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Population dynamics of autotrophic picoplankton in relation to environmental factors in a productive lake

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ABSTRACT

Spatial and seasonal fluctuations in autotrophic picoplankton (APP) abundance in a eutrophic, dimictic lake (Lake Aydat, France) were measured concurrently with a variety of environmental variables. Cell number ranged from 0.03 to 2.36×10^6 cells $\cdot$ ml^{-1} (highest concentrations were >5-fold higher than in oligotrophic lakes) and averaged 24 ± 7% of total picoplankton abundance (APP + heterotrophic bacteria). APP abundance (1) peaked in spring simultaneously with heterotrophic flagellate and ciliate densities, (2) decreased during the nitrogen-limited and summer stratification period, and (3) increased with fall turnover. In summer-autumn, the contribution of single-cell eukaryotic (up to 66%) and colonial prokaryotic (18%) forms to total abundance peaked in the bottom waters. Multivariate regression analyses suggest that >40% variance in APP number changes may be explained by ciliate abundance (at 0–4 m depth-range), heterotrophic flagellate number and oxygen concentration (5–9 m), and ciliate carbon biomass (10–14 m). The model accounting for changes in heterotrophic bacterial abundance (5–9 m) indicates chlorophyll *a* concentration ($r^2 = 58$%) and ciliate abundance ($r^2 = 34$%) as dominant covariates. The data presented here suggest that micrograzers control APP abundance in Lake Aydat.

Introduction

Autotrophic picoplankton (APP, 0.2–2.0 μm) are major components of the photosynthetic biomass of marine and freshwater ecosystems (cf. Stockner, 1988). These organisms can at times be responsible for a substantial part of the primary production in oligotrophic lakes. However, in more productive lakes, their standing stock increases (e.g. Fig. 1 in Stockner, 1991). This trend is not yet clear, since little is known about the quantitative and functional importance of algal picoplankton in productive waters (Burns and Stockner, 1991; Vörös et al., 1991).

Furthermore, it is essential to know the factors controlling changes in APP abundance. They are now included as a part of the freshwater (Stockner and Porter, 1988) and marine (Hagström et al., 1988; Longhurst, 1991) aquatic food webs. Factors known to affect the abundance of phototrophic picoplankton include nutrient supply (Stockner, 1987; Hardy et al., 1986; Stockner and Shortreed, 1988;

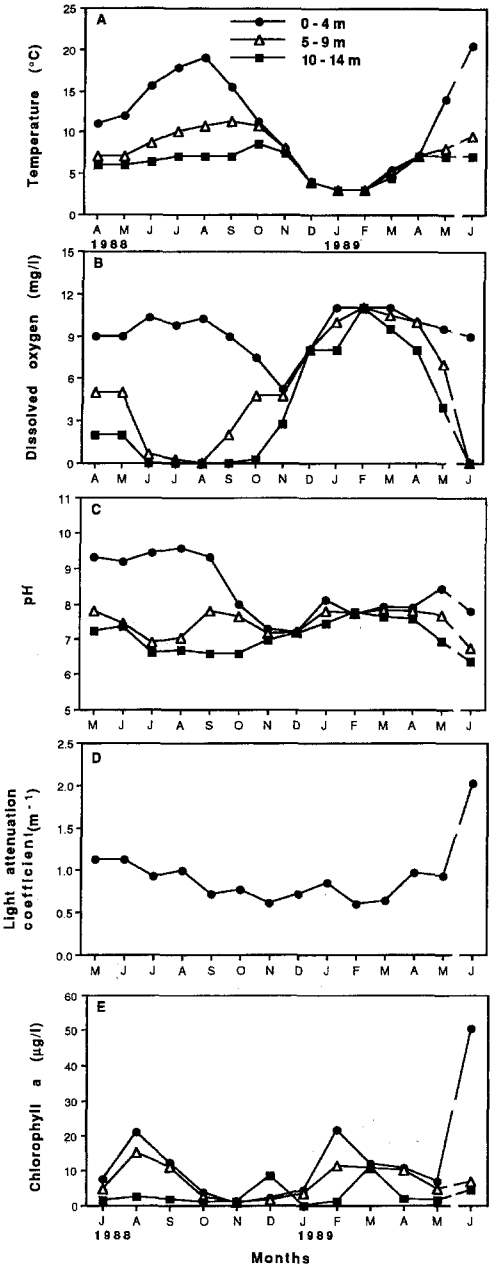

Figure 1. Seasonal and spatial changes in some physical and chemical data in Lake Aydat. Data not available for June 1989

Shortreed and Stockner, 1990; Vörös et al., 1991; Wehr, 1991), water temperature (Krempin and Sullivan, 1981; Caron et al., 1985; Joint, 1986; Jochem, 1988), light attenuation (Pick, 1991), and micrograzers (Weisse, 1988; Nagata, 1988; Wehr, 1991). However, the combined relative contribution of these factors to the seasonal variations of APP cell number within lakes has not been established.

In this study, the spatial and seasonal changes in phototrophic picoplankton populations in the eutrophic Lake Aydat (France) were related to biological, chemical, and physical data, including temperature, light attenuation, nutrient (NO_3–N, NH_4–N, PO_4–P) concentrations, and micrograzer (heterotrophic flagellates and ciliates) densities.

Material and methods

Site and sampling

Lake Aydat is a small (area = 60.3 ha, maximum depth = 15.5 m) eutrophic, dimictic lake, located at 825 m altitude in the French "Massif Central" (e.g. Sime-Ngando and Hartmann, 1991). Samples were taken from April 1988 to July 1989 at a central location in the lake, usually between 10:00 and 13:00 h. Samples were collected weekly (from June to November 1988), biweekly (March, May 1989), or monthly (April, May, and December 1988; January, February, April, and July 1989). The levels of sampling were integrated over depth-ranges: 0–4 m, 5–9 m and 10–14 m, corresponding respectively to epi-, meta-, and hypolimnion when the lake is strongly stratified (Sime-Ngando and Hartmann, 1991). 0–4 m samples were collected by using a flexible plastic tube, provided with a rope connecting the ballasted bottom of the tube with the surface. With this system, surface water samples are collected (in triplicate) by simple capillarity. 5–9 and 10–14 m samples are composite samples of an equal amount of water sampled with a Van-Dorn bottle at 1 m intervals. The sampling method is presented elsewhere (Sime-Ngando and Hartmann, 1991). Sub-samples (30 ml) were immediately fixed with buffered alkaline formaldehyde (final concentration 2% v/v), refrigerated in the dark, and analyzed (i.e. preparation of slides and counting, see below) the next day.

Autotrophic picoplankton (APP)

To determine APP numerical abundance, 5 to 10 ml sub-samples were filtered onto black Nuclepore membranes (0.2 µm porosity). Membranes were mounted between a slide and glass cover slip, with a non-fluorescent immersion oil (Olympus). Observations were made with an Olympus HBS microscope equipped with an epifluorescence illuminator HB2-RFL, a HBO-100 W mercury lamp, and a neofluar objective lens 100/1.25. Both free-living and colonial APP fluorescing yellow to orange (phycoerythrin-containing cells = prokaryotes) or red (non-phycoerythrin-containing cells = eukaryotes) were easily observed under blue light excitation (T. Sime-Ngando, unpublished photomicrographs). They were counted separately and considered as autotrophic, according to Tsuji et al. (1986). A set of Olympus

filters BP 490, DM 500, and O 515 was used with a supplementary excitation filter EY-455 improving the optical quality of the observed cells. At least 300 cells were counted in 15 to 35 fields, as has previously been described (Sime-Ngando et al., 1991). Phycocyanin containing APP which are more properly enumerated under green light excitation (Pick, 1991) were not taken into account, due to the absence of green light filters on our microscope when this study was carried out. They sometimes appear a dull red under blue light excitation when larger algae were illuminating the microscopic field of view, but were easily distinguished from eukaryotic APP (>1 μm) by their smaller size (<0.8 μm).

Other parameters and statistical analyses

APP data were statistically analyzed as: total (i.e. sum of different APP groups, see below), single-cell prokaryotic and eukaryotic, and colonial (i.e. the number of cells that existed in colonial form; mainly consisting of prokaryotes) cell numbers.

A parallel study (Sime-Ngando, 1991) generated data on: water temperature, pH, dissolved oxygen concentration, Secchi disk depths, nitrate-N, ammonium-N, and orthophosphate-P, as well as chlorophyll *a* concentration, heterotrophic bacterial, heterotrophic flagellate and ciliate abundances, and ciliate carbon biomass. Temperature, dissolved oxygen, and pH were measured with automated in situ probes and averaged over the appropriate depth ranges. Secchi disk depths (Ds) were transformed into light attenuation coefficient (k) according to Poole and Atkins (1929): $k = 1.7/\mathrm{Ds}$. Such estimates were within published extinction values for Lake Aydat (Amblard, 1988). Heterotrophic (i.e. non-pigmented) bacteria and flagellates were enumerated using the 4′,6′-diamino-2-phenylindole (DAPI) epifluorescence microscopical technique (Porter and Feig, 1980). Ciliates were counted in vivo, after concentration by passive filtration, according to Sime-Ngando et al. (1990). Ciliate biomass was calculated from the mean cell volume (of each taxon) which was determined by measuring cell dimension with a micrometer and approximating the cell shapes to geometrical figures (cf. Sime-Ngando and Hartmann, 1991). The dry weight biomass was obtained with the conversion factor of Gates et al. (1982), i.e. $1\ \mu m^3 = 0.279$ pg. The carbon biomass was calculated according to Finlay (1982), assuming that carbon represents 47.1 % of the dry weight.

APP abundances over time were related with other variables by linear pairwise correlations and step-wise multiple regressions. Nitrogen (i.e. NO_3–N, NH_4–N) and phosphorus (i.e. PO_4–P) concentrations which were measured only from August 1988 to February 1989, were excluded from step-wise regressions. APP counts were tested by analysis of variance (ANOVA) for differences between depths or seasons.

Results

Physical and chemical environment

The period of thermal stratification in Lake Aydat generally begins in late April and lasts into October (Amblard, 1988; Sime-Ngando, 1991). Maximum surface tempe-

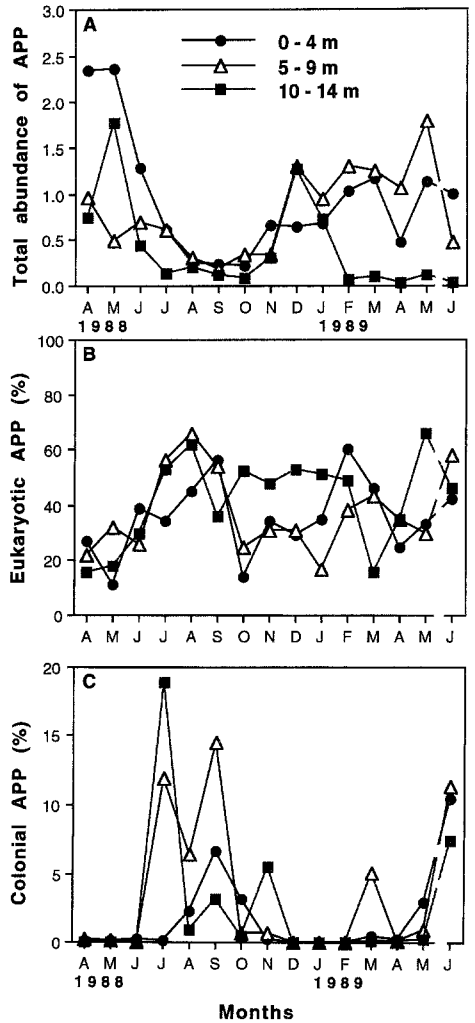

Figure 2. Seasonal and spatial changes in autotrophic picoplankton (APP) abundance ($\times 10^6$ cells $\cdot$ ml^{-1}) and the percentages of single-cell eukaryotic and colonial prokaryotic forms. Data not available for June 1989

rature (~ 20 °C) occurred in August 1988 and earlier (July) the next year (Fig. 1 A), due to more stable summer weather during the second year. The upper 4 m of the water column were generally well-oxygenated throughout the year. In contrast, oxygen concentration in the bottom waters declined rapidly with thermal stratification (Sime-Ngando, 1991). Oxygen was undetectable from June to August in the metalimnion, and from June to October in the hypolimnion (Fig. 1 B). The water column pH (measured from May 1988) was generally alkaline (mean pH = 7.6), although acidic pHs (5.9 to 6.9) occurred in the anoxic bottom waters during the

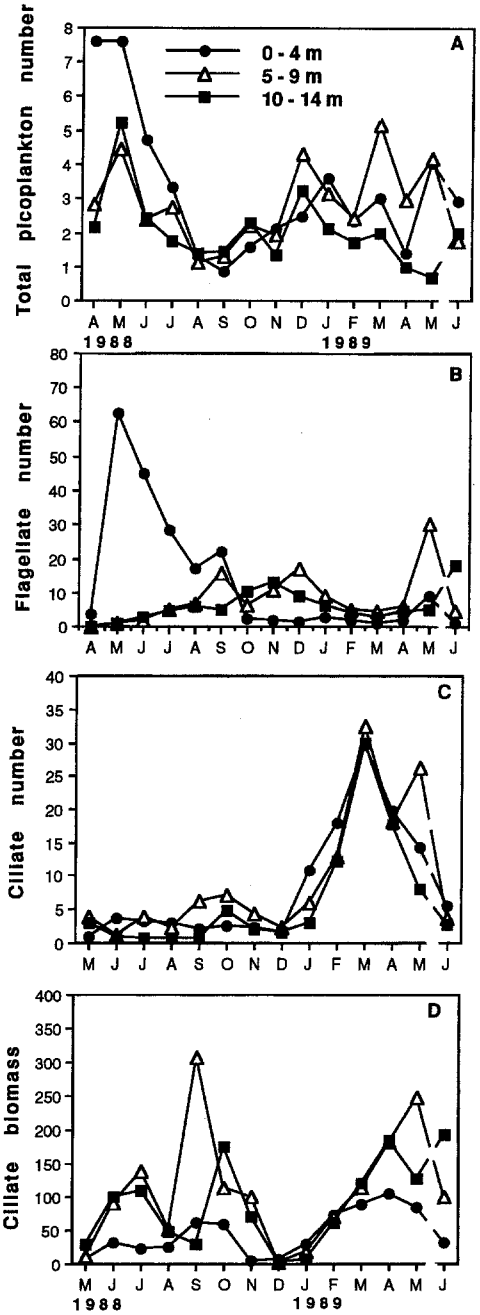

Figure 3. Seasonal and spatial changes in the abundances of total picoplankton (autotrophs + heterotrophs, $\times 10^6$ cells $\cdot$ ml^{-1}), heterotrophic flagellates ($\times 10^3$ cells $\cdot$ ml^{-1}), and ciliates ($\times 10^3$ cells $\cdot$ l^{-1}), and the carbon biomass of ciliates (μg C $\cdot$ l^{-1}). Note the absence of samples in June 1989

thermal stratification period (Fig. 1C). Light attenuation coefficient (measured from May 1988) peaked in July 1989 with surface temperature (Fig. 1A,D). Both parameters were significantly correlated ($r=0.62$, $p<0.05$).

Chlorophyll *a* concentration (measured from July 1988) varied from 0.02 to 50.34 $\mu g \cdot l^{-1}$ and peaked in the surface layer in July 1989 with temperature and light attenuation coefficient (Fig. 1A,D,E). Surface pigment concentration was significantly correlated to surface temperature ($r=0.55$, $p<0.05$) and to the light attenuation coefficient ($r=0.82$, $p<0.001$), indicating that the level of downward irradiance was mainly due to phytoplankton.

Spatial distribution

The number of autotrophic picoplankton (APP) ranged from 0.03 to 2.36×10^6 cells $\cdot$ ml^{-1} (Fig. 2A), and averaged 24% (standard deviation = 7%) of total picoplankton (APP + heterotrophic bacteria, Fig. 3A). For the entire sampling period, mean (± standard deviation) cell abundance of APP declined with depth from $0.94 \pm 0.67 \times 10^6$ cells $\cdot$ ml^{-1} (0–4 m) to $0.80 \pm 0.47 \times 10^6$ cells $\cdot$ ml^{-1} (5–9 m) and $0.41 \pm 0.51 \times 10^6$ cells $\cdot$ ml^{-1} (10–14 m). There was a significant difference (ANOVA, $p<0.05$) in APP cell number between 0–4 and 10–14 m.

At all depths, the community was numerically dominated (>50% of total cell number) by single-cell prokaryotic APP (likely cyanobacteria of *Synechococcus* and *Synechocystis* types). Mean contributions of other APP groups for 0–4, 5–9, and 10–14 m, respectively, were as follows: 35, 38, and 42% (single-cell eukaryotic APP), and 1.8, 3.4, and 2.4% (cells in colonial form) (cf. Fig. 2B,C). Aggregated APP in Lake Aydat consist mainly of prokaryotic colonies of 4 cells (Sime-Ngando, unpublished photomicrographs).

Temporal distribution

Autotrophic picoplankton (APP) number peaked in May (1988 for 0–4 and 10–14 m, 1989 for 5–9 m) along with heterotrophic flagellate abundance (at 0–4 m in 1988 and at 5–9 m in 1989) (Figs. 2A, 3B). Two phases were observed in APP dynamics through the water column. (1) In summer (1988), cell number generally decreased when proportions of both eukaryotic and colonial APP forms increased (Fig. 2A,B,C). The decreasing trend in APP cell number was more pronounced and rapid in the epilimnion, and coincided with a similar trend in flagellate number (Figs. 2A, 3B). (2) In autumn (1988), APP abundance increased and peaked by the end of the year for the two deepest layers, and later in spring (March 1989) for 0–4 m. The peak in the surface depth (0–4 m) coincided with that (observed for all depths) of the small oligotrichous ciliates of the genus *Strobilidium* (≤20 μm) and the scuticociliate *Cyclidium glaucoma* (30 μm) (Sime-Ngando, 1991). In the bottom waters (10–14 m), APP abundance decreased significantly (>100 fold) from December 1988 to February 1989 and remained low until the end of the sampling period. In contrast, the carbon biomass of *Strobilidium* and *Cyclidium* increased significantly (>100 fold) and peaked in April 1989 (Figs. 2A, 3C,D).

Table 1. Coefficient of linear pairwise correlation between the seasonal abundance of both autotrophic picoplankton (APP) and heterotrophic bacteria, and environmental variables in Lake Aydat. Only variables with $0.0001 \leq p \leq 0.05$ are listed. Blank = $p > 0.05$, $n = 12$ for chlorophyll, 14 for light attenuation, and 15 for other variables (cf. Figs. 1, 2, 3). Nutrients were excluded from analyses due to an insufficient number of points of comparison (5 degrees of freedom, cf. Fig 4).

Variable	Prokaryotic APP	Eukaryotic APP	Colonial APP	Total APP	Heterotrophic bacteria
0–4 m					
Light attenuation			0.91		
Chlorophyll			0.82		
Heterotrophic bacteria	0.93			0.89	1
5–9 m					
Temperature	−0.69			−0.67	
Oxygen	0.71	0.51		0.70	0.52
Ciliate abundance	0.68	0.60		0.73	0.58
10–14 m					
Ciliate biomass		−0.69		−0.62	
Heterotrophic bacteria		0.69		0.62	1

In the surface layer, there was a significant difference (ANOVA, $p < 0.05$) in cell number between spring 1988 and other seasons, for both APP and heterotrophic bacteria. Similar differences were also observed for APP in the bottom waters, but not for heterotrophic bacteria.

Correlations with environmental data

The strongest correlations for autotrophic picoplankton (APP) abundance were with biological variables (Table 1). In the upper water column (0–4 m), changes in prokaryotic APP abundance were positively correlated with changes in heterotrophic bacterial density. In addition, colonial APP abundance was positively correlated with chlorophyll *a* concentration. Prokaryotic and eukaryotic APP cell numbers were positively correlated with ciliate number at 5–9 m while eukaryotic APP abundance was negatively correlated with ciliate biomass at 10–14 m.

Ciliate abundance (0–4 m), flagellate number and oxygen concentration (5–9 m), and ciliate biomass (10–14 m) were the dominant factors in the multivariate models of APP number changes (Table 2). Multiple regression analysis did not produce a multivariate model for heterotrophic bacterial number changes for 0–4 and 10–14 m; chlorophyll *a* concentration and ciliate abundance were the dominant correlates for 5–9 m (Table 2).

Table 2. Multiple regression coefficient for autotrophic picoplankton and heterotrophic bacteria abundances versus environmental covariates in Lake Aydat. Nutrients were excluded from analyses due to an insufficient number of points of comparison (5 degres of freedom, cf. Fig. 4). Multiple regression did not produce a multivariate model for heterotrophic bacteria at 0–4 and 10–14 m.

Covariate	Coefficient	r^2	Equation constant
Autotrophic picoplankton			
0–4 m			
Ciliate abundance	0.024	0.41	0.45
5–9 m			
Flagellate abundance	0.027	0.68	0.08
Oxygen concentration	0.083	0.52	
10–14 m			
Ciliate biomass	−0.004	0.45	0.61
Heterotrophic bacteria			
5–9 m			
Chlorophyll	−0.096	0.58	1.96
Ciliate abundance	0.062	0.34	

Discussion

The numerical abundance ($0.03-2.36\times10^6$ cells $\cdot$ ml^{-1}) of autotrophic picoplankton (APP) in Lake Aydat falls within the range of published values ($0.4-2\times10^6$ cells $\cdot$ ml^{-1}) for APP abundance for productive lakes. In less productive systems, maximum APP densities range from 0.075×10^6 cells $\cdot$ ml^{-1} (ultra-oligotrophic lakes) to 0.5×10^6 cells $\cdot$ ml^{-1} (mesotrophic lakes) (e.g. Stockner, 1991 and comparative table therein).

The dominance of free-living prokaryotic cells among the APP in Lake Aydat agrees with results from most aquatic systems, including temperate and subarctic lakes (Burns and Stockner, 1991; Pick, 1991; Stockner and Shortreed, 1991; Fahnenstiel and Carrick, 1992), open ocean and coastal marine environments (Joint, 1986; Waterbury et al., 1986; Campbell and Carpenter, 1987). However, the numerical importance (range, 11–66%; mean, 38% of total abundance, of red-fluorescing APP (free-living eukaryotes) in the water column was sufficiently high not to be overlooked. This is similar to the results from the hypereutrophic zone of Lake Balaton (Hungary) where eukaryotic APP (EAPP) constituted over 80% of the total APP abundance (Vörös et al., 1991). In oligotrophic freshwater, EAPP generally constitute a minor component of APP populations (Caron et al., 1985; Hardy et al., 1986; Nagata, 1986; Pick and Caron, 1987; Weisse, 1988; Kennaway and Edwards, 1989). However, Fahnenstiel et al. (1991) found EAPP from oligotrophic Laurentian Great Lakes (Lakes Huron and Michigan) to constitute over 50% of the total APP abundance. These authors pointed out the lack of EAPP abundance data in other freshwater environments, because of methodological limitations.

APP cell number significantly decreased (about 2-fold, see results) from the surface to the deepest waters. This was apparent in winter and spring (Fig. 2A). Although spatial distribution of APP abundance is scarce in freshwater ecosystems,

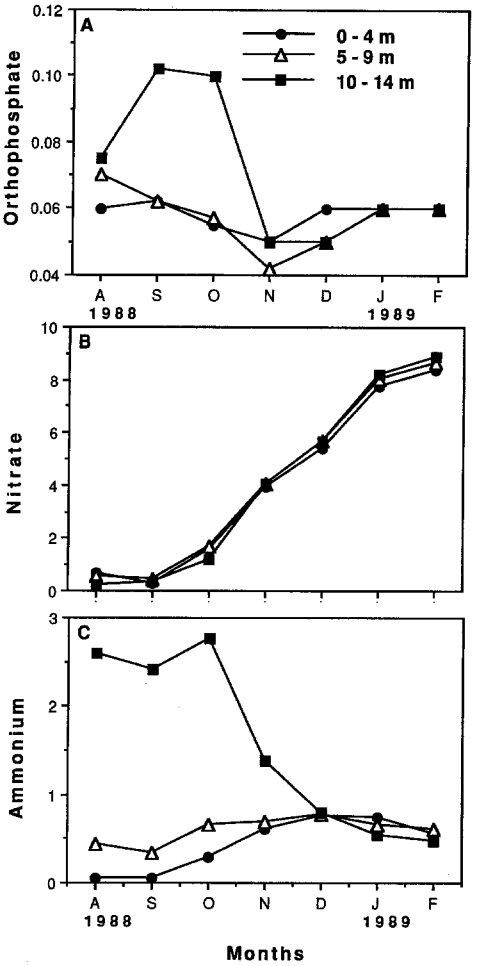

Figure 4. Spatio-temporal variations of phosphorus (PO_4–P) and nitrogen (NO_4–N, NH_4–N) levels ($\mu mol \cdot l^{-1}$) in Lake Aydat

similar trends have been reported for other lakes, such as meso-eutrophic Lake Constance in Central Europe (Weisse and Kenter, 1991), eutrophic Lake Hayes and oligotrophic Lake Manapouri both in New Zealand (Burns and Stockner, 1991). In Lake Aydat, mean contributions of eukaryotic and colonial cells to the total APP number were relatively higher in the bottom waters than in the surface (see results). In Laurentian Great Lakes, Fahnenstiel et al. (1991) found EAPP to exhibit a subsurface abundance maximum during the period of thermal stratification. The temporally acidic bottom waters of Lake Aydat (Fig. 1C) may represent a suitable environment for EAPP growth. These organisms usually increase in both number and diversity with increasing acidity (e.g. Stockner and Shortreed, 1991).

The pattern of seasonal APP abundance in Lake Aydat was quite similar for all depths. Seasonal abundance peaked in May (generally with microzooplankton density, decreased in summer-stratified period, and increased with fall turnover (Fig. 2A). Similar seasonal pattern was reported by Vörös et al. (1991) for the hypereutrophic zone of Lake Balaton. In other lakes, APP cell numbers generally peak in summer or early fall (Caron et al., 1985; Fahnenstiel et al., 1986; Nagata, 1986), similar to brackish (Jochem, 1988) and marine waters (Krempin and Sullivan, 1981; El Haq and Fogg, 1986; Joint et al., 1986). However, the spring peaks might have been missed in most of the seasonal studies on APP, due to the general low sampling frequency of these studies which mainly concentrated on the summer period. For example, the seasonal distribution of APP in Lake Constance investigated on a biweekly basis over four consecutive years showed recurrent peaks in spring and late summer (Weisse and Kenter, 1991).

In Lake Aydat where PO_4-P levels (Fig. 4A) are generally non-limiting for phytoplankton growth throughout the year (Amblard, 1988), the decline of APP growing in the summer was likely affected by the low nitrate levels (Fig. 4B). Although nutrients were measured for a short-time period, APP cell numbers were significantly ($P<0.01$, $df=5$) and positively correlated with nitrate concentrations in all depths. In addition, ammonium concentration (Fig. 4C), which may be preferred over nitrate by cyanobacteria (Klemer, 1991), was significantly ($P<0.01$, $df=5$) and positively correlated with prokaryotic APP abundance in the surface waters. These correlations agree with those of other studies in which freshwater algal picoplankters generally increase in number in response to pulses of nitrogen (e.g. Wehr, 1991).

In August 1988 and in July 1989, chlorophyll *a* concentration peaked in the surface waters (Fig. 1E), due to the development of filamentous blue-green algae, dominated by N_2-fixing species (e.g. Sime-Ngando, 1991; Sime-Ngando and Hartmann, 1991). The summer bloom of filamentous algae in Lake Aydat generally contributes to a decrease in nitrogen concentrations (Amblard, 1988) which may account for the strong limitation of APP growth, due partly to the competitive exclusion of APP by larger phytoplankton. This N-limitation may also help explain the occurrence of colonial APP in summer-autumn (Fig. 2C). The prevalence of microaggregated APP cells in the plankton when nutrient limitation is most severe was reported from the epilimnion of a eutrophic lake (Pedros-Alio and Brock, 1983) as well as from the epilimnion and deep chlorophyll layer of an ultra-oligotrophic lake (Klut and Stockner, 1991). These authors suggest that aggregated cells may have enhanced survival value over the free-living mode of existence.

Indications of APP growth limitation by competitive exclusion by larger phytoplankton relative to nitrogen utilization in this study are consistent with observations from other lakes (Stockner, 1987; Hardy et al., 1986; Stockner and Shortreed, 1988; Shortreed and Stockner, 1990; Vörös et al., 1991; Wehr, 1991). However, chlorophyll concentration in Lake Aydat was significantly correlated with surface temperature, but not with inorganic nitrogen concentrations. This implies that factors other than light and nutrients, such as temperature, can also control the natural assemblage of phytoplankton. However, the lack of correlation between pigment concentration and inorganic forms of nitrogen could be an outcome of the paucity of nutrient data during this study. Some freshwater (Caron et al., 1985) and

marine (Krempin and Sullivan, 1981; Joint, 1986; Jochem, 1988) studies (mainly focusing on *Synechococcus*) showed a general trend of increasing APP abundance with temperature. In summer, light attenuation may provide the best prediction ($r^2 = 53\%$) of epilimnetic cyanobacterial abundance (Pick, 1991).

Step-wise multipe regression analysis suggested that APP numbers within Lake Aydat may be controlled by micrograzers. The model included ciliate abundance and ciliate biomass as the single dominant covariates for 0–4 and 10–14 m, respectively (Table 2). In addition to flagellate abundance, the model that accounted for changes in 5–9 m APP number also includes oxygen concentration as a dominant correlate (Table 2). Oxygen concentration ($r = -0.87$, $p < 0.01$) and APP abundance ($r = -0.69$, $p < 0.01$) were negatively correlated with water temperature at 5–9 m. Such correlations indicate that changes in APP number may also be influenced by seasonal changes in the lake. However, in the multivariate model for 5–9 m, flagellate abundance explains 1.3-fold more variance in APP number changes than did oxygen concentration (Table 2). Furthermore, APP abundances in other depths, including surface waters, were not significantly correlated with temperature (Table 1).

The negative correlation between APP number and ciliate biomass in the deepest waters (Table 1, 2) indicates a predator-prey relationship. Previous work in Lake Aydat (Sime-Ngando and Hartmann, 1991) clearly revealed a rapid intrinsic growth of hypolimnetic ciliates (doubling time = 5.3 h) feeding selectively on large picoplankton cells such as APP (mean volume > 0.1 μm^3), rather than on small cells such as heterotrophic bacteria (mean volume < 0.1 μm^3, Sime-Ngando et al., 1991). The latter organisms were positively correlated with APP in the deepest waters, but were not correlated with micrograzer density (Table 1). In addition, the multiple regression analysis produced a multivariate model for heterotrophic bacteria only for 5–9 m where chlorophyll concentration explained 1.7 fold more variance in their cell number changes than did ciliate abundance (Table 2).

The data presented here highlight the complexity and our incomplete understanding of processes which control APP abundance in eutrophic lakes. Nevertheless, the data suggest micrograzer-control of APP abundance in Lake Aydat, complimenting other reports (using different approaches) of tight coupling between APP and microzooplankton (Campbell and Carpenter, 1986; Sherr et al., 1986; Sherr and Sherr, 1987; Fahnenstiel et al., 1991). Clearly, this study was inadequate to distinguish all factors influencing seasonal variations of APP. Thus it leaves unanswered the nature and the role of a variety of metazoan sources of predation (e.g. review in Stockner, 1991). Seasonal in situ studies offer a promising approach to the elucidation of the functional role of autotrophic picoplankton in aquatic ecosystems.

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