobiol 154(4):625–46.
- Tietjen TE, Wetzel RG. 2003. Seasonal and spatial distribution of bacterial biomass and the percentage of viable cells in a reservoir of Alabama. J Plankton Res 25(12):1521-34.
- Utermöhl H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton. Methodik. Mitteilungen Internationale Limnologie 9(1):1–38.
- Viner AB. 1985. Thermal stability and phytoplankton distribution. Hydrobiologia 125(1-3):47–69.