

Plankton food web structure in a eutrophic polymictic lake with a history of toxic cyanobacterial blooms

*Maria Moustaka-Gouni*¹ and *Elisabeth Vardaka*²

Department of Botany, School of Biology, Aristotle University of Thessaloniki, GR-541 24 Thessaloniki, Greece

Evangelia Michaloudi

Laboratory of Ichthyology, School of Biology, Aristotle University of Thessaloniki, GR-541 24 Thessaloniki, Greece

Konstantinos Ar. Kormas

Department of Animal Production and Aquatic Environment, GR-383 34 Nea Ionia, Volos, Greece

Eleni Tryfon,³ *Helen Mihalatou*, *Spyros Gkelis*, and *Tom Lanaras*

Department of Botany, School of Biology, Aristotle University of Thessaloniki, GR-541 24 Thessaloniki, Greece

Abstract

We studied the seasonal dynamics of phytoplankton, bacterioplankton, heterotrophic nanoflagellates, ciliates, and metazoan plankton in the highly eutrophic polymictic Lake Kastoria (Greece), which has a history of toxic cyanobacterial blooms. An acute increase in the flushing rate of the lake during spring inhibited cyanobacterial biomass accumulation. During this transient oligotrophic period, which was characterized by abundant lake snow particles, the plankton food web was an inverted biomass pyramid (low autotrophic biomass and high heterotrophic biomass). Prokaryotes played a key role in these changes (cyanobacteria during periods of autotrophy and bacteria during periods of heterotrophy). In summer and autumn, toxic cyanobacterial blooms developed, and the microbial loop was weak. The microbial loop was weak because the heterotrophic nanoflagellates and nanociliates decreased to undetectable densities during the summer, when larger bacterivores (rotifers and small cladocera) were abundant. Toxic blooms may have a dual effect on heterotrophic nanoplankton: negative during the first bloom and postbloom period and positive during a following toxic bloom. Different species (*Cylindrospermopsis raciborskii*, *Aphanizomenon* spp., and *Microcystis aeruginosa*) and succession phases of toxic blooms may differentially affect the microbial food web structure.

In pelagic systems, phytoplankton and bacterioplankton constitute the complementary functional components that primarily produce new particulate matter by autotrophy and heterotrophy. Their carbon pool represents the base of grazing food chains and the microbial loop. Thus, the relative dominance of each functional component has significant implications for food web structure and the function and bio-

geochemistry of nutrients in aquatic systems (Cho and Azam 1990). The bacterial biomass has been found to make up a substantial fraction of the total planktic biomass in pelagic systems and even exceeds phytoplankton biomass in oligotrophic conditions (Cho and Azam 1990; Simon et al. 1992). With increasing nutrient enrichment and phytoplankton biomass, the ratio of heterotrophic to autotrophic biomass in freshwater and marine systems declines systematically (del Giorgio and Gasol 1995; Gasol et al. 1997).

Bacterioplankton are heavily grazed by a wide range of organisms such as heterotrophic and mixotrophic flagellates, ciliates, rotifers, and cladocerans (e.g., Sanders et al. 1989). Heterotrophic nanoflagellates and ciliates, the principal bacterivores, constitute the link between the microbial loop and the grazing food chain through their consumption by metazoan plankton. In lakes, on a seasonal scale, cladocerans exert the highest negative effect on heterotrophic nanoflagellates during summer (Gasol et al. 1995). Pronounced minima or even gaps in the plankton size spectra appear only in connection with high *Daphnia* biomass (Tittel et al. 1998). High daphnid biomass was related to a bumpy plankton size spectrum on a seasonal scale in a highly eutrophic polymictic flushed lake (Gaedke et al. 2004). Copepods select for larger particle size than cladocera, thus suppressing ciliates and releasing heterotrophic nanoflagellates from ciliate predation (Sommer et al. 2003).

¹ Corresponding author (mmustaka@bio.auth.gr).

² Present address: Department of Fisheries and Aquaculture Technology, Technological Educational Institute of Thessaloniki, Campus of Nea Moudania, P.O. Box 157, GR-632 00 Nea Moudania, Greece.

³ Present address: Administration of Environmental Planning, Hellenic Ministry for the Environment, Physical Planning and Public Works, GR-112 51 Athens, Greece.

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In eutrophic lakes, the phytoplankton include dominant organisms that, because of their large size, are well protected against grazing (Sommer et al. 1986). However, they are affected by density-independent losses caused mainly by flushing and settling (Scheffer 1998). According to the top-down control, as Sommer and Stibor (2002) cite, "the distribution of phytoplankton biomass to size classes does not reflect the menu offered to the herbivores but the leftovers after feeding." The ratio of zooplankton to phytoplankton biomass declines sharply in shallow lakes above a total phosphorus (TP) threshold of 0.1 mg L^{-1} (Jeppesen et al. 1997). In lakes with $\text{TP} > 0.1 \text{ mg L}^{-1}$, the cyanobacteria exceed 70% of the total phytoplankton biomass (Watson et al. 1997). A massive increase in the biomass of cyanobacteria leads to water blooms that are considered one of the most undesirable consequences of eutrophication. Flushing a lake with clean water can help eliminate colonial cyanobacteria (Scheffer 1998).

Blooms of toxic cyanobacteria are common in eutrophic lakes throughout the world. *Microcystis*, *Aphanizomenon*, and *Cylindrospermopsis* are among the most common genera that include species that have been documented to produce toxins (Sivonen and Jones 1999). Toxins are released into the water in large amounts after the bloom collapses (Harada and Tsuji 1998). The ecological implications of cyanobacterial toxins in aquatic food webs, such as the reduced grazing potential of larger zooplankton and the failure of sensitive protozoa to develop, have been pointed out by Christoffersen (1996). On the other hand, it is known that toxic *Nodularia spumigena* blooms provide a potential food source for the heterotrophic food chain in the Baltic Sea (Engström-Öst et al. 2002). Furthermore, bacteria can efficiently degrade microcystins (MCs) in natural waters with a previous cyanobacterial history, and heterotrophic nanoflagellates respond quickly to the bacterial growth (Christoffersen et al. 2002).

Toxic cyanobacterial blooms are common in Lake Kastoria, and MCs constitute an inherent component of the lake's system. Toxins were identified in the lake for the first time in 1987 (Lanaras et al. 1989). Moreover, Lake Kastoria is one of the few lakes worldwide in which the temporal and spatial distribution of MC-LR has been studied (Cook et al. 2004). High MC-LR concentrations (max. = $3,186 \mu\text{g L}^{-1}$) were detected in samples collected from inshore stations. The percentage of MC-containing samples in water-bloom samples was 100%, and it is the highest reported percentage in the literature (Gkelis et al. 2005). In addition to MCs, other bioactive peptides (anabaenopeptins) produced by cyanobacteria have been identified in Lake Kastoria (Gkelis et al. 2005).

The objective of this study was to quantify the plankton community components (functional groups, taxonomic groups, and dominant species) in a lake with a previous history of toxic cyanobacterial blooms and identify the possible effects of these blooms on the microbial food web structure. An acute increase in the flushing rate of the lake in spring 1999 inhibited cyanobacteria biomass accumulation and provided the opportunity to quantify the plankton community components during the transient oligotrophic conditions. The present study contributes to the understanding of the possible

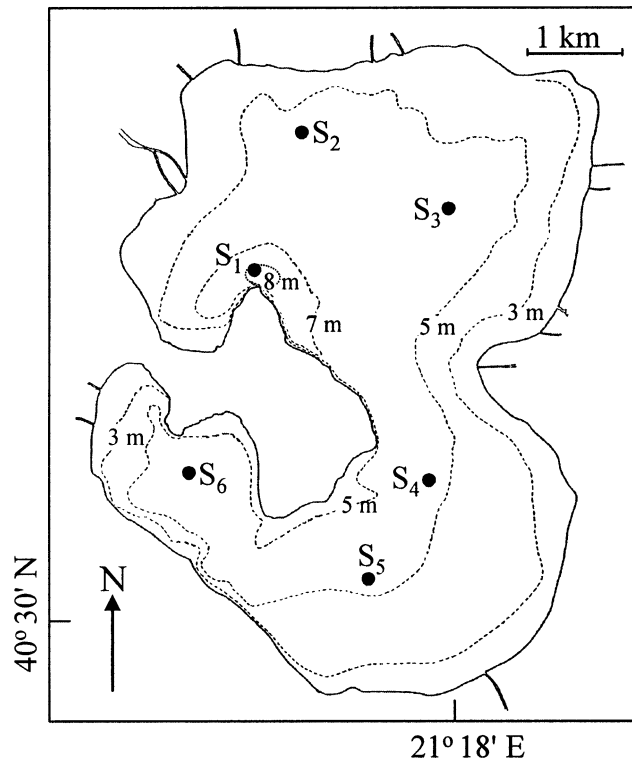


Fig. 1. Map of Lake Kastoria with 3-, 5-, 7-, and 8-m depth contours. The six sampling stations (S_1 , S_2 , S_3 , S_4 , S_5 , and S_6) in the lake are indicated with solid circles.

effects of toxic cyanobacteria on plankton food web structure at the ecosystem level, an issue that has recently been the focus of intensive research (Christoffersen 1996; Christoffersen et al. 2002; Engström-Öst et al. 2002).

Methods

Study site and sampling—Lake Kastoria ($40^{\circ}30'N$, $21^{\circ}18'E$) (Fig. 1) is a polymictic lake with a 24-km^2 surface area, a maximum depth of 8 m, an average depth of 4 m, and a long water retention time ($>2 \text{ yr}$). It is an urban lake that had been receiving sewage effluents for years until 1995. Unlike natural lakes, the discharge from Lake Kastoria is regulated with respect to maintaining a constant water level, particularly when the lake volume increases because of winter inflows. In March 1999, the highest known water level (629.48 m above sea level) was recorded, after an increase in depth of 0.25 m in the previous 3 months (Ministry of Agricultural Development and Food unpubl. data). Lake managers lowered the water level by releasing large amounts of surface water at distinct times in March and April. From March to April, the inflow of cooler and denser water ($6.0\text{--}12.5^{\circ}\text{C}$) flushed out the warmer lake water ($7.8\text{--}17.1^{\circ}\text{C}$). The highest flushing rate was 0.53% of the lake volume per day (calculated from water level changes). The fluctuations of flushing rate calculated from daily sum of outflow on the basis of weekly-biweekly measurements in spring 1999 (Tolikas 2000) are shown in Fig. 2.

Sampling was conducted at six stations (Fig. 1) in the

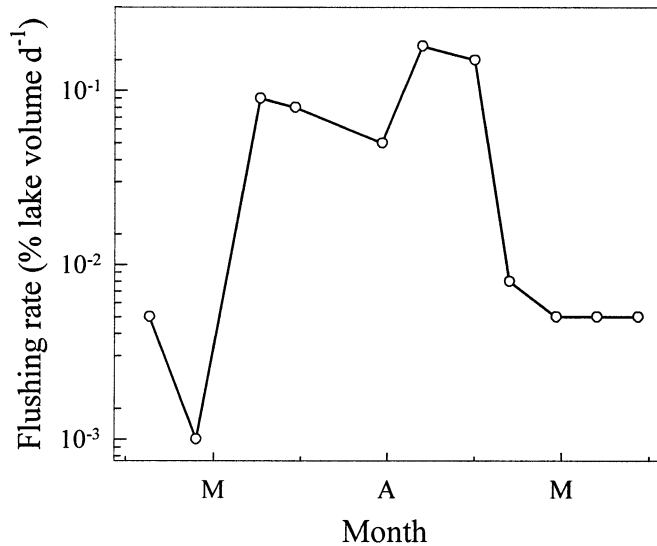


Fig. 2. Flushing rate (% lake volume d⁻¹) from March to May 1999 in Lake Kastoria (data from Tolikas 2000).

deeper areas of the lake's basin (depth = >4 m). Water samples for the determination of oxygen, nutrients, TP, chlorophyll *a* (Chl *a*), phytoplankton, bacterioplankton, heterotrophic nanoflagellates, and ciliates were collected with a Nansen-type sampler from the surface (0–1 m) and the bottom layer (1 m above sediment). Water temperature, pH, and transparency were measured in situ using a portable WTW-type pH meter and a Secchi disk. Sampling was carried out from November 1998 to October 1999 monthly during the cold period and biweekly during the warm period of the year. Ice cover in the lake prohibited sampling in December 1998.

For the zooplankton study, samples from the whole water column were collected from the six sampling stations (Fig. 1) from March to October 1999, monthly or biweekly (during summer). Sampling was performed with an electric pump MARCO 6.102 UP3 12V, with a nominal flow rate of 14 L min⁻¹. At least 30 liters of water was filtered each time, through filter with a net size of 50 μm, and preserved in 4% (v/v) formalin.

Chemical analyses—Dissolved oxygen was determined using the Winkler method (Strickland and Parsons 1968), and the concentrations were converted to saturation values (%). Chl *a* in water samples filtered on to Whatman GF/C filters was determined spectrophotometrically in 90% methanol extracts using the equation of Talling and Driver (1963). Dissolved inorganic nutrient concentrations (soluble reactive phosphorus [SRP], nitrate nitrogen [NO₃-N], nitrite nitrogen [NO₂-N], and dissolved silicon [SiO₂-Si]) in samples filtered through Whatman GF/C filters were determined using the methods of the American Public Health Association (1976), except for ammonia nitrogen (NH₄-N), which was determined by the method of Liddicoat et al. (1976). Dissolved inorganic nitrogen (DIN) expresses the total nitrate, nitrite, and ammonia nitrogen. TP was determined after persulfate digestion according to the American Public Health Association (1976).

Phytoplankton and heterotrophic protists—Phytoplankton in live and preserved samples were examined with a light microscope and identified using taxonomic keys. At least 500 individuals of phytoplankton and heterotrophic protists (colorless nanoflagellates >5 μm and ciliates) were counted for each sample (Lugol-preserved) with an inverted microscope. Pigmented nanoflagellates belonging to chlorophytes (*Phacotus lenticularis*), cryptophytes (*Rhodomonas* and *Cryptomonas* species), and prymnesiophytes (*Chrysochromulina parva*) were easily distinguished from colorless flagellates (*Bodo* species and chrysoomonads) in the live and preserved material with a light microscope. Mean cell or filament volume was estimated using geometric formulae after measuring the dimensions of 30 individuals (cells or filaments). The cell and filament volume estimates were converted to biomass (wet weight) by assuming a density of 1 g cm⁻³. Conversion of phytoplankton cell volume into cellular carbon was made according to the equation of Rocha and Duncan (1985). Carbon biomass was estimated using the conversion factors of 220 fg carbon μm⁻³ for colorless nanoflagellates (Børsheim and Bratbak 1987) and 140 fg carbon μm⁻³ for ciliates (Putt and Stoecker 1989).

MC analysis—Composite samples (made by mixing water samples from the whole water column from all six stations) collected from March to October 1999 and preserved in 4% (v/v) formalin were used for MC quantification. MC extraction was performed according to Gkelis et al. (2005). MCs were quantified in the extracts using the Envirologix Microcystin Plate Kit according to the manufacturer's instructions. The negative control, three standards, and the samples were all analyzed in duplicates. The microtiter plates were read at 450 and 630 nm, and B₀ values (%) were calculated. Samples with a coefficient of variation (C.V.) percentage of >15% were not accepted. Results are given in microgram MC-LR equivalents per liter of water. The presence of MCs during the study period was confirmed by high-pressure liquid chromatography for samples collected in July, August (Gkelis et al. unpubl. data), and October (Gkelis et al. 2005).

Picoplankton—Samples for bacterial counts were preserved in particle-free 2% (v/v) formaldehyde. Bacteria were enumerated by DAPI (4',6-diamidino-2-phenylindole) direct epifluorescence counts (Porter and Feig 1980). The final concentration of the fluorescing dye DAPI was 10 μg ml⁻¹. Water samples were filtered through black polycarbonate Millipore filters (0.2-μm pore diameter). Filters were mounted in slides using paraffin oil. Filtered volume varied between 1 and 2 ml. Bacteria were counted at ×1,000 magnification with an IM 35 ZEISS epifluorescence microscope using a 100-W mercury lamp. Ultraviolet excitation (G 365, FT 395, LP 420, ZEISS filter set) was used for bacterial counting. At least 20 fields (200–800 cells) were counted per slide. Mean cell volume was estimated using geometric formulae, and measurements of the size of several cells were estimated using an ocular micrometer. Cell volume estimates were converted to bacterioplankton biomass (wet weight) by assuming a density of 1 g cm⁻³. Carbon biomass was estimated using a conservative conversion factor of 120 fg carbon μm⁻³. Bacteria having complex forms (budding bac-

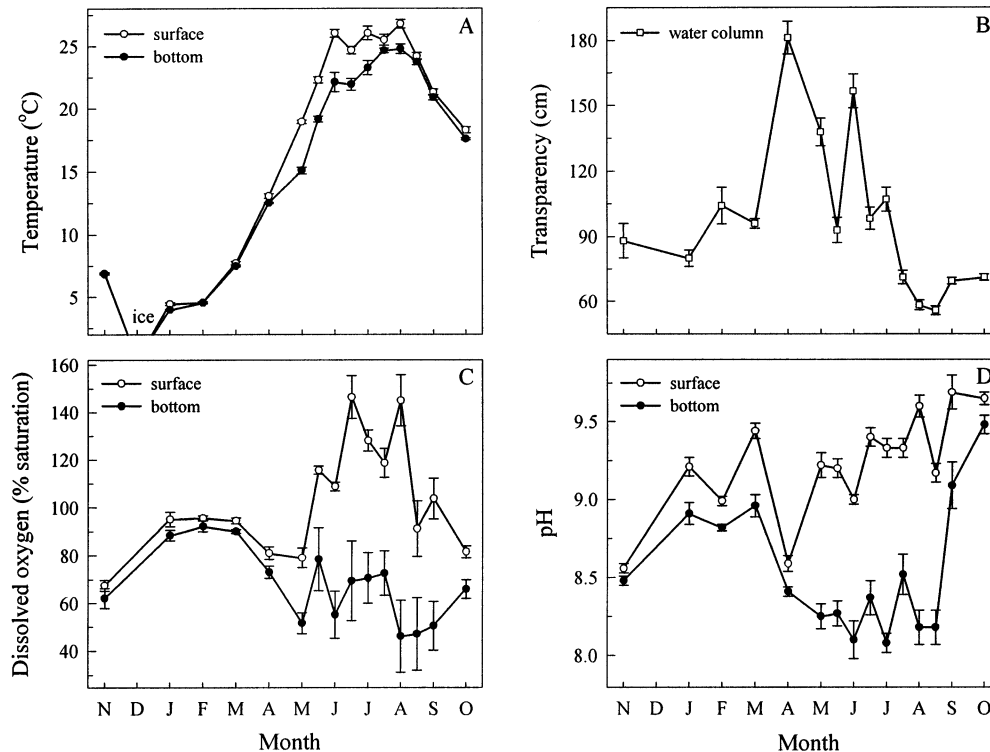


Fig. 3. Physical and chemical parameters in Lake Kastoria from November 1998 to October 1999. (A) Temperature, (B) transparency, (C) dissolved oxygen (% saturation), and (D) pH. Values are means and refer either to the surface or bottom layers (A, C, D) or to the whole water column (B) from all six stations. Bars represent standard deviation.

teria) with a colony size of up to 30 μm are considered grazing resistant. They were counted with an inverted microscope, and their carbon biomass was estimated similarly to that for picoplanktic bacteria.

Synechococcus-type picophytoplankton were counted occasionally in unpreserved samples with an IM 35 ZEISS epifluorescence microscope using a 100-W mercury lamp for green excitation (BP 546, FT 580, LP 590, ZEISS filter set). Counts and estimation of carbon biomass were determined as for heterotrophic bacteria.

Zooplankton—For each sample (total volume of 100 ml), five counts of 1-ml subsamples were made on a Sedwick-Rafter cell, with a light microscope to estimate abundance. Biomass was calculated using individual dry weight data, while the converting factor of 0.4 was used for the calculation of carbon biomass.

Size classes—Picoplankton were defined as microorganisms $<2 \mu\text{m}$. Nanoplankton included organisms with their longest dimension between 2 and 20 μm . Microplankton included autotrophs $>20 \mu\text{m}$ and heterotrophs in the range of 20–300 μm . Macrozooplankton were defined as heterotrophs $>300 \mu\text{m}$.

Statistical analysis—Pearson correlation analysis was used to determine relationships between physical and biological parameters (Legendre and Legendre 1998). Principal component analysis (PCA) was used to determine relation-

ships between individual plankton components and physical and chemical parameters of the water (Legendre and Legendre 1998). When necessary, log transformation of values was made to achieve normality.

Results

Physical-chemical parameters—There was a strong seasonal cycle of water temperature ranging from 0°C to $26.8^\circ\text{C} \pm 0.4^\circ\text{C}$ with vertical gradients from May to August (Fig. 3A). Water transparency, which was generally low (annual mean = $97.9 \pm 36.9 \text{ cm}$), varied considerably between 22 March and 14 June (Fig. 3B). Dissolved oxygen varied noticeably in time and space, decreasing to $46.2\% \pm 15.1\%$ saturation at the bottom water layer during the summer (Fig. 3C). The pH mean values ranged from 8.1 ± 0.1 to 9.7 ± 0.1 (Fig. 3D). Mean SRP concentrations varied between 1.1 ± 0.1 and $32.5 \pm 2.8 \mu\text{g L}^{-1}$ (Fig. 4A). Nitrate nitrogen dropped to low levels in summer (min. = $4.8 \pm 1.9 \mu\text{g L}^{-1}$) (Fig. 4B), while ammonia nitrogen was undetectable in June (Fig. 4C). Dissolved silicon was in low concentrations throughout the year (max. = $415.3 \pm 6.7 \mu\text{g L}^{-1}$) (Fig. 4D). DIN dropped to low levels ($<30 \mu\text{g L}^{-1}$) in March, June, and October (Fig. 4E). Total phosphorus (annual mean = $189.3 \pm 201.0 \mu\text{g L}^{-1}$) reached its highest concentrations in May ($626.2 \pm 145.5 \mu\text{g L}^{-1}$) and July ($513.9 \pm 80.7 \mu\text{g L}^{-1}$) (Fig. 4F).

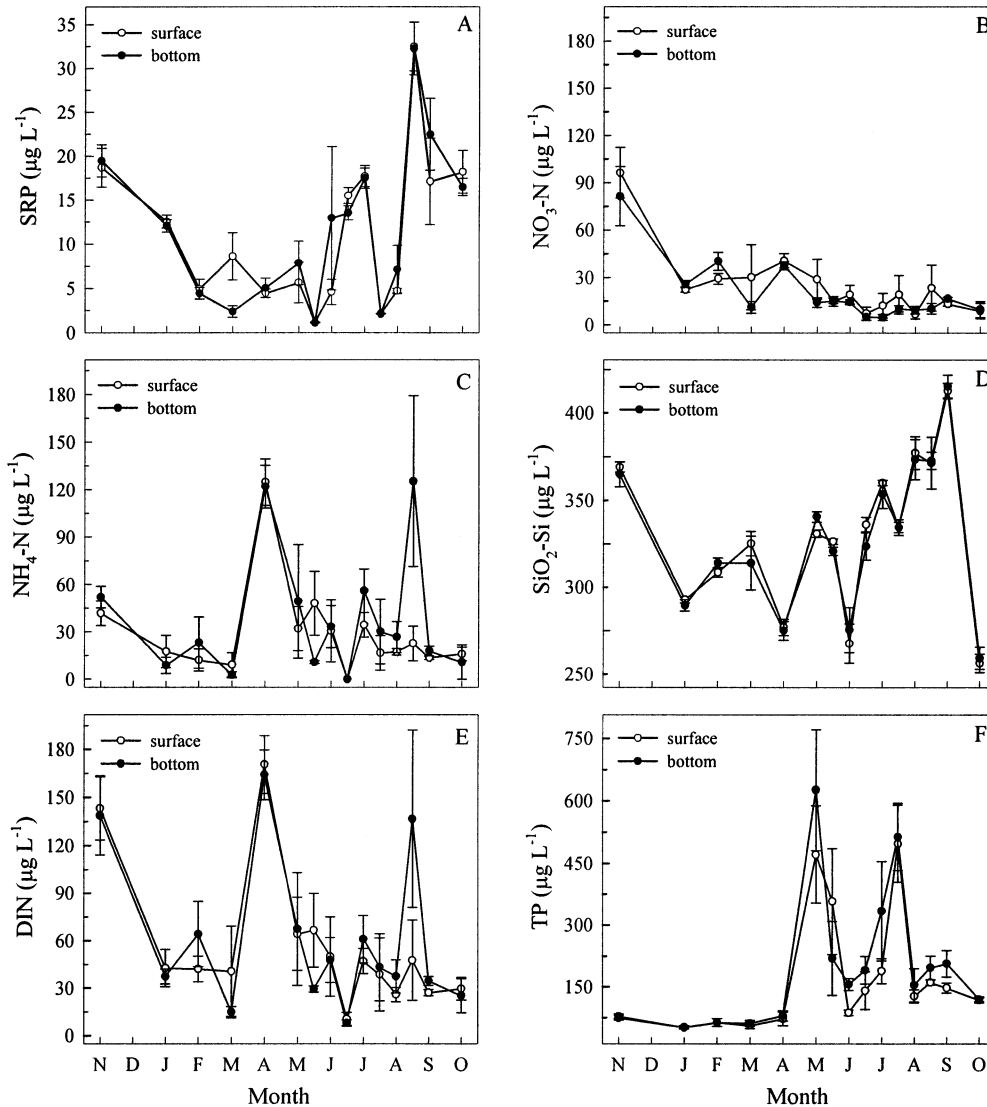


Fig. 4. Chemical parameters in Lake Kastoria from November 1998 to October 1999. (A) Soluble reactive phosphorus (SRP), (B) nitrate nitrogen ($\text{NO}_3\text{-N}$), (C) ammonia nitrogen ($\text{NH}_4\text{-N}$), (D) dissolved silicon ($\text{SiO}_2\text{-Si}$), (E) dissolved inorganic nitrogen (DIN), and (F) total phosphorus (TP). Values are means and refer to the surface or bottom layers from all six stations. Bars represent standard deviation.

Autotrophs—Mean Chl *a* concentrations varied from 8.7 ± 1.1 to $112.0 \pm 20.5 \mu\text{g L}^{-1}$ (Fig. 5A). Phytoplankton biomass showed abrupt seasonal changes, reaching low levels from 15 April to 14 June and vertical differences from summer to autumn (Fig. 5B). The biomass dropped dramatically to very low levels ($66.7 \pm 10.5 \mu\text{g carbon L}^{-1}$) in April following a flushing rate increase in late March (Fig. 2) after a reduction in DIN (Fig. 4E). Cyanobacterial biomass, and particularly the biomass of the dominant species *Limnothrix redekei*, showed an almost identical pattern to that of the total phytoplankton biomass from November to June (Fig. 5C,D). The biomass of known toxic cyanobacteria (*Cylindrospermopsis raciborskii*, *Aphanizomenon* spp., and *Microcystis aeruginosa*) increased during the rest of the year (June–October) (Fig. 5E–G). Nanophytoplankton biomass reached peak values in summer when a spatially uneven dis-

tribution was observed (Fig. 5H). Picophytoplankton ranged from 11 to $340 \times 10^6 \text{ cells L}^{-1}$.

From 15 April to 14 June, the phytoplankton biomass remained very low. During the same time, abundant aggregates of transparent particles (370×10^3 to $5,503 \times 10^3 \text{ L}^{-1}$) were observed in the lake. Inclusions of phytoplankton, heterotrophic nanoplankton, and debris were observed in the transparent mucuslike particles of variable shape and size (up to $700 \mu\text{m}$).

Microcystins—Concentrations of MCs ranged from undetectable levels up to $34.0 \mu\text{g MC-LR equivalents L}^{-1}$ (Fig. 6). Very low concentrations were recorded from March to June, and then MC concentrations increased following the increase of the known MC-producing cyanobacteria biomass (Fig. 5F,G).

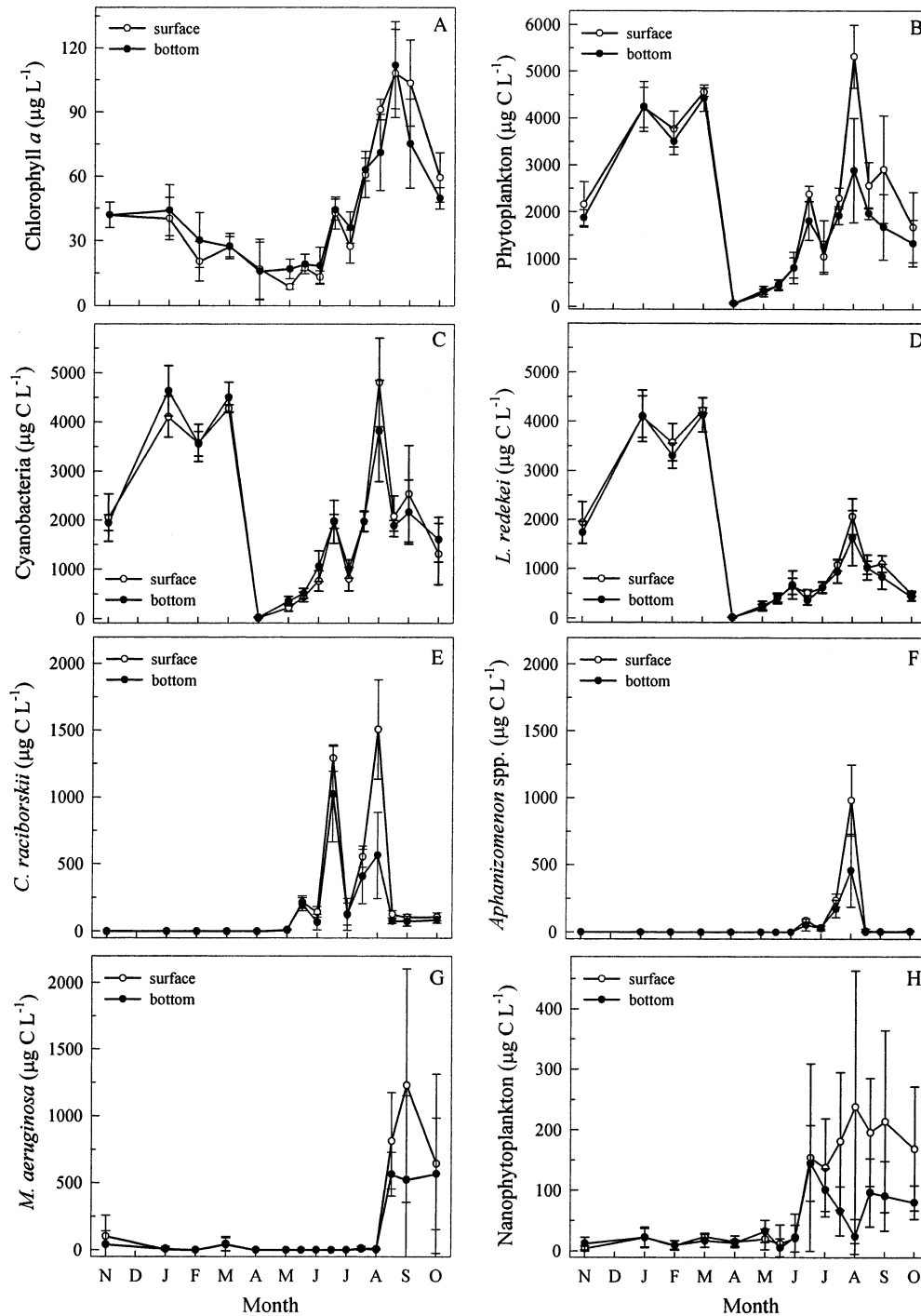


Fig. 5. Biological parameters in Lake Kastoria from November 1998 to October 1999. (A) Chlorophyll *a*, (B) total phytoplankton biomass, (C) total cyanobacteria biomass, (D) *Limnothrix redekei* biomass, (E) *Cylindrospermopsis raciborskii* biomass, (F) *Aphanizomenon* spp. biomass, (G) *Microcystis aeruginosa* biomass, and (H) nanophytoplankton biomass. Values are means and refer to the surface or bottom layers from all six stations. Bars represent standard deviation.

Heterotrophs—Bacterial abundance increased sharply from March ($3.0 \pm 0.3 \times 10^9$ cells L^{-1}) to May ($12.9 \pm 0.9 \times 10^9$ cells L^{-1}), showing minor spatial differences (Fig. 7A). Bacterial biomass showed a very similar pattern to that of the abundance, differing only during summer, when it

reached higher biomass values at the bottom water layer (Fig. 7B).

Heterotrophic nanoflagellates were observed in low densities throughout the year (annual mean = $1.5 \pm 1.9 \times 10^5$ cells L^{-1}). After the steep drop of their abundance on 29

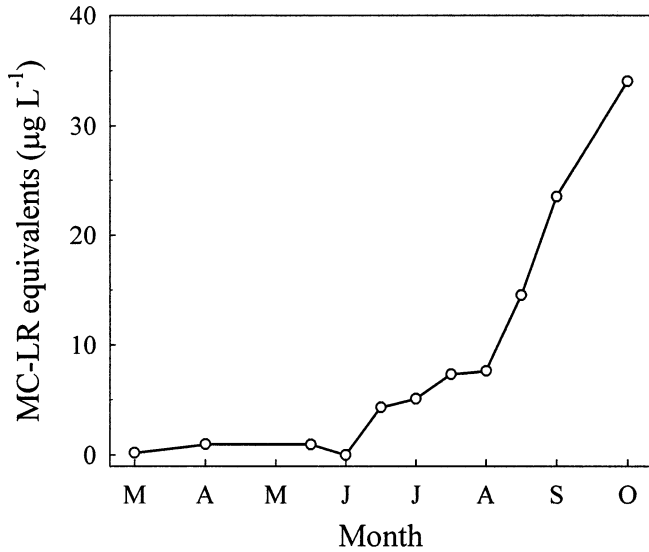


Fig. 6. Microcystin-LR (MC-LR) equivalent concentrations in Lake Kastoria from March to October 1999. Values refer to composite samples.

May, associated with their inclusion in the transparent particles-aggregates, they somewhat recovered on 14 June but remained close to zero from 29 June to 26 July (Fig. 7C). Nanociliates were observed in low numbers throughout the year (annual mean = $0.05 \pm 0.1 \times 10^5$ cells L⁻¹) (Fig. 7D).

Large ciliates (>50 µm) were rarely observed in countable numbers but formed a pronounced peak on 31 August ($163.4 \pm 379.1 \mu\text{g carbon L}^{-1}$) (Fig. 8A).

Rotifers and nauplii exhibited strong fluctuations in time and space, reaching high biomass levels in summer (max. = 64.2 ± 26.7 and $39.9 \pm 18.4 \mu\text{g carbon L}^{-1}$, respectively) (Fig. 8B). Cladocera were abundant from 14 June to 26 July (Fig. 8C). Copepods that exhibited strong fluctuations in time and space were the dominant group in the zooplankton community in terms of biomass (Fig. 8C). The most important zooplankton species, in terms of biomass, were the *Daphnia* spp., *Ceriodaphnia pulchella*, *Diaphanosoma mongolianum*, and *Brachionus calyciflorus* (Fig. 8D-F). The overall size distribution of the zooplankton community (Fig. 9) was dominated by the group that composed a size fraction of up to 300 µm, which was almost entirely made up of rotifers and nauplii.

Relationships between physical, chemical, and biological parameters—PCA was used to examine the relationships of individual plankton components and how they were grouped in relation to the physical and chemical parameters from March to October (Fig. 10), when all zooplankton components were included in the study. The first two axes with the largest eigenvalues accounted for 34% and 20% of the variance in the data. When considering the variables that weighted most heavily in axis I, it can be seen that spring

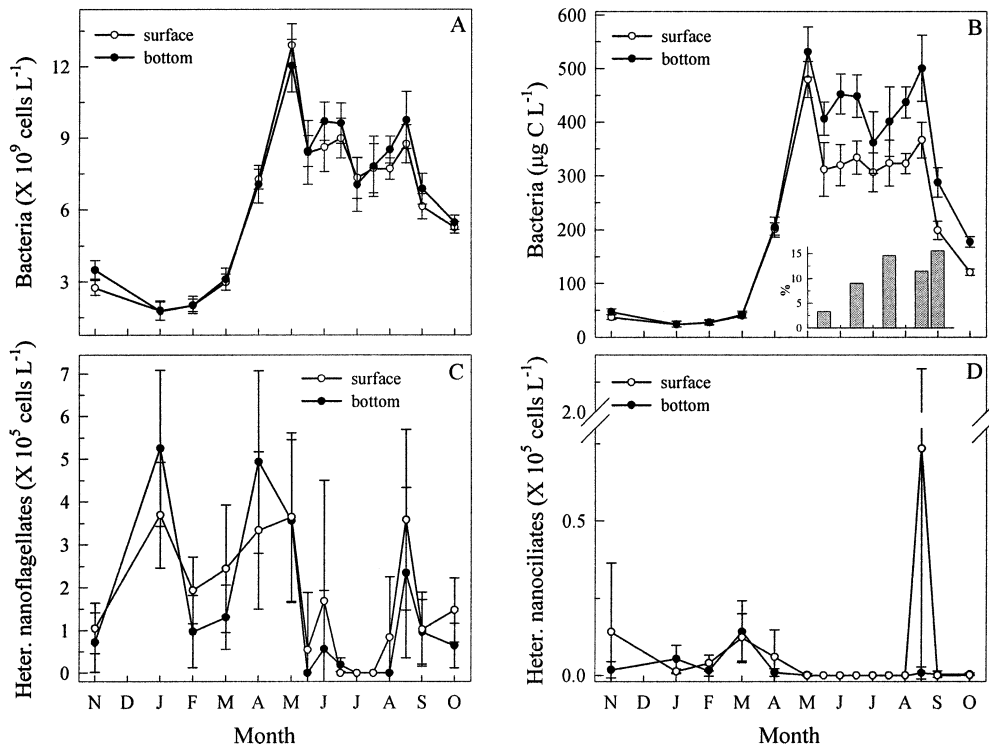


Fig. 7. Biological parameters in Lake Kastoria from November 1998 to October 1999. (A) Bacteria abundance, (B) bacteria biomass (inset: percentage of grazing-resistant bacteria to the picoplanktonic bacteria biomass at the bottom water layer of the deepest station), (C) heterotrophic nanoflagellates abundance, and (D) heterotrophic nanociliates abundance. Values are means and refer to the surface or bottom layers from all six stations. Bars represent standard deviation.

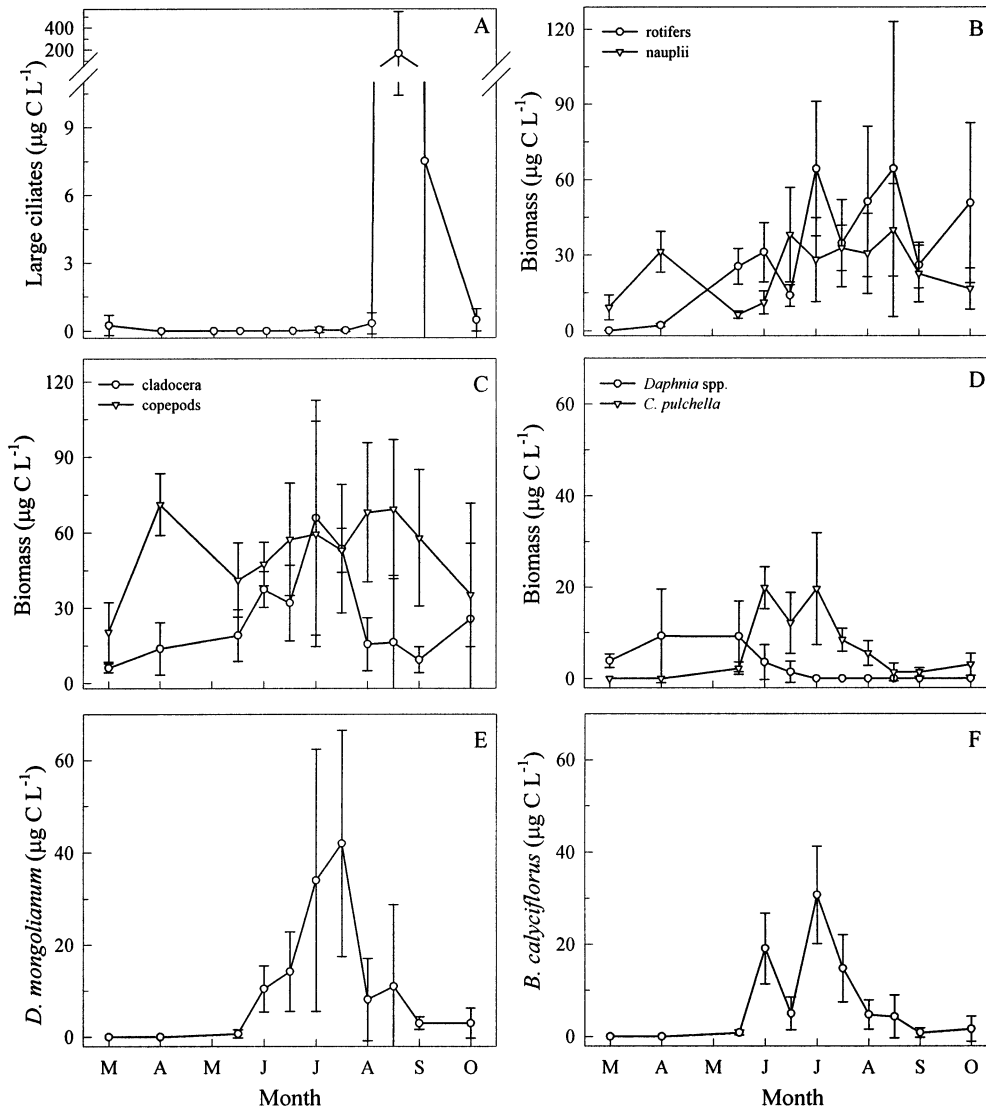


Fig. 8. Zooplankton biomass in Lake Kastoria from March to October 1999. (A) Large ciliates, (B) rotifers and nauplii, (C) cladocera and copepods, (D) *Daphnia* spp. and *Ceriodaphnia pulchella*, (E) *Diaphanosoma mongolianum*, and (F) *Brachionus calyciflorus*. Values are means and refer to data from all six stations. Bars represent standard deviation.

samples are differentiated by having higher values of heterotrophic nanoplankton, while summer and autumn samples show higher biomass of rotifers, small cladocera, nauplii, nanophytoplankton, large phytoplankton, known toxic cyanobacteria, and bacteria. Along axis II, April–August has a noticeably higher biomass of zooplankton components. Heterotrophic nanoplankton and known toxic cyanobacteria are clearly separated, showing a negative topology.

Biomass distribution of plankton components—The biomass distribution of plankton components in the autotrophic and heterotrophic compartments based on their size is presented in Table 1. Autotrophic microplankton and heterotrophic picoplankton were the two major components of the plankton community throughout the study, despite considerable fluctuations over time. Nanophytoplankton constituted

a small fraction (5%) of the autotrophic biomass, although they were abundant in summer. Nanophytoplankton and picophytoplankton contributed maximally to the autotrophic carbon (25% and 16%, respectively) when heterotrophic picoplankton were dominant in the plankton carbon pool ($B:A > 1$). Heterotrophic nanoplankton constituted a negligible fraction (1%) of the total heterotrophic carbon biomass throughout the study period, with the highest contribution (5%) when $B:A > 1$. The contributions of micro- and macrozooplankton to the heterotrophic carbon biomass were closely related (18 and 13%, respectively) throughout the study period.

No correlation was found between the heterotrophic and autotrophic compartment biomass (Fig. 11A). However, the ratio of heterotrophic to autotrophic carbon was strongly negatively correlated with autotrophic biomass (Fig. 11B).

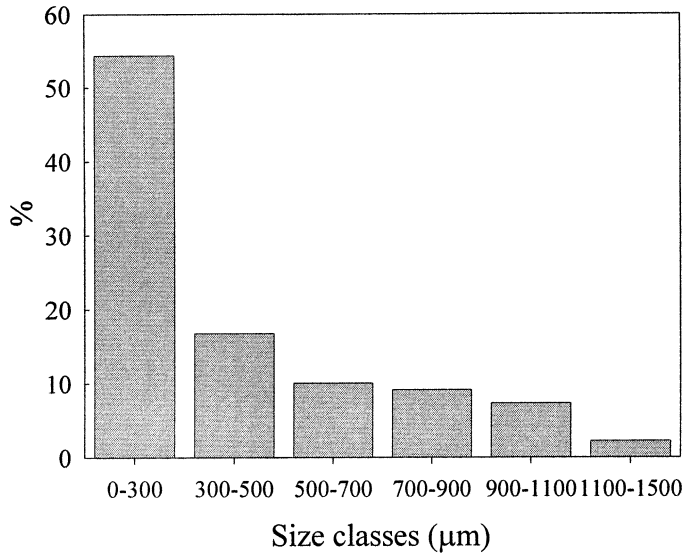


Fig. 9. Size frequency distribution of the zooplankton community expressed as a percentage (%) of the total biomass in Lake Kastoria from March to October 1999.

In a similar way, the ratio of bacteria to autotrophic carbon was also strongly negatively correlated with autotrophic biomass (Fig. 11C), whereas the ratio of bacteria to heterotrophic biomass was not correlated at all with the autotrophic biomass (Fig. 11D).

Discussion

In Lake Kastoria, phytoplankton constituted the largest carbon compartment in the plankton carbon pool (Table 1), which is common in eutrophic waters (Simon et al. 1992). The zooplankton : phytoplankton carbon ratio was low on average (<0.22), and it decreased with increasing TP (Fig. 12). Similar results have been reported for Danish shallow eutrophic lakes (Jeppesen et al. 1997). The dominance of plankton community biomass by autotrophs in Lake Kastoria can be explained by the dominance of filamentous and toxic cyanobacteria, which are well defended against grazing and the inability of microphagous herbivores (rotifers, nauplii, and small cladocera) to control cyanobacterial biomass. There has been controversy concerning the herbivore control of plants since Hairston et al. (1960) proposed the general picture of green plants in which green plants are abundant, and obvious depletions of plants by herbivores are exceptions. Sommer et al. (2001) reported that herbivore control of phy-

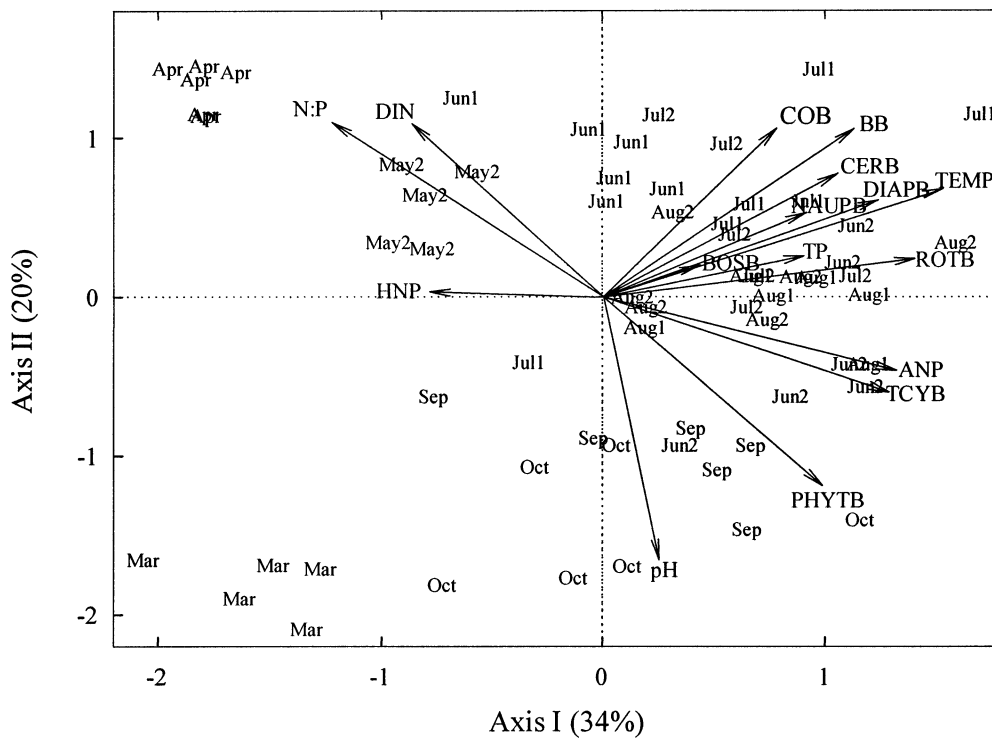


Fig. 10. Two-dimensional PCA ordination of the water samples of Lake Kastoria from March to October 1999. Physical, chemical, and biological parameters are indicated as vectors. TEMP, water temperature (°C); DIN, dissolved inorganic nitrogen ($\mu\text{g L}^{-1}$); N:P, atomic ratio of inorganic nitrogen to phosphorus; TP, total phosphorus ($\mu\text{g L}^{-1}$); PHYTB, phytoplankton biomass; TCYB, known toxic cyanobacterial biomass; ANP, autotrophic nanoplankton biomass; BB, bacterioplankton biomass; HNP, heterotrophic nanoplankton biomass; COB, copepods biomass; CERB, *Ceriodaphnia* biomass; DIAPB, *Diaphanosoma* biomass; BOSB, *Bosmina* biomass; NAUPB, nauplii biomass; ROTB, rotifers biomass. All biomass data are given in $\mu\text{g carbon L}^{-1}$.

Table 1. Biomass distribution of the plankton components in the autotrophic and heterotrophic compartments and the total plankton carbon pool of Lake Kastoria, based on component size during different periods of the study. First is given the whole study period (WSP), followed by the three periods separated on the basis of the different bacterial:autotrophic biomass (B:A) ratios. Mean values ($\mu\text{g C L}^{-1}$) (upper row) and percentages (lower row).

	Periods			
	WSP	B:A > 1	0.5 < B:A < 1	B:A < 0.5
Autotrophs	1,903 81%*	60 16%*	628 57%*	2,439 84%*
Picophytoplankton		10† 16%‡	30†	10†
Nanophytoplankton	94 5%‡	15 25%‡	14 2%‡	123 5%‡
Autotrophic microplankton	1,809 95%‡	35 59%‡	614 98%‡	2,315 95%‡
Heterotrophs	439 19%*	305 84%*	469 43%*	449 16%*
Heterotrophic picoplankton	301 69%§	203 67%§	370 79%§	297 66%§
Heterotrophic nanoplankton	4 1%§	15 5%§	2 0%§	3 1%§
Microzooplankton	79 18%§	33 11%§	33 7%§	95 21%§
Macrozooplankton	56 13%§	54 18%§	65 14%§	54 12%§

* Total plankton carbon.

† Indicates one value.

‡ Autotrophic carbon.

§ Heterotrophic carbon.

toplankton biomass depends not only on the plant but also on the herbivore functional diversity.

Phytoplankton (cyanobacterial) biomass decreased dramatically after a flushing rate increase in March that followed DIN reduction. Although the flushing rate was relatively low (0.53% of the lake volume per day), it was effective in eliminating cyanobacteria. Further flushing in April negatively affected cyanobacterial biomass for 2 months. Flushing pulses in the range of 1–2% of the lake volume per day in a sufficient frequency (20–30 d) are considered very effective in breaking cyanobacterial biomass increase (Padisák et al. 1999). It is also known that even a small increase in the flushing rate may lead to the disappearance of slow-growing cyanobacteria, if nutrient reduction has already occurred (Scheffer 1998). From 15 April to 14 June, the abundant phytoplankters in the lake were substituted by abundant transparent mucuslike particles. At the same time, an increase in water transparency (Fig. 3B) could indicate a clear water phase of low phytoplankton biomass caused by zooplankton grazing according to the Plankton Ecology Group model (Sommer et al. 1986). However, this clear water state cannot be attributed to zooplankton grazing, since zooplankters were found in low numbers, but to density-independent losses of phytoplankton caused by flushing and sinking. Sedimentation may have played an additive role in phytoplankton losses at the end of May, when phytoplankton and lithogenous particle inclusion was observed in abun-

dant (up to $5,503 \times 10^3 \text{ L}^{-1}$) and large ($>500 \mu\text{m}$ in largest dimension) transparent aggregates.

Temperature seemed to be a major determinant of bacterioplankton seasonality in Lake Kastoria ($r = 0.813$, $p < 0.001$), as has been demonstrated in many other systems (e.g., Pick and Caron 1987). Experimental data suggest that the limitation of bacterial growth in winter is an effect of temperature on substrate uptake or assimilation (Pomeroy and Wiebe 2001). In summer, the highest bacterial abundance and biomass were observed at the bottom water layer where the dissolved oxygen was relatively low (min. = $46.2\% \pm 15.1\%$ saturation). There, up to 30% of the bacteria cells were large ($0.8 \mu\text{m}^3$ cell volume), an average of eight times larger than those in the richer in oxygen surface layers. The tendency for a higher abundance and larger bacterial cells in the low oxygen layers is in agreement with previous observations in anoxic hypolimnia and has been explained by species shift and reduced predation (Cole et al. 1993).

Structure of plankton community and its food web: In Lake Kastoria, bacteria had a dominant role in the heterotrophic compartment of the plankton carbon pool, generally constituting $>50\%$, regardless of the size of the autotrophic carbon pool (Fig. 11D). The B:A ratio increased dramatically in low autotrophic biomass (Fig. 11C). The ratio of heterotrophic (H) to autotrophic carbon biomass (H:A) increased sharply up to 6.4 with decreasing autotrophic carbon $<450 \mu\text{g carbon L}^{-1}$ (H:A ~ 1) (Fig. 11B). These patterns, describing the seasonal dynamics of H:A and B:A, reflect an inverted biomass pyramid representing the food web during the transient oligotrophic conditions in Lake Kastoria. The relationships describing the seasonal dynamics of H:A and B:A in the lake show remarkable similarity to the patterns observed in a large number of marine and freshwater systems along trophic gradients (Cho and Azam 1990; Simon et al. 1992; del Giorgio and Gasol 1995).

The occurring shifts in the B:A ratio in Lake Kastoria reflect a seasonally variable structure of the plankton community and its food web (Table 1). From April to May with the B:A > 1 , all plankton size classes were well represented in the carbon pool, allowing the functioning of the microbial loop. From June to October with a low B:A ratio (<0.5), the size distribution in plankton showed the pronounced peaks in the size classes of autotrophic microplankton and heterotrophic picoplankton (Table 1), both peaks being due to prokaryotes. The peak in heterotrophs that is expected in the size of crustaceans according to Sprules et al. (1983) shifted to a smaller size (rotifers, nauplii, and small crustaceans). For autotrophs, the nonuniform size distribution is attributable to the accumulation of inedible or less-edible cyanobacteria, which is characteristic of eutrophic conditions (Sommer et al. 1986).

Although all size classes were present in Lake Kastoria, the size class of heterotrophic nanoplankton was temporarily (29 June–26 July) empty (Fig. 7C,D), while at the same time, autotrophic nanoplankton were abundant (Fig. 5H). The decline of heterotrophic nanoplankters sized $5\text{--}12 \mu\text{m}$ to undetectable levels could be attributed to a strong predation by daphnids, which prefer prey in this size. Additionally, there should be a higher vulnerability of heterotrophic nanoplank-

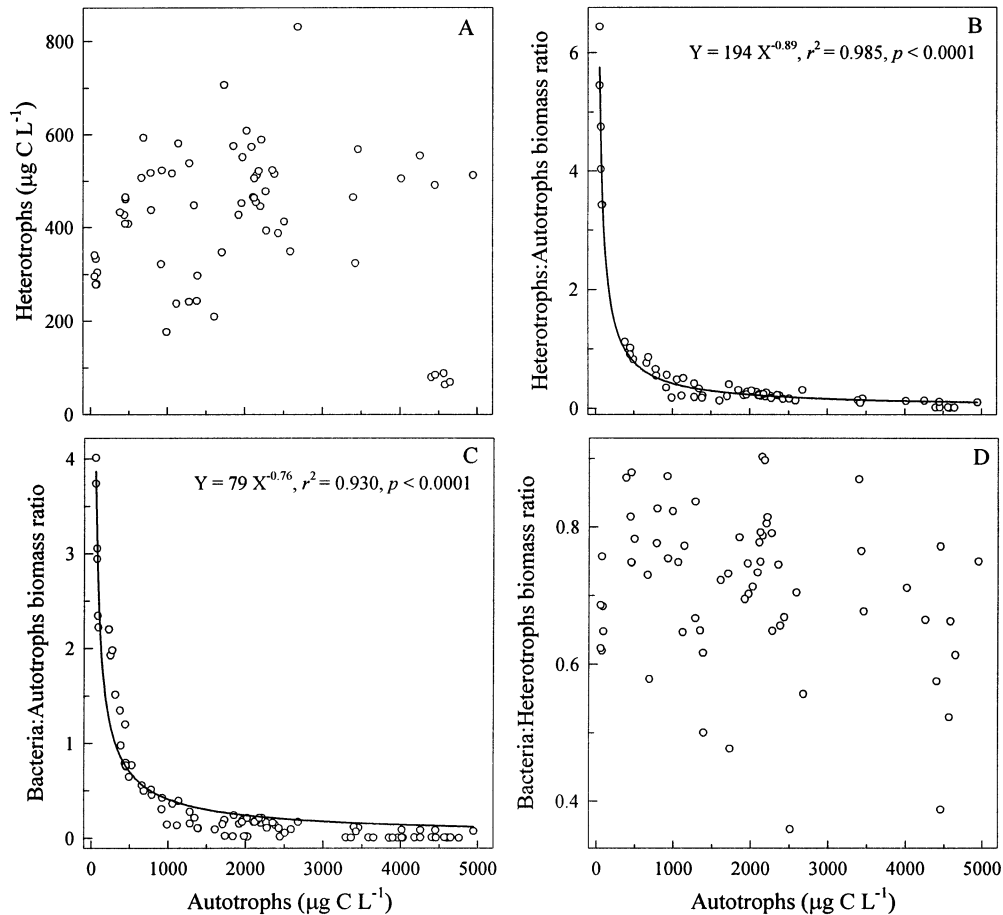


Fig. 11. Relationships between the plankton compartment biomass in Lake Kastoria from March to October 1999. (A) The biomass of heterotrophs versus autotrophs, (B) the ratio of heterotroph: autotroph biomass versus autotroph biomass, (C) the ratio of bacteria: autotroph biomass versus autotroph biomass, and (D) the ratio of bacteria: heterotroph biomass versus autotroph biomass.

ters to high daphnids abundance than that of the equally sized autotrophs. A precondition for both circumstances is a high abundance of large daphnids (Tittel et al. 1998; Gaedke et al. 2004). However, in Lake Kastoria, the overall size composition of zooplankton was dominated by sizes up to 300 μm (Fig. 9).

Food limitation could not be the cause of the breach in heterotrophic nanoplankton seasonal distribution. Bacteria retained relatively high values of abundance and biomass during the summer season. The relatively constant bacterial biomass in summer may have resulted from the grazing control, and in the diminishment of heterotrophic nanoplankton, metazoan plankton may account for most of grazing control. In Lake Kastoria, the zooplankton community was, especially during summer, composed of highly efficient bacterivores, the cladocera *C. pulchella* and *D. mongolianum*, and the rotifer *B. calyciflorus*. These bacterivores probably controlled the bacterial biomass, which showed a summer minimum that coincided with the bacterivores' biomass peak (Fig. 8D–F). The consideration of bacteria as a food source for rotifers and cladocera has been long recognized in eutrophic lakes (e.g., Gliwicz 1969).

During July, when heterotrophic nanoplankton decreased,

grazing-resistant bacteria were present and composed 14.6% of the picoplanktic bacteria biomass (Fig. 7B inset) at the bottom water layer of the deepest station with low oxygen concentration (30.8% saturation). Their occurrence could not be attributed to protozoa-grazing pressure as in other eutrophic lakes (Jürgens and Güde 1994), since heterotrophic nanoplankton were undetectable. However, the grazing-resistant bacteria appeared in May before the decrease of heterotrophic nanoplankton. Another possible explanation is that these budding bacteria ($>10 \mu\text{m}$), which are well adapted to low oxygen environments, are resistant to the small cladocera that dominate the zooplankton community during this period (Fig. 8D,E).

The breach in heterotrophic nanoplankton seasonal distribution may have resulted from unfavorable environmental conditions for their growth. Heterotrophic nanoplankton constituted the plankton component in PCA (Fig. 10) that has the highest negative relationship with the known toxic cyanobacteria dominating in toxic blooms. The heterotrophic nanoflagellates and nanociliates are considered the most sensitive planktic organisms when toxic cyanobacterial blooms are present (Christoffersen 1996).

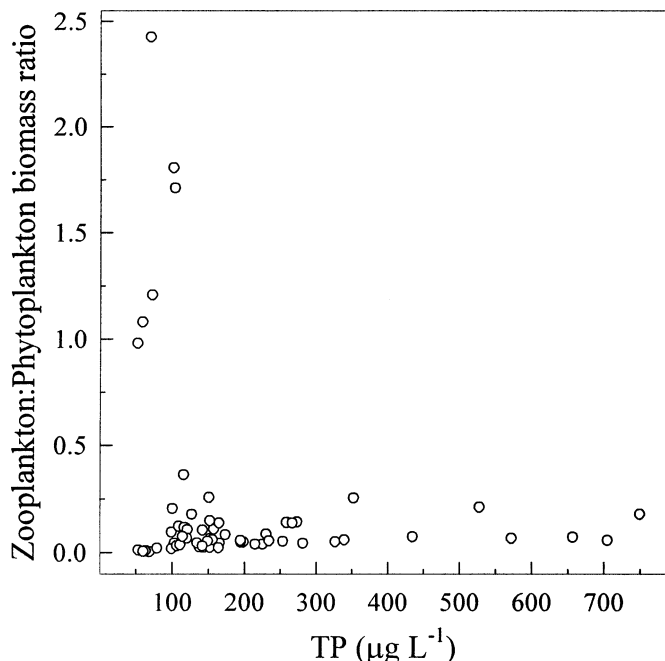


Fig. 12. The ratio of zooplankton:phytoplankton biomass versus total phosphorus (TP) concentration in Lake Kastoria from March to October 1999.

Possible effects of toxic blooms on the microbial food web: In Lake Kastoria during the summer decrease of heterotrophic nanoplankton, the known toxic cyanobacteria biomass increased, forming the first summer bloom (Fig. 5E,F). The concentration of MCs also increased (Fig. 6). The first summer bloom consisted of *C. raciborskii* (*Aphanizomenon* had a minor contribution), and it collapsed on 9 July following an unusual decrease in water temperature on 29 June. Adequate explanations for the irregularities of *C. raciborskii* blooms have been provided by both laboratory and fieldwork (Padisák 1998).

The second toxic bloom ($7.6 \mu\text{g MC-LR equivalents L}^{-1}$), which consisted of *C. raciborskii* and *Aphanizomenon* species, was recorded on 11 August. At this time, heterotrophic nanoflagellates represented by *Bodo* species were present in low numbers in contrast to the abundant autotrophic nanoflagellates (*Cryptomonas* and *Rhodomonas* species). During the postbloom period (31 August) when *Cylindrospermopsis* and *Aphanizomenon* biomass decreased, *M. aeruginosa* (Fig. 5G) formed a third toxic bloom ($14.5 \mu\text{g MC-LR equivalents L}^{-1}$). At the same time, heterotrophic nanoplankton (flagellates and ciliates) reached relatively high numbers, and bacterial abundance and biomass also increased (Fig. 7A–D). This coincidental increase of MC, bacteria, and heterotrophic nanoplankton may indicate either bacterial degradation of MCs and a positive response of heterotrophic nanoplankton to bacteria increase or the presence of MC-tolerant heterotrophic nanoplankton. In association with the increase of bacteria, heterotrophic nanoflagellates, and nanociliates, large ciliates constituting the link between an active microbial loop and the grazing food chain formed a pronounced biomass peak (Fig. 8A). Bacteria can quickly degrade MCs in natural waters with a previous history of toxic cyanobac-

terial blooms, and heterotrophic nanoflagellates respond positively to the bacterial growth (Christoffersen et al. 2002). Toxic cyanobacteria blooms provided a potential food source for the heterotrophic food chain in mesocosm experiments conducted in the Baltic Sea (Engström-Öst et al. 2002). In Lake Kastoria from September to October, when *M. aeruginosa* comprised the entire cyanobacteria biomass and MCs increased to $34 \mu\text{g MC-LR equivalents L}^{-1}$, a simultaneous reduction in the numbers of heterotrophic nanoflagellates and nanociliates and bacteria was observed. A reduction in the abundance of nanoflagellates during a toxic bloom of *Microcystis* was also observed in a Danish lake (Christoffersen 1996).

In Lake Kastoria, which has a previous history of toxic cyanobacterial blooms, heterotrophic nanoflagellates abundance throughout the year (annual mean = 1.5×10^5 cells L^{-1}) was close to the threshold density of 3×10^5 cells L^{-1} , and the annual mean ratio (50,611:1) of bacteria to heterotrophic nanoflagellates was greater than the highest ratio for a large number of lakes (Sanders et al. 1992). Nanociliates were observed in low numbers throughout the year (annual mean = 0.05×10^5 cells L^{-1}), which is lower than those reported in other eutrophic lakes (Pace 1982; Christoffersen et al. 1990). The annual mean ratio (11:1) of autotrophic to heterotrophic nanoplankton abundance was high in comparison to the 3:1 ratio found in other aquatic systems (Pick and Caron 1987). Larger bacterivores (rotifers and small cladocera) were abundant during the summer. The microbial food web was weak in structure because of the decrease of heterotrophic nanoplankton to undetectable numbers when the first toxic bloom developed (*C. raciborskii* and *Aphanizomenon* species). During the second toxic bloom, which consisted of the same cyanobacteria species heterotrophic nanoflagellates were present in low numbers. On the contrary, when MCs concentration was higher during the third toxic bloom consisting of *M. aeruginosa*, a well-established microbial food web was observed, indicating a positive effect of this species. Species composition (*Cylindrospermopsis*, *Aphanizomenon*, and *Microcystis* species) and a succession of toxic blooms may differentially affect the microbial food web structure.

References

- AMERICAN PUBLIC HEALTH ASSOCIATION. 1976. Standard methods for the examination of water and waste water, 14th ed. American Public Health Association.
- BØRSHEIM, K. Y., AND G. BRATBAK. 1987. Cell volume to cell carbon conversion factors for a bacterivorous *Monas* sp. enriched from seawater. *Mar. Ecol. Prog. Ser.* **36**: 171–175.
- CHO, B. C., AND F. AZAM. 1990. Biogeochemical significance of bacterial biomass in the ocean's euphotic zone. *Mar. Ecol. Prog. Ser.* **63**: 253–259.
- CHRISTOFFERSEN, K. 1996. Ecological implications of cyanobacterial toxins in aquatic food webs. *Phycologia* **35**: 42–50.
- , S. LYCK, AND A. WINDING. 2002. Microbial activity and bacterial community structure during degradation of microcystins. *Aquat. Microb. Ecol.* **27**: 125–136.
- , B. RIEMANN, L. R. HANSEN, A. KLYSNER, AND H. B. SØRENSEN. 1990. Qualitative importance of the microbial loop and plankton community structure in a eutrophic lake during a bloom of cyanobacteria. *Microb. Ecol.* **20**: 253–272.

- COLE, J. J., M. L. PACE, N. F. CARACO, AND G. S. STEINHART. 1993. Bacterial biomass and cell size distributions in lakes: More and larger cells in anoxic waters. *Limnol. Oceanogr.* **38**: 1627–1632.
- COOK, C. M., E. VARDAKA, AND T. LANARAS. 2004. Toxic cyanobacteria in Greek freshwaters, 1987–2000: Occurrence, toxicity and impacts in the Mediterranean region. *Acta Hydrochim. Hydrobiol.* **32**: 107–124. [doi: 10.1002/ahch.200300523]
- DEL GIORGIO, P., AND J. M. GASOL. 1995. Biomass distribution in freshwater plankton communities. *Am. Nat.* **146**: 135–152.
- ENGSTRÖM-ÖST, J., AND OTHERS. 2002. Effects of toxic cyanobacteria on a plankton assemblage community development during decay of *Nodularia spumigena*. *Mar. Ecol. Prog. Ser.* **232**: 1–14.
- GAEDKE, U., A. SEIFRIED, AND R. ADRIAN. 2004. Biomass size spectra and plankton diversity in a shallow eutrophic lake. *Int. Rev. Hydrobiol.* **89**: 1–20. [doi: 10.1002/iroh.200310661]
- GASOL, J. M., P. A. DEL GIORGIO, AND C. M. DUARTE. 1997. Biomass distribution in marine planktonic communities. *Limnol. Oceanogr.* **42**: 1353–1363.
- , A. M. SIMONS, AND J. KALFF. 1995. Patterns in the top-down versus bottom-up regulation of heterotrophic nanoflagellates in temperate lakes. *J. Plankton Res.* **17**: 1879–1903.
- GKELIS, S., V. HARJUNPÄÄ, T. LANARAS, AND K. SIVONEN. 2005. Diversity of hepatotoxic microcystins and bioactive anabaenopeptins in cyanobacterial blooms from Greek freshwaters. *Environ. Toxicol.* **20**: 249–256.
- GLIWICZ, Z. M. 1969. Studies on the feeding of pelagic zooplankton in lakes with varying trophy. *Ekol. Pol. A* **17**: 663–708.
- HAIRSTON, N. G., F. E. SMITH, AND L. B. SLOBODKIN. 1960. Community structure, population control, and competition. *Am. Nat.* **94**: 421–425.
- HARADA, K.-I., AND K. TSUJI. 1998. Persistence and decomposition of hepatotoxic microcystins produced by cyanobacteria in natural environment. *J. Toxicol.-Toxin Rev.* **17**: 385–403.
- JEPPESEN, E., J. P. JENSEN, M. SØNDERGAARD, T. L. LAURIDSEN, L. J. PEDERSEN, AND L. JENSEN. 1997. Top-down control in freshwater lakes: The role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia* **342/343**: 151–164.
- JÜRGENS, K., AND H. GÜDE. 1994. The potential importance of grazing-resistant bacteria in planktonic systems. *Mar. Ecol. Prog. Ser.* **112**: 169–188.
- LANARAS, T., S. TSITSAMIS, C. CHLICHLIA, AND C. M. COOK. 1989. Toxic cyanobacteria in Greek freshwaters. *J. Appl. Phycol.* **1**: 67–73.
- LEGENRE, P., AND L. LEGENDRE. 1998. Numerical ecology, 2nd ed. Elsevier.
- LIDDICOAT, M. I., S. TIBBITS, AND M. I. BUTLER. 1976. The determination of ammonia in natural waters. *Water Res.* **10**: 567–568.
- PACE, M. L. 1982. Planktonic ciliates: Their distribution, abundance, and relationship to microbial resources in a monomictic lake. *Can. J. Fish. Aquat. Sci.* **39**: 1106–1116.
- PADISÁK, J. 1998. Sudden and gradual responses of phytoplankton to global climate change: Case studies from two large, shallow lakes (Balaton, Hungary and the Neusiedlersee Austria/Hungary), p. 111–125. *In* D. C. George, J. G. Jones, P. Puncochar, C. S. Reynolds, and D. W. Sutcliffe [eds.], Management of lakes and reservoirs during global change. Kluwer.
- , J. KÖHLER, AND S. HOEG. 1999. The effect of changing flushing rates on development of late summer *Aphanizomenon* and *Microcystis* populations in a shallow lake, Müggelsee, Berlin, Germany, p. 411–423. *In* G. Tundisi and M. Sraskraba [eds.], Theoretical reservoir ecology and its applications. Backhuys.
- PICK, F. R., AND D. A. CARON. 1987. Pico- and nanoplankton biomass in lake Ontario: Relative contribution of phototrophic and heterotrophic assemblages. *Can. J. Fish. Aquat. Sci.* **44**: 2164–2172.
- POMEROY, L. R., AND W. J. WIEBE. 2001. Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. *Aquat. Microb. Ecol.* **23**: 187–204.
- PORTER, K. G., AND Y. S. FEIG. 1980. The use of DAPI for identifying and counting aquatic microflora. *Limnol. Oceanogr.* **25**: 943–948.
- PUTT, M., AND D. K. STOECKER. 1989. An experimentally determined carbon-volume ratio for marine oligotrichous ciliates from estuarine to coastal waters. *Limnol. Oceanogr.* **34**: 1097–1103.
- ROCHA, O., AND A. DUNCAN. 1985. The relationship between cell carbon and cell volume in freshwater algal species used in zooplankton studies. *J. Plankton Res.* **7**: 279–294.
- SANDERS, R. W., D. A. CARON, AND U.-G. BERNINGER. 1992. Relationships between bacteria and heterotrophic nanoplankton in marine and fresh waters: An inter-ecosystem comparison. *Mar. Ecol. Prog. Ser.* **86**: 1–14.
- , K. G. PORTER, S. J. BENNETT, AND A. E. DEBIASE. 1989. Seasonal patterns of bacterivory by flagellates, ciliates, rotifers, and cladocerans in a freshwater planktonic community. *Limnol. Oceanogr.* **34**: 673–687.
- SCHEFFER, M. 1998. Ecology of shallow lakes. Population and community biology ser. 22. Kluwer.
- SIMON, M., B. C. CHO, AND F. AZAM. 1992. Significance of bacterial biomass in lakes and the ocean: A comparison to phytoplankton and biogeochemical implications. *Mar. Ecol. Prog. Ser.* **86**: 103–110.
- SIVONEN, K., AND G. JONES. 1999. Cyanobacterial toxins, p. 41–111. *In* I. Chorus and J. Bartram [eds.], Toxic cyanobacteria in water: A guide to public health significance, monitoring and management. E. & F. N. Spon.
- SOMMER, U., Z. M. GLIWICZ, W. LAMPERT, AND A. DUNCAN. 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.* **106**: 433–471.
- , F. SOMMER, B. SANTER, C. JAMIESON, M. BOERSMA, C. BECKER, AND T. HANSEN. 2001. Complementary impact of copepods and cladocerans on phytoplankton. *Ecol. Lett.* **4**: 545–550.
- , AND H. STIBOR. 2002. Copepoda–Cladocera–Tunicata: The role of three major mesozooplankton groups in pelagic food webs. *Ecol. Res.* **17**: 161–174.
- , AND OTHERS. 2003. *Daphnia* versus copepod impact on summer phytoplankton: Functional compensation at both trophic levels. *Oecologia* **135**: 639–647. [doi: 10.1007/s00442-003-1214-7]
- SPRULES, W. G., J. M. CASSELMAN, AND B. J. SHUTER. 1983. Size distribution of pelagic particles in lakes. *Can. J. Fish. Aquat. Sci.* **40**: 1761–1769.
- STRICKLAND, J. D. H., AND T. R. PARSONS. 1968. A practical handbook of seawater analysis. *Fish. Res. Board Can.* **167**: 1–311.
- TALLING, J. F., AND D. DRIVER. 1963. Some problems in the estimation of chlorophyll a in phytoplankton, p. 142–146. *In* Proceedings of the conference on Primary Productivity Measurement, Marine and Freshwater, Univ. of Hawaii, August 21–September 6, 1961. U.S. Atomic Energy Commission, Division of Technical Information TID-7633.
- TITTEL, J., B. ZIPPEL, W. GELLER, AND J. SEEGER. 1998. Relationships between the plankton community structure and plankton size distribution in lakes of Northern Germany. *Limnol. Oceanogr.* **43**: 1119–1132.
- TOLIKAS, D. 2000. Existing sediment control measures—proposals for new structures, determination of discharge, sediment and water quality in the torrents of Kastoria Lake basin. Technical Report, Department of Civil Engineering, Aristotle Univ. of Thessaloniki. [In Greek.]
- WATSON, S., E. MCCAULEY, AND J. DOWNING. 1997. Patterns in phytoplankton taxonomic composition across temperate lakes of differing nutrient status. *Limnol. Oceanogr.* **42**: 487–495.

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