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APPLIED ISSUES

Effects of eutrophication on seasonal patterns of mesozooplankton in a tropical reservoir: a 4-year study in Pampulha Lake, Brazil

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SUMMARY

1. Pampulha Lake has undergone rapid eutrophication. Annual maxima of total phosphorus and conductivity increased steadily from 1993 to 1996. Nitrogen quickly decreased after macrophyte removal in 1994, but increased again in the following years
2. The zooplankton was dominated by *Daphnia gessneri, D. laevis, Diaphanosoma birgei* and *Thermocyclops decipiens*. The biomass of major zooplankton organisms, including *Daphnia* and rotifers, increased during the period covered in this study.
3. Autocorrelation coefficients have confirmed the existence of recurrent seasonal patterns for both chemical and biological variables.
4. *Daphnia,* calanoid copepods and rotifers showed clear and recurrent seasonal patterns. Cyclopoid copepods and *Diaphanosoma* had temporal patterns more affected by long-term trophic changes. Other organisms such as *Moina, Ceriodaphnia* and *Bosmina* exhibited high temporal variability with no recurrent patterns.
5. There was a strong and positive correlation between total phosphorus and *Daphnia* biomass. Seasonal patterns of this cladoceran were also inversely associated with sestonic C:P ratios. Thus, *Daphnia* may be limited primarily by phosphorus and not by total food availability as expressed by particulate carbon.
6. This study suggests that increasing eutrophication has changed the structure as well as seasonal patterns of the zooplankton community in Pampulha Reservoir.

Introduction

Striking characteristics of most ecosystems are the spatial and temporal patterns observed in structural as well as functional components. Analysis of this variability can yield insights into the forces structuring these ecosystems (Kratz *et al.*, 1987). Temporal variability is poorly understood in tropical freshwater zooplankton. Early studies were based mainly on samples collected by expeditions, and thus provided little information on temporal and spatial patterns (i.e. Kiefer, 1933; Wright, 1936). In the last 30 years, more knowledge concerning temporal dynamics of tropical zooplankton has accumulated (Saunders & Lewis, 1988a). According to Nilssen (1984), long-term studies have been concentrated in a relatively small number of tropical lakes such as Lake George, Lake Chad in Africa and Lake Lanao in the Phillipines. In Central and South America, Lake Gatun in Panama, Lake Valencia in Venezuela and Lake Bishop in Brazil have been intensively studied. A growing number of lakes and reservoirs in Brazil have been studied in the past decade (Tundisi *et al.*, 1995), but these studies have usually been restricted to faunal comparisons (Brandorf, 1978; Matsumura-Tundisi *et al.*, 1981; Brandorf *et al.*, 1982; Arcifa, 1984; Sendacz *et al.*, 1985; Bonecker & Lansac-Tôha, 1996). Several other studies

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have covered just one or two seasonal cycles (Rocha *et al.*, 1982; Sendacz, 1984; Pinto-Coelho, 1987).

Nilssen (1984), reviewing the limnological work from tropical freshwater systems, stressed the need to study artificial tropical lakes. He gave persuasive reasons for this statement: (i) there are many more artificial lakes in the tropics than natural lakes and this number is increasing; (ii) tropical reservoirs possibly have functional and structural properties much more similar to small temperate lakes as opposed to the large, old, deep and biologically complex tropical lakes which have been more intensively studied and (iii), despite their great economic and social importance, tropical artificial lakes suffer from an array of environmental problems such as eutrophication, overfishing, introductions of exotic fauna, biocide contamination and intense forest clear-cutting in their catchment areas.

Contrary to a commonly held belief, seasonal fluctuations are frequently observed in tropical lakes. Despite low seasonal variation in temperature, these lakes demonstrate seasonal patterns in zooplankton abundance and community structure (Lewis, 1979; Twombly, 1983). There are several hypotheses to explain the seasonality of tropical zooplankton including mixing regimes (Saunders & Lewis, 1988a), wind (Beadle, 1981), fluctuations in water level (Brandorf & Andrade, 1978; Bozelli, 1994), precipitation (Nilssen, 1984) and changes in phytoplankton (Infante & Riehl, 1984). Major components of zooplankton such as copepods and cladocerans often have contrasting seasonal patterns (Infante, 1982; Rocha *et al.*, 1982; Sendacz, 1984; Saunders & Lewis, 1988b). In Lake Valencia, the cladocerans suffered a steady decrease during a long-term study (Infante, 1982). In some Brazilian reservoirs, such as the eutrophic Billings Reservoir in São Paulo state, increases in zooplankton biomass have been observed during the rainy season (Sendacz, 1984), whereas in the nearby eutrophic Paranoá Reservoir the zooplankton biomass decreased during the rainy season (Pinto-Coelho, 1987).

Most lakes and reservoirs in south-eastern Brazil suffer from eutrophication, so it is important to understand the major effects of eutrophication on the structure of their zooplankton communities. The responses of zooplankton to eutrophication are regulated by food availability and fish and invertebrate predation as well as the characteristics of the physical environment. Since the influence of these three categories of ecological factors may vary considerably from one lake to another it is not an easy task to establish a relationship between trophic state and zooplankton structure (Ravera, 1996). Several studies have demonstrated that tropical zooplankton populations change in response to increased levels of nutrient input. Cyclopoids, cladocerans and rotifers become more abundant with eutrophication while calanoids tend to disappear (Matsumura-Tundisi *et al.*, 1981; Arcifa, 1984; Sendacz *et al.*, 1985 Freire & Pinto-Coelho, 1986).

The objective of this study was to analyse the effects of increasing eutrophication on seasonal trends of zooplankton in a eutrophic reservoir. This study is based on a data set covering four complete seasonal cycles. The seasonal trends in zooplankton were compared with seasonal courses of some major environmental variables commonly used to assess the progress of eutrophication.

Methods

Study area

Pampulha Reservoir is a shallow, eutrophic water body with a surface area of 2.4 km^2 and a volume of 12×10^6 m^3. The maximum depth (z_{max}) is 17 m and the mean depth (z_{mean}) is around 6.0 m. It is situated in Belo Horizonte city, (19°55′09′′S, 43°56′47′′W; altitude 790 m above sea level). This is one of the largest cities in Brazil with more than 2.5 million inhabitants. The reservoir water level does not fluctuate seasonally since the tulip-shaped surface outflow operates year round.

The climate of the region is classified as B-2 tropical climate with a moderated hydric deficit (Ferreira, 1992). The coolest period is usually restricted to the period from May to July. During 1993–95, average monthly maximum air temperature ranged from 27 to 35 °C with means between 21 and 26 °C and an average of minimum temperatures between 14 and 19 °C. The rainy season occurs in the hottest months, from November to March. The mean annual rainfall was about 1400–1600 mm (data from 5th Meteorological District of Agriculture Ministry, Belo Horizonte).

The reservoir was constructed in 1938 and, since 1970, has been suffering from eutrophication as a result of the input of untreated domestic wastewater. Extensive blooms of cyanobacteria including *Microcystis aeruginosa* (Kütz, 1846), *M. flos-aquae* (Kirchn,

1898), *M. viridis* (Lemm 1903) and *Woronichinia naegeliana* (Elenk., 1933), as well as macrophyte increases (*Eichhornia crassipes*, (Martius), Solms., 1888) have been regularly reported over the last decade (Goodwin, 1997; Greco, 1996). At the end of 1993, the city administration undertook an intensive program aimed at the complete removal of macrophyte coverage. More than 1000 000 m^2 of the macrophyte *Eichhornia crassipes* were removed between October 1993 and February 1994.

Sampling

Samples for plankton and water analysis were taken monthly from February 1993 to December 1995 at a station located in the central region of the reservoir (depth = 7.0 m). In 1996, samples were taken every two weeks. Previous studies (Giani *et al.*, 1988) have demonstrated that this sampling point effectively characterizes the plankton composition as well as the chemical characteristics of the lake water.

The following abiotic variables were measured: water temperature, water transparency (Secchi disk), pH, conductivity (μS cm^{-1}, at 25 °C), dissolved oxygen concentrations (mg O_2 L^{-1}), ammonia, nitrite, nitrate (μg N L^{-1}) and total phosphorus (μg P-PO_4 L^{-1}). Water temperature was measured using a YSI thermistor. Oxygen was determined using the Winkler method (Pomeroy & Kirschman, 1945). Conductivity and pH were measured using a Jenway 3446 electro-chemistry analyser.

Particulate organic carbon and chlorophyll *a* measurements were taken in 1994, 1995 and 1996. All other variables were measured between 1993 and 1996. Chlorophyll *a* determinations were conducted according to Lorenzen (1967). Particulate carbon was measured using a modified DQO method (APHA 1992). Determinations of inorganic nitrogen and phosphorus were performed using standard spectrophotometric methods after Mackereth *et al.* (1978).

Zooplankton replicate samples were taken using a 5.1-L Schindler–Patalas plankton trap at four different depths: 0, 2, 4 and 6 m. Samples were filtered through a 90-μm mesh net and rapidly transferred to 300 mL polyethylene vials containing Rose Bengal and kept on ice. After some minutes, a solution of sugar-formalin, buffered to pH 7.0, was added to the flasks to achieve a final formalin concentration of 4%.

In the laboratory, zooplankton samples were usually completely counted. Subsamples were taken using a nonselective Stempel pipette of 5 mL capacity only when more than 1000 individuals were present in the samples. All counted samples remain in our zooplankton collection for further studies and taxonomic checks.

Zooplankton identification was carried-out with reference to Matsumura-Tundisi (1984) and Fernando *et al.* (1987) for *Daphnia* spp., El-Moor-Loureiro (1990) and Korovchinsky (1992) for *Diaphanosoma*, Reid (1985; 1987), Sendacz & Kubo (1982), Matsumura-Tundisi (1983; 1986) and Dussart *et al.* (1984) for copepoda. All copepoda determinations were checked by Dr Janet W. Reid of the Smithsonian Institute, Washington, U.S.A. Copepods were counted separately in the categories adult males, egg carrying females, females, copepodites and nauplii. The adults were identified to species level. Only rotifers larger than 90 μm were considered in this study.

Each individual was measured; copepods from the top of cephalothorax to the furca (excluding the furcal rami) and cladocerans from the top of the head to the base of the distal carapace spine. Measurements were made using a M-3 Leica stereomicroscope equipped with a 10× ocular micrometer.

Biomass (B) of zooplankton was estimated using allometric equations:

$$B = a^{*}L^{b} \qquad (1)$$

where L is the length in millimetres and the parameters a and b were specific for each species (Bottrell *et al.*, 1976; McCauley, 1984 and Masundire, 1994). Calculations of individual biomass and length were performed using a computer program written in Turbo Pascal.

Integrated biomass values were obtained by integrating biomass from different depths using the rectangle algorithm (Bartsch, 1988).

$$I = \int_{a}^{b} f(x)\mathrm{d}x = \frac{b-a}{n} {}^{*}(y_a + y_1 + y_2 + \cdots + y_{n-1}) \qquad (2)$$

where I = integrated biomass (g DW m^{-2}); a, b = depth interval (m); n = number of partitions (samples) along the limits to be integrated and y = biomass values for each depth x (g DW m^{-3}). All of these calculations were also performed using a Turbo Pascal computer program.

Principal component analyses (PCA) and autocorrelation functions (ACF) were carried out using a systat package version written for the MS-DOS operating

system (Wilkinson, 1990). Prior to the PCA analysis, all variables were transformed as follows:

$$\text{trans } f(x) = \log(x + 1) \quad (3)$$

Because all variables must have normalized distributions before running a PCA analysis (Valentin, 1995), the transformed variables were tested for normality. The PCA analysis via R-mode used Pearson correlation coefficients to estimate the dependence between each pair of variables. For ACF calculations, only samples taken at monthly intervals were considered.

Before plotting abiotic or biotic values against time, each sampling date was transformed into an integer number according to the Julian scale beginning on 1 January 1993 and ending on 31 December 1996. All time calculations and plots were obtained using a program written in Turbo Pascal, making it possible to maintain the real time intervals between the sampling dates in the plots.

Results

Water transparency was very low at Pampulha Reservoir, with Secchi readings usually less than 1.0 m. In 1993, transparency was higher, reaching values around 2.0 m during the dry season. After macrophyte removal, which occurred between October 1993 and February 1994, Secchi readings usually remained less than 1.0 m (Fig. 1). During most years, minimum values occurred during the rainy season, especially in December, when it often rains heavily for several days without any interruption.

A clear and recurrent seasonal trend was observed in water temperature. Differences in surface water temperatures between summer and winter were greater than 7 °C (Fig. 1). The lowest temperatures, around 18 °C, occurred during the winter months of July and August when the water column was normally well mixed. During summer, the water column remained stratified and temperatures higher than 26 °C were frequently observed. A maximum of 30 °C was measured in January 1995.

A clear seasonal pattern was also observed in conductivity, reflecting the crucial role that the rainy season plays in lake chemistry (Fig. 1). There was a regular increase from 200 to 220 μS cm^{-1} in March–April to 250–350 μS cm^{-1} in September–October, just before the beginning of the rainy season. Moreover, there was a long-term increase in conductivity that can be observed by comparing the annual maximum values for 1993 (263 μS cm^{-1}), 1994 (321 μS cm^{-1}), 1995 (340 μS cm^{-1}) and 1996 (376 μS cm^{-1}).

Values of pH higher than 8.0 were common in surface waters, especially during the second half of the dry season (July–September) when colonial cyanobacteria bloomed and there was stable thermal stratification (Fig. 2). In 1993, pH values were more homogeneous in the water column than in subsequent years, probably due to the absence of surface blooming of a colonial cyanobacteria in that particular year. Dissolved oxygen was the abiotic variable which varied the most (Fig. 2). Surface values were always much higher than bottom oxygen concentrations and this difference increased throughout 1994, whereas the opposite was observed in 1995. In 1996, surface oxygen concentrations peaked several times, suggesting that oxygen availability in this lake is in delicate balance. Bottom dissolved oxygen concentrations remained very low, except for very short periods during mixing.

Total phosphorus, like conductivity, had both seasonal and long-term temporal patterns. On a seasonal basis, total phosphorus concentrations increased during the dry season, reaching annual maxima between September and October. A clear long-term increase from 1993 to 1995 was also observed, with steadily increasing annual maximum concentrations (6 m): 85 μg $P\text{-}PO_4$ L^{-1} in 1993, 212 μg$P\text{-}PO_4$ L^{-1} in 1994, 335 μg $P\text{-}PO_4$ L^{-1} in 1995 and 400 μg $P\text{-}PO_4$ L^{-1} in 1996 (Fig. 2).

Inorganic dissolved nitrogen (ammonia + nitrite + nitrate) always remained above, 1.0 mg L^{-1}. Like total phosphorus, dissolved inorganic nitrogen peaked at the end of the dry season, mainly in October. Nitrogen decreased markedly after macrophyte removal in 1993/1994; however, a tendency to increase was noticed in 1995 and 1996 (Fig. 1).

After macrophyte removal there was a rapid response of phytoplankton biomass. Chlorophyll *a* concentrations reached values as high as 0.43 g m^{-2} in July 1994 (Fig. 3); however, in later years, annual maxima of chlorophyll *a* were restricted to a range of 0.12–0.20 g m^{-2}. Chlorophyll *a* concentrations peaked twice a year, the first usually at the beginning of the dry season in April–May and the second in September–October.

Pampulha Reservoir showed high availability of sestonic carbon with integrated concentrations of particulate organic carbon (POC) reaching a maximum of

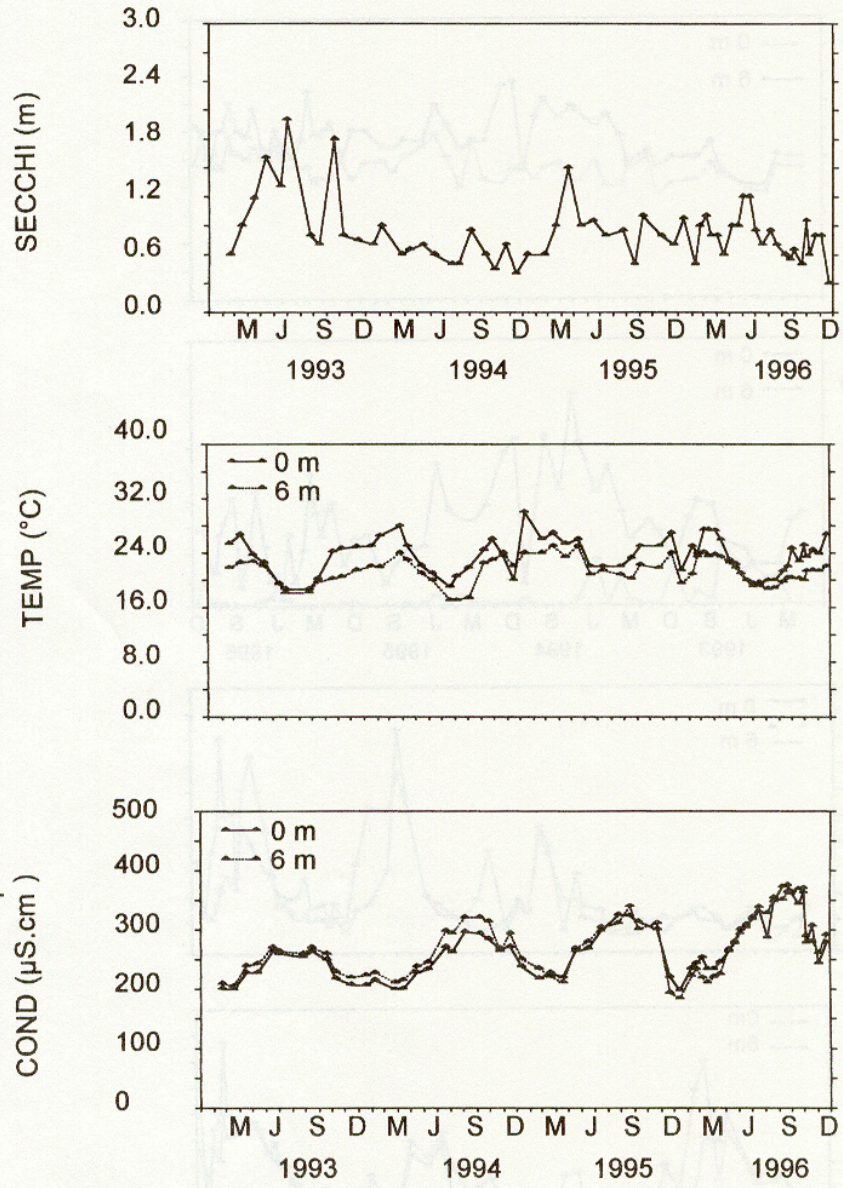

Fig. 1 Temporal variation (1993–96) of Secchi disk, water temperatures and conductivity in Pampulha Reservoir, Belo Horizonte, Brazil.

43 g C m^{-2} in May 1995 (Fig. 3). A seasonal cycle could also be detected with higher concentrations during the dry season (May–October).

Zooplankton biomass was dominated by large cladocerans (Fig. 4) including *Daphnia gessneri* (Herbst, 1967); *D. laevis* (Birge, 1878) and *Diaphanosoma birgei* (Korínek, 1981). *Daphnia laevis* was particularly abundant in 1993, 1995 and 1996. In 1995, this population reached an annual maximum of 6.7 g DW m^{-2} in October. In 1996, two seasonal peaks were observed, one in June (8.3 g DW m^{-2}) and another in November (8.9 g DW m^{-2}). The second most important organism, in terms of biomass, was *D. birgei* (Fig. 4). This species was especially abundant during 1994 when it reached an integrated biomass peak of about 1.8 g DW m^{-2} in June. On a seasonal basis, *Diaphanosoma* also showed a tendency to peak when *Daphnia* biomass was low during the first half of the dry season, or after the

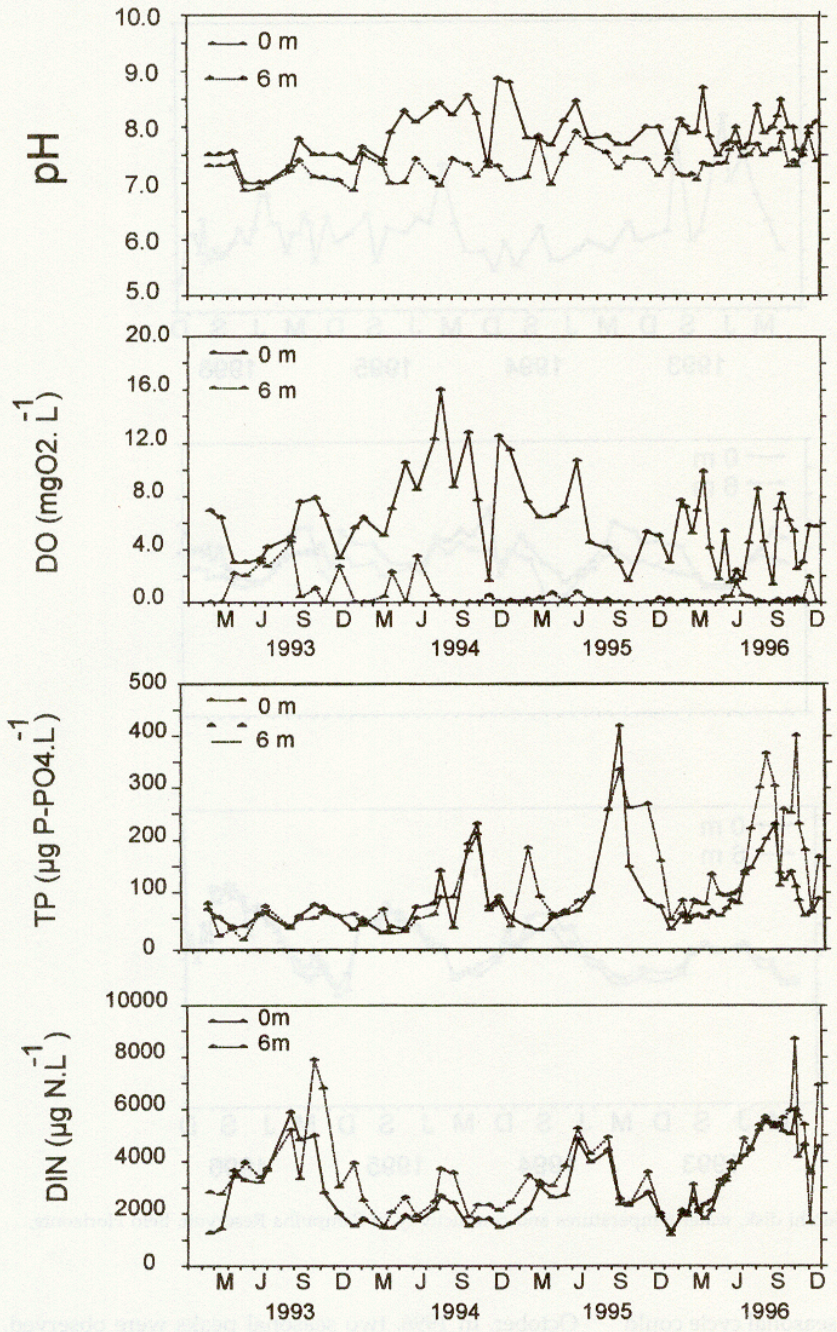

Fig. 2 Temporal variation (1993–96) of pH, dissolved oxygen, total phosphorus and inorganic nitrogen in Pampulha Reservoir, Belo Horizonte, Brazil.

massive development of *Daphnia* populations during the second half of the dry season.

Scolodiaptomus corderoi (Wright (Reid); 1987) was present at a higher biomass before macrophyte removal. In 1993, for instance, the biomass of this calanoid copepod reached a maximum of 0.04 g DW m^{-2} in August–September (Fig. 4). It practically disappeared in 1994, but returned in 1995 with a lower biomass (annual maximum = 0.04 g DW m^{-2} in September). In 1996 calanoids were practically absent from the lake. Cyclopoid copepods, consisting almost exclusively of *Thermocyclops decipiens* (Kiefer, 1929), also showed clear and recurrent seasonal cycles with annual maxima always occurring between

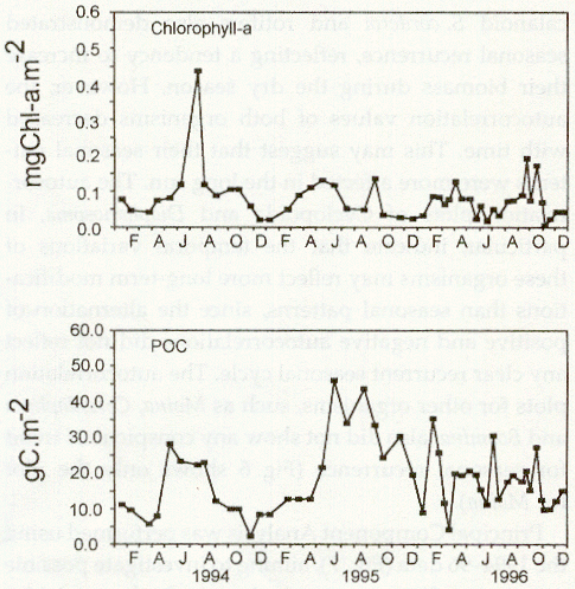

Fig. 3 Temporal variation (1994–96) of chlorophyll *a* and particulate organic carbon in Pampulha Reservoir, Brazil.

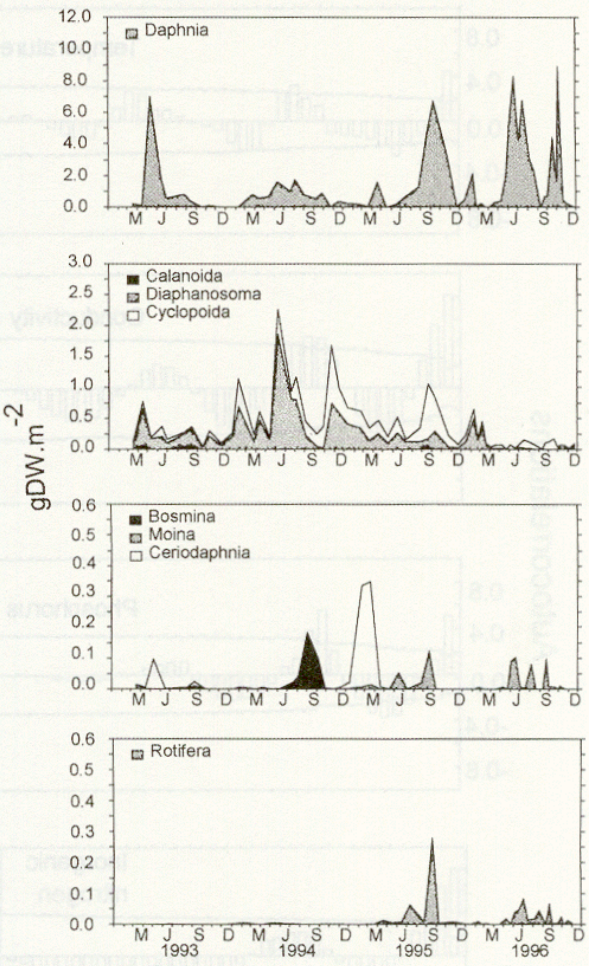

Fig. 4 Temporal variations (1993–96) of integrated biomass of major zooplankton species in Pampulha Reservoir, Brazil.

October and December, just before the beginning of the rainy season (Fig. 4). The annual maximum biomass for 1994 was observed in November (0.94 g DW m^{-2}). In 1995, the annual maximum was 0.88 g DW m^{-2}, measured in September. In 1996 their densities decreased and the annual maximum was registered in October (0.16 g DW m^{-2}).

Other cladocerans such as *Bosmina longirostris* (O F. Müller, 1785), *Ceriodaphnia cornuta* (Sars, 1885) and *Moina* spp., occurred in the lake but at relatively low biomass and for restricted and non-recurrent periods of time (Fig. 4). *Ceriodaphnia cornuta* peaked in May 1993 (0.10 g DW m^{-2}) and in March 1995 (0.30 g DW m^{-2}). *Bosmina* had its maximum biomass in the dry season of 1994 (0.18 g DW m^{-2}) whereas *Moina* spp. became more abundant later in 1995 and 1996; this cladoceran peaked three times during the dry season of 1996, reaching biomasses in the range 0.08–0.10 g DW m^{-2}. Larger rotifers, mostly *Brachionus calyciflorus* (Pallas, 1766), were especially abundant in 1995 and 1996. In these years, they were always found in high numbers between July and September. The highest biomass of rotifers was measured in September 1995 (0.27 g DW m^{-2}).

The autocorrelation plots of abiotic variables with conspicuous seasonality, such as temperature, showed a pattern of alternating positive and negative autocorrelation values (Fig. 5). Surface water temperatures showed positive autocorrelations for times 1–2, negative correlations for times ranging from 3 to, 10 and positive correlations for times raging from 11 to 14. This alternation of positive and negative values continued until time 36.

Conductivity and total phosphorus exhibited similar patterns of alternating positive and negative autocorrelations, indicating the existence of seasonal recurrence. However, the autocorrelation plots of total phosphorus and inorganic nitrogen showed a trend of decreasing autocorrelations, or even lost the alternation of periods with negative and positive values with increasing time. This probably reflects long-term

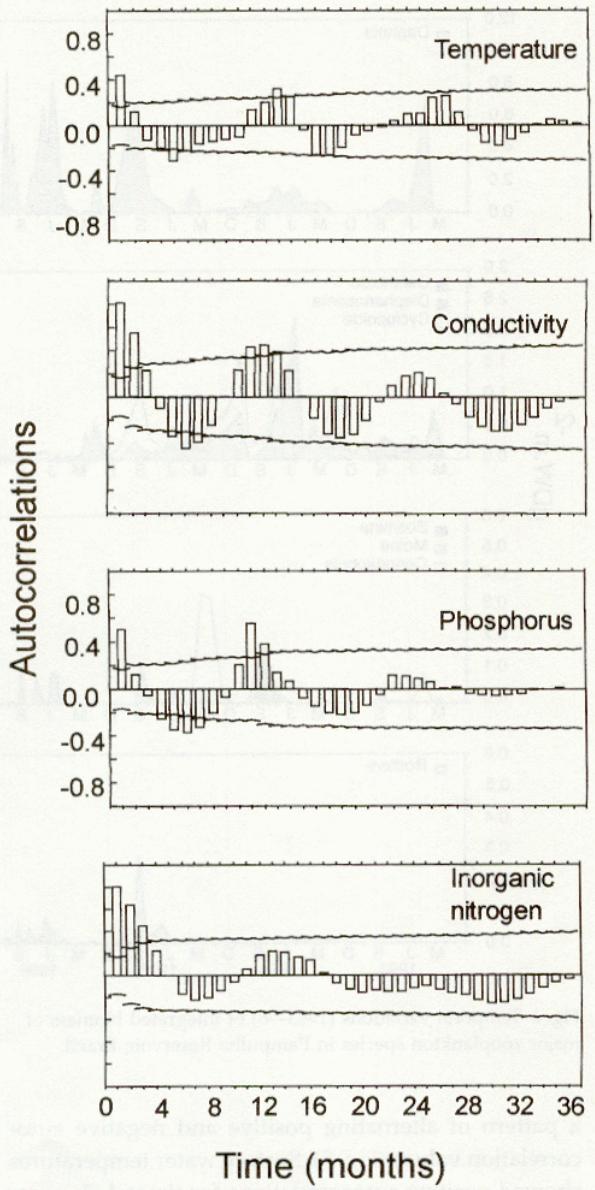

Fig. 5 Autocorrelation plots of temperature, conductivity, total phosphorus and inorganic nitrogen from surface water of Pampulha Reservoir, Brazil, for monthly samples from January 1994 to December 1996. Standard errors are indicated.

modifications, since nitrogen and phosphorus had increased over the study period (Fig. 5).

The autocorrelation plots for the major components of zooplankton also revealed alternating patterns of positive and negative values with increasing time lags (Fig. 6). The autocorrelation plot for *Daphnia* shows clearly the recurrence of seasonal patterns. The calanoid *S. corderoi* and rotifers also demonstrated seasonal recurrence, reflecting a tendency to increase their biomass during the dry season. However, the autocorrelation values of both organisms decreased with time. This may suggest that their seasonal patterns were more affected in the long run. The autocorrelation plots of Cyclopoida and *Diaphanosoma*, in particular, indicate that the temporal variations of these organisms may reflect more long-term modifications than seasonal patterns, since the alternation of positive and negative autocorrelations did not reflect any clear recurrent seasonal cycle. The autocorrelation plots for other organisms, such as *Moina*, *Ceriodaphnia* and *Bosmina*, also did not show any conspicuous trend for seasonal recurrence (Fig. 6 shows only the plot for *Moina*).

Principal Component Analysis was performed using the 1994–96 data (Fig. 7), aiming to investigate possible associations between zooplankton and other variables commonly used to describe eutrophication. The following variables were considered: water conductivity, dissolved oxygen, pH, total phosphorus and inorganic nitrogen and food availability (POC and chlorophyll *a*). Only the most abundant zooplankton organisms were considered: *Daphnia*, *Diaphanosoma*, *Moina*, cyclopoid copepods and rotifers. The first three axes explained 61.9% of the total variance (Table 1).

The most important zooplankton organisms in terms of biomass, *Daphnia* and *Diaphanosoma*, were clearly separated along axis one. *Daphnia* formed a tight cluster with total phosphorus, inorganic nitrogen, conductivity, particulate carbon, rotifers and *Moina*. The first axis also isolated a second cluster formed by surface pH, chlorophyll *a*, dissolved oxygen and Cyclopoida. Being a eutrophic ecosystem, Pampulha lake showed close associations between algal biomass (chlorophyll *a*), water transparency, dissolved oxygen and pH. These variables were also associated with *Diaphanosoma* (see plot of factor 1 vs. factor 3). Therefore, the two variables associated with food availability for zooplankton appeared in quite different regions of the first axis. POC was associated with *Daphnia* in one cluster whereas chlorophyll *a* was weakly associated with *Diaphanosoma* and dissolved oxygen. Thus, the first axis possibly describes two ecological scenarios: (i) one characterized by dominance of *Daphnia* in the zooplankton, associated with higher availability of sestonic carbon, phosphorus and nitrogen as well as high conductivity levels and (ii) a second characterized

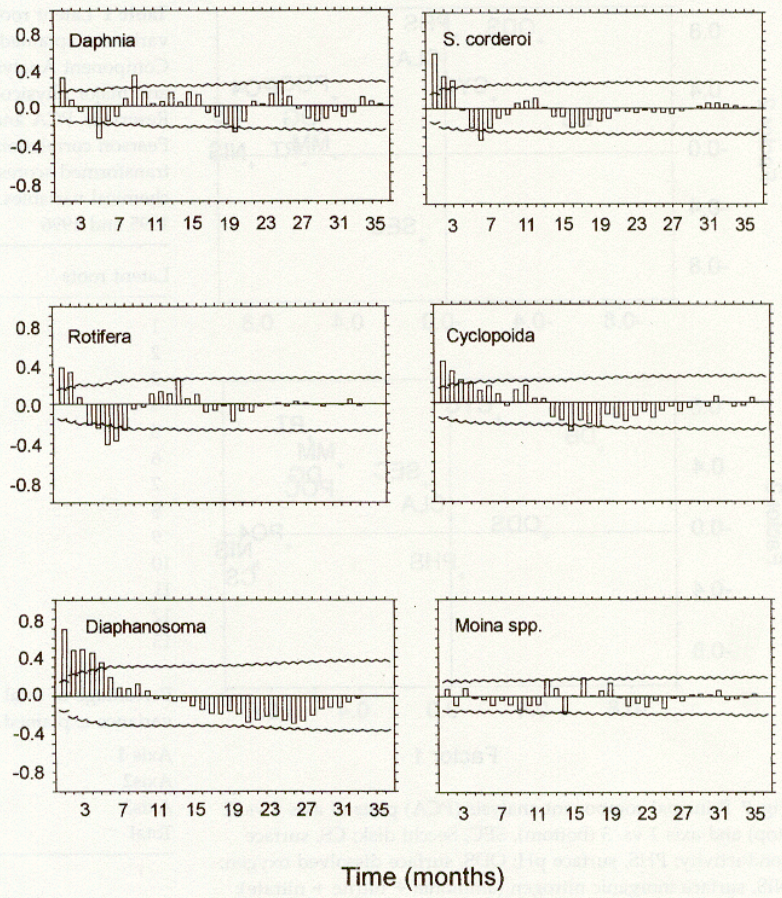

Fig. 6 Autocorrelation plots of zooplankton from Pampulha Reservoir, Brazil, for monthly samples from January 1994 to December 1996. Data are log-transformed. Standard errors are indicated.

by the dominance of *Diaphanosoma* in the zooplankton with high algal biomass and moderate levels of nitrogen and phosphorus.

The second axis possibly reflected the turbidity factor. The cluster formed by particulate carbon (detritus) and chlorophyll (algae particles) is situated in the positive region of axis two; both variables contribute to increased turbidity in the lake. The Secchi depth was isolated in the negative region of the second axis. The third axis probably reflects a gradient of nutrient availability, since nitrogen, phosphorus and conductivity form a tight cluster in the negative region of this axis.

The sestonic C:P ratio also showed large variations in Pampulha Reservoir. The highest values were found shortly after the rainy season, between February and May, when C:P ratios higher than ninety were observed (Fig. 8). The seasonal course of the dominant zooplankter, *Daphnia* spp., seems to be inversely associated with the sestonic C:P ratios. All seasonal maxima of this cladoceran occurred when C:P ratios were lower than twenty-five (Fig. 8).

Discussion

Long-term studies focusing on the temporal dynamics of zooplankton from temperate regions are relatively abundant in the literature, both for medium and large lakes (Gulati, 1978; Goldman *et al.*, 1979; Prophet, 1982; Einsle, 1988; Scavia *et al.*, 1988; Ravera, 1996) and also for reservoirs, small lakes and ponds (i.e. Kratz *et al.* 1987; Benndorf *et al.*, 1988; Mark *et al.* 1994). Such studies demonstrate the existence of clear and recurrent seasonal patterns for most groups of zooplankton. On the other hand, long-term studies in tropical lakes are scarce. Zooplankton from some tropical lakes and reservoirs undergo large but nonrecurring temporal variations in their abundance, while other tropical

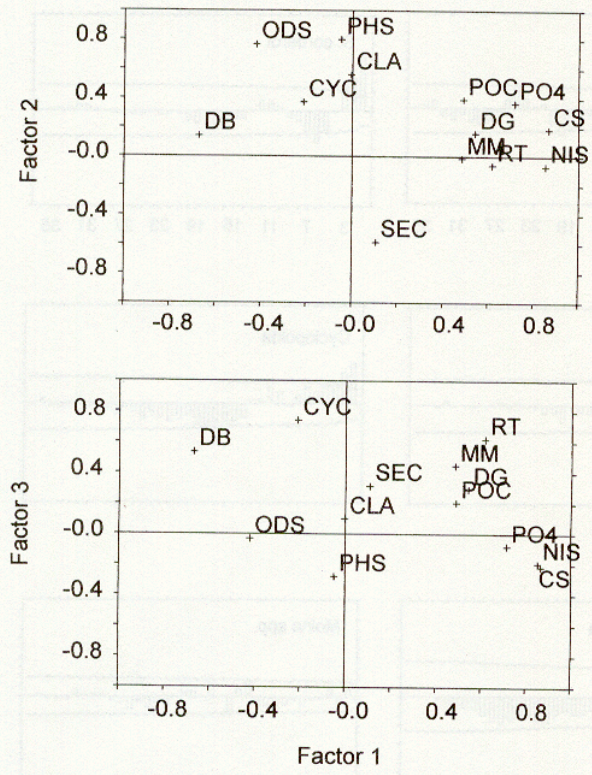

Fig. 7 Principal component analysis (PCA) plots of axis 1 vs. 2 (top) and axis 1 vs. 3 (bottom). SEC, Secchi disk; CS, surface conductivity; PHS, surface pH; ODS, surface dissolved oxygen; NIS, surface inorganic nitrogen (ammonia + nitrite + nitrate); PO4, surface total phosphorus; CLA, chlorophyll *a*; POC, particulate organic carbon. Organisms symbols: CYC, Cyclopoida; DG, *Daphnia*; DB, *Diaphanosoma*; MM, *Moina*; RT, rotifera.

Table 1 Latent roots, eigenvalues and percentage of total variance explained by the first three axes of Principal Component Analysis (PCA) based on zooplankton organisms and major physico-chemical characteristics of Pampulha Reservoir. PCA analysis was carried-out using a matrix of Pearson correlation coefficients of zooplankton biomass (log-transformed scores; µg DW m^{-2}) and surface values of chemical variables. The PCA used only data from years 1994, 1995 and 1996

Latent roots	Eigenvalues	
1	3.832	
2	2.401	
3	1.819	
4	1.103	
5	0.941	
6	0.776	
7	0.613	
8	0.469	
9	0.351	
10	0.307	
11	0.191	
12	0.138	
13	0.057	
Percentage of total variance explained	% each axis	% cumulative
Axis 1	29.476%	29.476%
Axis2	18.469%	47.945%
Axis3	13.990%	61.935%
Total	61.935%	

lakes are permanently dominated by a simple community of small organisms, such as small cladocerans and rotifers (Pinto-Coelho 1987; Saunders & Lewis 1988a; Bonecker & Lansac-Tôha 1996). Moreover, the prevalence of early stages of copepods is a common feature in shallow and unstable tropical waters, such as lagoons, which suffer intense and periodic influence of sea water (Attayde, 1996).

The present study shows recurrent seasonal cycles not only in physicochemical variables but also in zooplankton populations. The autocorrelation plots of major zooplankton organisms such as *Daphnia* showed an obvious pattern of alternating negative and positive autocorrelations. Other zooplankters, such as *Diaphanosoma*, exhibited temporal variations that seem to reflect the long-term changes in the trophic status of the reservoir. Finally, there is a third group of opportunistic organisms, including *Moina* and *Ceriodaphnia*, that shows neither a recurrent seasonal trend nor long-term trend; these population peaks seem to occur over short periods of time under specific (and unstable) conditions.

The seasonal courses of physicochemical variables can also be divided into three groups. To a first group belong variables such as water temperature and conductivity, which exhibited a very clear and recurrent seasonal pattern. A second group of variables, including total phosphorus and inorganic nitrogen, exhibited seasonality but also showed long-term changes during the four years covered in this study. These long-term changes are clearly reflected in their autocorrelation plots. Finally, a third group of variables, including oxygen and pH, showed temporal variability but these patterns were not recurrent on a seasonal basis.

Phosphorus, nitrogen and chlorophyll *a* are widely used to monitor the progress of eutrophication in aquatic ecosystems (Vollenweider, 1979). Principal

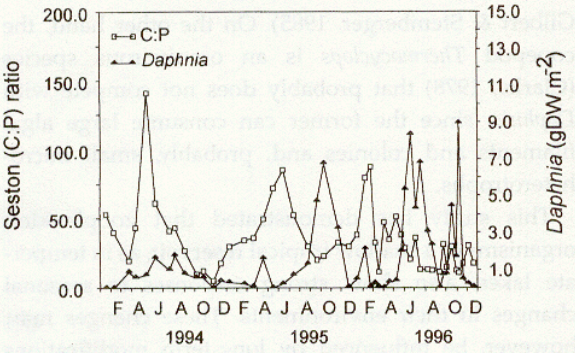

Fig. 8 Temporal variation of sestonic C:P ratios and integrated biomass of *Daphnia* in Pampulha Reservoir.

component analysis showed that *Daphnia* biomass was related to the temporal dynamics of most of these parameters in Pampulha Reservoir. Thus, the increases of *Daphnia* biomass, conductivity, total phosphorus and nitrogen observed in 1995 and 1996 can be associated with the increased eutrophication of this reservoir during this period.

A significant relationship was found between *Daphnia* biomass and total phosphorus ($r_{pearson}$ = 0.355, $P < 0.015$, $n = 49$). Increases in both variables are associated with eutrophication (Gutelmakher & Makartsura 1990; Mazumder, 1994; Shahady & Redfield, 1994). The present study also shows an inverse association between *Daphnia* biomass and C:P ratios (Fig. 8). *Daphnia* seems to have one of the highest P-contents of zooplankton organisms (up to 2.0% of dry weight) and thus, it has one of the highest P-requirements (Sterner & Hessen, 1994). It has previously been demonstrated that *Daphnia* can be P-limited; thus *Daphnia galeata* suffer from P-limitation if the C:P ratio is higher than 100 (Urabe & Watanabe, 1992). Hessen (1992), reviewing several studies about P-limitation in zooplankton, suggests that *Daphnia* may suffer from P-limitation at C:P ratios varying from 50 to 62.5. The present study showed that the development of large populations of this cladoceran only occurred when C:P ratios were lower than 50.

All measures of food availability in Pampulha Reservoir (Chlorophyll *a*, POC and total phosphorus) were at least an order of magnitude higher than the amount required to give maximal growth or maximal ingestion in laboratory experiments with high food quality (Geller, 1975). Thus, the zooplankton of Pampulha should be limited by food quality. The inverse association found in this study between sestonic C:P ratios and *Daphnia* ($r_{Pearson}$ = –0.243, $P < 0.078$, $n = 49$) may be an indication that food quality may be a key factor regulating zooplankton populations in this lake.

Like total phosphorus, inorganic nitrogen could also explain temporal shifts in the structure of the zooplankton community. The correlation coefficient between inorganic nitrogen and *Daphnia* biomass was also significant ($r_{Pearson} = 0.319$, $P \leq 0.025$, $n = 49$). *Daphnia* usually builds up a large population in the dry season in Pampulha Lake with the population maximum frequently coinciding with increases in ammonia concentrations. There is also experimental evidence that respiration and nutrient excretion by *Daphnia* is intense enough to reduce the amounts of dissolved oxygen and to increase ammonia concentrations in lake water. In previous experiments, it has been demonstrated that excretion by *Daphnia* and differential uptake of phosphorus by water-column bacteria contribute to increased N:P ratios in lake water (Pinto-Coelho *et al.*, 1997b). Nitrogen levels in the reservoir also responded rapidly to macrophyte management (Pinto-Coelho & Araújo, 1998).

No long-term increase in chlorophyll *a* concentrations was observed. A possible explanation for this may be related to the biomass increase of *Daphnia*, especially *D. laevis* when observed in 1995 and 1996. The Pearson correlation coefficient between this cladoceran and chlorophyll *a* was negative, but nonsignificant ($r_{Pearson} = -0.135$, $P \leq 0.355$, $n = 49$). The increase in zooplankton biomass may have offset an expected increase in phytoplankton biomass during this period.

Zooplankton population structure may not be regulated only by 'bottom up' forces such as nutrient or food availability. Fish predation is often an important factor explaining zooplankton community structure (Christoffersen *et al.*, 1993). However, there is evidence that fish predation plays only a secondary role in Pampulha reservoir, perhaps because the fish fauna is dominated by non-planktivorous species (Godinho *et al.*, 1992). Furthermore, the lake is very turbid; water transparency is an important factor since fish predation is mostly based on visual stimuli (O'Brien, 1979). In this context, Carvalho (1984) has observed increases in *Daphnia* populations associated with increases in turbidity in Amazonian lakes. In addition, frequent oxygen depletion or algal toxins produced by extensive algal blooms have caused massive fish mortalities in recent years (Pinto-Coelho *et al.* 1997a). In this context, diel vertical migration, which may be an efficient

predator avoidance mechanism (Gliwicz, 1986), is not observed in *Daphnia* or several other zooplankton species in this lake (Da Costa & Pinto-Coelho, 1997).

Invertebrate predators may be more influential than fish in Pampulha Lake. The most important predators are the cyclopoids *Mesocyclops aspericornis* (Daday 1906), *M. meridianus* (Kiefer 1926), *Metacyclops mendocinus* (Wierzejski 1892), the rotifer *Asplanchna* sp. and larvae of the dipteran *Chaoborus* sp. during the rainy season. Occasionally, some predatory planktonic flatworms have also been observed. *Asplanchna* and *Mesocyclops* spp. mostly consume small individuals such as *Ceriodaphnia* and *Bosmina*. Invertebrate predation may help to explain why these small cladocerans occur in low biomass in Pampulha lake.

Diaphanosoma and *Daphnia* are filter-filtering cladocerans of similar dimensions; their quite different seasonal trends in Pampulha Reservoir may be indicative of interspecific competition. The Pearson correlation coefficient between the biomass of these cladocerans was negative but non significant ($r_{Pearson} = -0.181$, $P <= 0.213$, $n = 49$). PCA analysis showed that *Daphnia* was associated with total phosphorus, inorganic nitrogen and particulate carbon. This suggests that *Daphnia* may be consuming not only algae and bacteria but also microheterotrophs and detritus. Recent studies have demonstrated that several species of *Daphnia* are able to consume a large spectrum of food items including sestonic particles, bacteria, algae, protozoans and rotifers (Pace & Vaqué, 1994; Jürgens, 1994). *Diaphanosoma*, on the other hand, was weakly associated with chlorophyll *a* and with moderate levels of nutrients, especially nitrogen ($r_{Pearson} = -0.623$, $P <= 0.0001$, $n = 49$). This may explain why *Diaphanosoma* tended to increase in the first half of the dry season when nitrogen concentrations were usually low. Despite some evidence indicating that *Diaphanosoma* is a very efficient bacteria feeder (e.g. Gliwicz, 1977), the lack of association with POC and the weak association with chlorophyll *a* seem to indicate that *D. birgei* may be exploiting mainly algal food particles in Pampulha Reservoir.

Moina, rotifers and cyclopoids have seasonal cycles similar to that of *Daphnia*, being more abundant during the dry season. Such co-occurrence, however, does not necessarily indicate that these organisms do not compete for food. Despite being smaller than *Daphnia*, several studies have demonstrated that rotifers compete with *Daphnia* for food (Gilbert, 1985, 1988, 1989; Gilbert & Stemberger, 1985). On the other hand, the copepod *Thermocyclops* is an omnivorous species (Clarke, 1978) that probably does not compete with *Daphnia*, since the former can consume large algal filaments and colonies and, probably, small microheterotrophs.

This study has demonstrated that zooplankton organisms of a shallow tropical reservoir, as in temperate lakes, also show strong responses to seasonal changes in their environments. These changes may, however, be influenced by long-term modifications such as eutrophication.

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