

Does the plankton community follow the horizontal water quality heterogeneity in a tropical urban reservoir (Guarapiranga reservoir, São Paulo, Brazil)?

Paula Yuri Nishimura^{1,*}, Patrícia do Amaral Meirinho¹, Viviane Moschini-Carlos² and Marcelo Luiz Martins Pompêo¹

¹ Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo. São Paulo-SP, Brazil.
² Departamento de Engenharia Ambiental, Universidade Estadual Paulista Júlio de Mesquita Filho, Campus Experimental de Sorocaba, Sorocaba-SP, Brazil.

* Corresponding author: mpompeo@ib.usp.br

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ABSTRACT

Does the plankton community follow the horizontal water quality heterogeneity in a tropical urban reservoir (Guarapiranga reservoir, São Paulo, Brazil)?

Reservoirs exhibit a marked degree of spatial heterogeneity, and environmental heterogeneity directly affects organism distribution and community composition. The objective of this study was to investigate the spatial horizontal heterogeneity of the planktonic communities along the longitudinal axis of the Guarapiranga reservoir (São Paulo, Brazil). We sampled nine stations along the Guarapiranga reservoir longitudinal axis for physical, chemical and biological variables. In addition, we analysed phytoplankton and zooplankton communities. To explore the data, we applied multivariate techniques, such as cluster hierarchical analysis and discriminant analysis. Our results showed a clear tendency towards compartmentalisation of the epilimnetic layers in this reservoir, especially when based on water quality. Three main compartments were observed: 1) the Embu-Graçu region, the upper part of the reservoir, more protected and less eutrophic; 2) the Parelheiros region, a very eutrophic branch of the reservoir; and 3) the lower part of the reservoir, with eutrophic and lacustrine characteristics. The groups formed by the cluster analysis based on the plankton data did not coincide with the groups based on water quality. These different outcomes indicate that the water quality, phytoplankton and zooplankton communities captured different features from the epilimnetic layer in the longitudinal axis of the Guarapiranga reservoir. Importantly, the phytoplankton and zooplankton communities in the dam region were altered, directly or indirectly, by copper sulphate treatment. Therefore, phytoplankton biomass is being driven by forces other than the forces intrinsic to the reservoir, such as human-induced losses. Consequently, zooplankton structure is being affected as well.

Key words: Phytoplankton, zooplankton, CSR-strategists, compartmentalisation.

RESUMEN

¿Sigue la comunidad planctónica la heterogeneidad de calidad horizontal del agua en un embalse tropical urbano (Embalse Guarapiranga, São Paulo, Brasil)?

Los embalses muestran un marcado grado de heterogeneidad espacial y la heterogeneidad ambiental afecta directamente a la distribución de los organismos y la composición de la comunidad. El objetivo de este estudio fue investigar la heterogeneidad espacial horizontal de las comunidades planctónicas a lo largo del eje longitudinal de Embalse Guarapiranga (Sao Paulo, Brasil). Se tomaron muestras en nueve estaciones a lo largo del eje longitudinal de Guarapiranga (datos físicos, químicos y biológicos). Además, se analizaron las comunidades de fitoplancton y zooplancton. Para explorar los datos, se aplicaron técnicas multivariantes, como el análisis de conglomerados jerárquico y análisis discriminante. Los resultados muestran una clara tendencia a la compartimentación de las capas epilimnéticas en este embalse, especialmente basada en la calidad del agua. Se evidenciaron tres compartimentos principales: 1) la región de Embu-Guaçu, cabecera del embalse, más protegida y menos eutrófica, 2) la región de Parelheiros, un tramo de río muy eutrófico y 3) la parte del embalse, cerca de la presa, con características eutróficas. Los grupos formados por el análisis de conglomerados jerárquico basado en los datos del plancton no coinciden exactamente con los grupos basados en la calidad del agua. Estos resultados indican que la calidad del agua y

Nishimura et al.

la comunidad del fitoplancton y zooplancton están influenciadas por diferentes características de la capa epilimnética en el eje longitudinal del Embalse Guarapiranga. Es importante destacar que el fitoplancton y zooplancton en el embalse fueron alterados, directa o indirectamente, por un tratamiento con sulfato de cobre. Por lo tanto, la biomasa del fitoplancton está condicionada por acciones humanas, distintas a las inherentes al embalse. En consecuencia, la estructura del zooplancton también está siendo afectada.

Palabras clave: Fitoplancton, zooplancton, estrategias CRS, compartimentación.

INTRODUCTION

Environmental heterogeneity, defined as spatial and temporal variation in the physical, chemical and biological environment, is a fundamental property of ecosystems (Scheiner & Willig, 2008). Regarding the spatial heterogeneity, there are two main approaches in ecology: 1) the physical heterogeneity of the organisms or ecological entities in the space and 2) the heterogeneity of qualitative or quantitative values of parameters in a continuum space (Dutilleul, 1993). These two different approaches are closely related because environmental heterogeneity directly affects the composition and distribution of organisms (Margalef, 1991). For example, as the environment gets more complex physically, the complexity of biological communities and diversity increases as well (Deshmuck, 1986).

Reservoirs exhibit a marked degree of spatial heterogeneity (Tundisi, 1996). The progressive physical, chemical and biological changes along the main axis of a reservoir (river-lake transition) frequently result in strong horizontal gradients (Nogueira et al., 1999). These gradients are not only attributed to the transformations of rivers into lakes but also to the great influence that rivers continue to exert in the reservoir (Marcé, 2007). Additional heterogeneity can result from the dendritic nature of reservoir basins (Kimmel et al., 1990) and from interactions with other ecosystems from the hydrographic basin. For example, if the tributary rivers exhibit distinct characteristics due to geological origin or human interference (Tundisi, 1996).

The above-mentioned abiotic factors that promote environmental horizontal heterogeneity are important to the structure and functioning of biotic communities. In particular, phytoplankton productivity and biomass are highly influenced by spatial variation, such as longitudinal gradients in basin morphology, flow velocity, water residence time, suspended solids, and light and nutrient availability (Kimmel *et al.*, 1990). Zooplankton organisms respond to changing quantity or quality of food resources by altering their reproductive performance, resulting in population increases near the source of food (Marzolf, 1990).

The objective of this study was to investigate the spatial horizontal heterogeneity of the planktonic communities along the longitudinal axis of the Guarapiranga reservoir (São Paulo, Brazil). Thus, we hypothesised the following:

- 1. the establishment of compartments with different water qualities will produce changes in phytoplankton community structure;
- 2. the zooplankton community structure will follow a compartmentalisation pattern similar to that shown by the phytoplankton community, as these two planktonic communities are closely related.

Therefore, we expect that water quality, phytoplankton and zooplankton data will exhibit similar compartmentalisation patterns in the Guarapiranga reservoir.

METHODOLOGY

Study site

This study was conducted in the Guarapiranga reservoir, a sub-basin of the Alto do Tietê basin, located at an altitude of 742 m in São Paulo city, Brazil (23°43'S/46°32'W, Fig. 1). The Guarapiranga basin has 639 km² of watershed area, and



Figure 1. The Guarapiranga reservoir, its main tributaries and the nine sampling stations. *Embalse de Guarapiranga, sus afluentes principales y las nueve estaciones de muestreo.*

the reservoir itself can store 194 million m³ of water. The maximum depth is 13 m and the average depth is 6 m. It is considered an urban polymictic reservoir with long retention times (185 days, Carvalho et al., 2007) and is mainly surrounded by the municipality of São Paulo (the largest South American city) on its right shore and partly on the left shore, totalling 70% of the reservoir's perimeter. The main tributaries are the Embu-Mirim River, the Embu-Guaçu River and the Parelheiros River, in addition to many other small streams and creeks. Guarapiranga's current uses are water supply, flood control, electric power generation and recreation. This reservoir supplies 3.7 million people in the São Paulo metropolitan area (20% of the São Paulo city population) (Whately & Cunha, 2006).

Since the 1960s, the Guarapiranga reservoir has been under eutrophication processes due to urban sewage water input (Rocha, 1976). As São Paulo city's population grew, Guarapiranga's watershed was impacted by urban expansion. The reservoir's surroundings were occupied mainly by illegal human settlements without proper sewage water catchments (Beyruth, 1996). Thus, sewage water was launched directly into the reservoir. Moreover, mineral and sand extraction contributed to the deforestation, erosion and sedimentation of the tributaries, and eutrophication problems remain today (Whately & Cunha, 2006). To control phytoplankton blooms, especially cyanobacteria, the addition of copper sulphate in the reservoir near the dam is a common action by the environmental agency.

Sampling and variable analyses

On October 27th, 2010, we sampled nine stations in the Guarapiranga reservoir (Fig. 1): "EG1", "EG2" and "EG3" at the Embu-Guaçu branch, "P1" and "P2" at the Parelheiros branch, "EM" at the Embu-Mirim branch, "C1" and "C2" at the central body of the reservoir and one sampling station at the "dam". Vertical profiles of temperature (T), dissolved oxygen (DO), pH and electric conductivity (EC) were measured at each sampling station at 50 cm intervals, from the surface to the bottom, with standard electrodes (YSI 556). The thermocline was considered as a drop of at least 1 °C in 1 m depth (Wetzel, 2001). Transparency was measured using a Secchi disk (Z_{SD}) , and euphotic depth (Zeu) was estimated by multiplying Z_{SD} by 2.4 (Arocena, 1999).

Integrated water samples (0-3 m) were collected with a plastic pipe to sample the entire euphotic zone in each sampling station. Subsamples were isolated, maintained at a cool temperature and stored in the dark until arrival at the laboratory. The integrated water samples were analysed for ammonium, nitrite and nitrate summed as total inorganic nitrogen (TIN, Mackereth et al., 1978), soluble reactive silica (SRSi) and soluble reactive phosphorus (SRP, Strickland & Parsons, 1960), total nitrogen (TN) and total phosphorus (TP, Valderrama, 1981), chlorophyll-a (Chla) corrected for phaeophytin using 90% acetone extraction (Lorenzen, 1967; Wetzel & Likens, 1991), and total solids (TS) and suspended solids (total: TSS, organic: OSS

Nishimura et al.

Table 1. Phytoplankton descriptor species (more than 5 % of the total biomass) sorted by taxonomic class, respective CSR-strategy classification and biomass in the nine sampling stations in the Guarapiranga reservoir longitudinal axis. *Especies descriptoras del fitoplancton (más de 5 % de la biomasa total) ordenadas por categoría taxonómica, la correspondiente clasificación según estrategias CRS y la biomasa, en las nueve estaciones de muestreo en el eje longitudinal del embalse Guarapiranga.*

Class Species		Sampling station/biomass (mg/l)								
		EG1	EG2	EG3	P1	P2	EM	C2	C1	Dam
Bacillariophyceae										
Urosolenia eriensis (H.L. Smith) Round & R.M. Crawford	R	6.5	15.2	8.1	-	-	-	-	-	-
Aulacoseira ambigua (Grunow) Simonsen	R	-	-	-	1.9	2.4	1.7	3.3	-	3.0
Cyclotella meneghiniana Kützing	R	-	-	11.6	-	-	-	-	-	1.9
Nitzschia fruticosa Hustedt	R	-	-	-	-	-	-	-	-	3.0
Chlorophyceae										
Botryococcus neglectus (West & G.S. West) J. Komárek & P.Marvan	S	-	-	-	-	-	-	-	1.8	-
Eudorina illinoisensis (Kofoid) Pascher	S	-	-	5.8	-	9.1	6.7	-	-	33.6
Acanthosphaera zachariasii Lemmermann	С	-	-	-	-	9.2	7.5	-	-	-
Actinastrum hantzschii var. subtile J. Woloszynska	С	-	-	1.4	-	-	-	-	1.3	4.0
Coelastrum indicum W.B. Turner	R	-	-	-	-	-	1.4	-	-	-
Desmodesmus denticulatus (Lagerheim) S.S. An, T. Friedl & E. Hegewald	C	-	-	-	-	-	-	-	-	1.2
Pediastrum duplex var. gracillimum West & G.S. West	R	-	-	4.6	1.8	1.6	-	-	2.7	1.5
Cryptophyceae										
Cryptomonas brasiliensis A. Castro, C. Bicudo & D. Bicudo	С	-	-	-	-	-	-	1.3	-	4.7
Cryptomonas curvata Ehrenberg	С	-	-	5.6	9.2	1.8	-	-	-	-
Chrysophyceae										
Dinobryon sertularia Ehrenberg	R	1.3	1.6	-	-	-	-	-	-	-
Cyanophyceae										
Dolichospermum spiroides (Kleb.) Wacklin, L. Hoffm. & Komárek	S	-	-	-	-	2.4	5.6	5.6	4.6	6.7
Aphanocapsa delicatissima West & G.S. West	С	-	3.2	5.6	12.1	19.4	11.3	11.8	-	21.4
Aphanocapsa incerta (Lemmermann) Cronberg & Komárek	С	-	-	-	-	-	-	-	1.2	-
Sphaerocavum brasiliense Azevedo & Sant'Anna	S	-	-	-	-	-	-	-	1.6	-
Phormidium sp.	R	-	-	3.8	-	-	-	-	-	-
Dinophyceae										
Peridinium gatunense Nygaard	S	-	-	-	13.4	3.1	3.4	-	2.6	-
Peridinium sp.	S	-	-	-	-	-	-	-	1.8	-
Gymnodinium fuscum (Ehrenberg) F. Stein	S	-	-	-	5.0	4.7	2.1	6.1	-	2.8
Euglenophyceae										
Trachelomonas volvocinopsis Svirenko	С	-	-	-	2.1	-	-	-	-	1.5
Xanthophyceae										
Tetraedriella spinigera Skuja	С	-	-	-	-	2.7	-	-	-	-
Zygnematophyceae										
Cosmarium sp.	R	-	-	-	-	-	-	-	-	4.9
Mougeotia sp.	R	-	-	-	-	-	1.5	-	1.5	4.6

Plankton horizontal heterogeneity in the Guarapiranga reservoir

Table 2. Zooplankton species sorted by main groups and density in the nine sampling stations in the Guarapiranga reservoir longitudinal axis. *Especies de zooplancton ordenadas por grupos principales y su densidad en las nueve estaciones de muestreo en el eje longitudinal del embalse Guarapiranga.*

Group	Sampling station/density (org/l)								
Species	EG1	EG2	EG3	P1	P2	EM	C2	C1	Dam
Copepoda Cyclopoida									
Acanthocyclops robustus (GO Sars, 1863)	-	-	-	-	-	-	-	0.03	0.02
Eucyclops subciliatus (Dussart, 1984)	-	0.01	-	-	-	-	-	-	-
Mycrocyclops anceps (Richard, 1897)	-	0.03	-	-	-	-	-	-	-
Thermocyclops decipiens (Kiefer, 1929)	0.01	0.01	-	26.14	1.16	0.03	0.26	1.11	0.07
Thermocyclops inversus (Kiefer, 1936)	-	-	-	0.26	0.10	-	-	-	-
Cladocera									
Bosmina longirostri (O.F. Muller, 1785)	0.01	-	0.62	0.40	0.72	0.03	0.74	-	0.07
Bosminopsis deitersi (Richard, 1895)	0.13	9.34	7.21	9.11	16.05	0.08	5.58	-	0.11
Ceriodaphnia cornuta (Sars, 1886)	-	0.37	-	-	-	-	-	-	0.02
Daphnia gessneri (Herbst, 1967)	-	0.01	0.04	0.07	0.06	-	-	-	-
Diaphanosoma birgei (Korinek, 1981)	-	0.03	-	-	0.11	0.11	0.11	-	0.09
Iliocryptus spinifer (Herrich, 1884)	-	0.04	-	-	-	-	-	-	0.02
Moina minuta (Hansen, 1899)	-	0.01	0.26	0.40	0.83	-	0.21	-	0.02
Simocephalus serrulatus (Koch, 1841)	-	0.06	-	-	-	-	-	-	-
Rotifera									
Anuraeopsis navicula (Rousselet, 1911)	0.33	-	2.28	5.55	4.64	0.88	0.95	1.39	5.49
Asplanchna sp.	-	-	0.57	0.79	-	8.33	0.47	-	-
Brachionus angularis (Gosse, 1851)	0.16	-	-	-	-	0.88	-	-	-
Brachionus calyciclorus (Bryce 1931)	-	0.34	-	3.17	6.19	3.95	5.69	5.11	17.84
Brachionus caudatus (Ahlstrom, 1940)	-	-	-	-	-	3.51	-	-	-
Brachionus mirus (Daday, 1905)	0.65	0.34	2.28	-	3.09	-	-	-	-
Collotheca sp1.	5.22	8.83	2.85	-	1.55	-	-	-	-
Collotheca sp2.	7.99	3.73	2.28	-	-	-	-	-	-
Collotheca sp3.	-	1.70	-	-	-	-	-	-	-
Conochilus coenobasis (Skorikov, 1914)	13.70	18.67	20.54	68.13	61.10	0.44	12.32	-	1.37
Conochilus unicornis Rousselet, 1892	18.75	31.24	38.80	38.03	70.38	-	11.37	0.46	2.06
Filinia opoliensis (Zacharias, 1898)	-	-	9.13	73.68	88.16	2.19	5.21	0.93	4.12
Gastropus hyptopus (Ehrenberg, 1838)	3.26	1.36	2.85	1.58	1.55	-	-	-	-
Hexarthra sp.	-	-	-	-	-	-	0.47	-	-
Kellicottia bostoniensis (Rousselet, 1908)	0.33	5.09	55.35	236.09	98.99	0.44	1.42	1.86	-
Keratella americana (Carlin, 1943)	0.33	9.17	16.55	7.13	20.88	18.86	9.95	17.19	41.85
Keratella cochlearis (Gosse, 1851)	4.73	6.79	20.54	33.27	75.79	29.82	28.91	34.37	283.37
Keratella lenzi (Hauer, 1953)	0.33	0.68	1.71	0.79	-	4.82	2.37	6.97	47.34
Keratella tropica (Apstein, 1907)	-	-	5.71	5.55	22.43	45.17	71.09	176.97	705.35
Lecane bulla (Gosse, 1851)	-	-	0.57	-	-	-	-	-	-
<i>Ploesoma</i> sp.	3.75	13.58	2.85	1.58	0.77	0.88	5.69	0.93	3.43
Polyarthra vulgaris (Carlin, 1943)	13.54	32.59	76.46	57.83	60.32	73.68	64.45	3.72	83.02
Proales sp.	-	-	-	-	-	4.82	-	0.46	1.37
Synchaeta sp.	3.10	4.07	10.27	10.30	10.05	19.74	22.27	2.32	19.90
Trichocerca sp.	1.14	1.36	1.14	1.58	1.55	3.07	0.47	0.46	7.55
Trichocerca similis (Wierzejski, 1893)	-	0.68	0.57	-	3.87	7.89	3.79	5.57	17.15

and inorganic: ISS) (Wetzel & Likens, 1991). The Trophic State Index (TSI) was calculated based on TP and Chla according to Lamparelli (2004) for Brazilian reservoirs.

Plankton sampling and analyses

Sub-samples (100 ml) of the integrated water column were isolated and preserved with Lugol's iodine solution for phytoplankton community analysis of each sampling station. Phytoplankton species were identified based on a specific bibliography in a Carl Zeiss ScopeA1 microscope (Oberkochen, Germany). Phytoplankton cells were counted using the settling technique (Utermöhl, 1958) in 2 ml settling chambers in a Carl Zeiss Axiovert40C inverted microscope. The determination of sedimentation time followed the protocol outlined by Lund et al. (1958). A minimum of 400 counting units (cells, colonies or filaments) were counted in each sample, giving a counting accuracy expressed in terms of 95 % confidence limits, of < 10 % for the entire phytoplankton population (Lund et al., 1958). Biovolume was obtained by geometric approximation, multiplying each species' density by the mean volume of its cells considering, whenever possible, the mean dimension of 30 individual specimens of each species (Hillebrand et al., 1999). Fresh algal biomass was estimated assuming a specific gravity for algal cells of 1 mg/mm³. Phytoplankton species that contributed to more than 5% of the total biomass of the sample were considered as descriptor species of the community and included in the data analysis. Species that contributed to more than 50% of the total biomass of the sample were considered dominant species (Lobo et al., 2002).

Descriptor phytoplankton species were assigned using CSR life strategies according to their morphological and physiological traits (Reynolds, 1988): (1) C-strategists: competitive species with a short lifespan, characterised by small cells with a high surface area-to-volume ratio from environments with low disturbance levels; C-strategists are capable of quickly acquiring nutrients; (2) R-strategists: ruderal species that are generally favoured by high-resource (nutrient and/or light) and high intensity of disturbance conditions (i.e., turbulent conditions); (3) S-strategists: stress-tolerant species with large single cells or colonies of small cells whose general motility allows them to regulate their position in the water column; S-strategists are slow growing and capable of conserving biomass and resources.

Zooplankton samples were collected in a 64 µm mesh net in a vertical array at a 0-3 m depth at each sampling station. Filtered volumes were estimated by geometric approximation (sampled depth and aperture area of the net) for the quantitative analysis. Zooplankton organisms were narcotised with carbonated water and preserved with a 4% formalin-sucrose solution. Zooplankton samples were identified according to specialised literature (e.g., Koste, 1978; Reid, 1985; Elmoor-Loureiro, 1997; Nogrady & Segers, 2002). Sub-samples of the zooplankton samples were counted in a Sedgwick-Rafter chamber for rotifers and in a counting chamber for crustaceans until 100 individuals of the most abundant species were reached.

Data analyses

Cluster hierarchical analyses were performed to assess the compartmentalisation of the sampling stations in the Guarapiranga reservoir based on the limnological variables (water quality) and the plankton communities. A first cluster hierarchical analysis (Ward's clustering method and Euclidean distance) was performed with all physical, chemical and biological variables (all included variables, see Supplementary information, Table S1, available at www.lim netica.net/internet). A second set of cluster hierarchical analyses (Ward's clustering method and Manhattan distance) was performed with the plankton community data: 1) phytoplankton descriptor species biomass, 2) phytoplankton CSR strategist biomass and 3) zooplankton individual species density.

To explore if the groups that originated from each cluster analysis were statistically distinct from each other, the groups were tested with simple or multiple discriminant analyses (Leg-



Figure 2. Sampling time and vertical profiles of temperature (T), dissolved oxygen (DO), pH and electric conductivity (EC) of the water in the nine sampling stations along the Guarapiranga reservoir longitudinal axis. *Hora de muestreo y perfiles verticales de temperatura (T), oxígeno disuelto (DO), pH y conductividad eléctrica (EC) del agua en las nueve estaciones de muestreo a lo largo del eje longitudinal del embalse Guarapiranga.*

endre & Legendre, 1998). To certify the independence of the variables, a tolerance level of 0.01 was established in the discriminant analysis. Correlation between phytoplankton and zooplankton communities was assessed using Spearman's rank correlation coefficient (between phytoplankton biomass and zooplankton density).

In all statistical analyses, water quality variables were transformed by range

$$\left[(x - x_{\min}) / (x_{\max} - x_{\min}) \right]$$

to maintain the same amplitude for all variables. Phytoplankton and zooplankton data were transformed by $[\log (x + 10)]$ to reduce the variance in the dataset. All analyses mentioned above were performed with STATISTICA (version 7.0) software.

RESULTS

Water quality and horizontal heterogeneity

Figure 2 shows the vertical profiles of the water column in the sampling stations followed by T, EC, pH and DO. Thermal stratification was only observed in P1, with a thermocline at a 0.5 m depth. In the other sampling stations, a gradual decrease in temperature towards the bottom was observed, without a thermocline per se. DO and pH followed the same pattern as temperature. EC values were homogenous along the water column in all sampling stations, except in EG3, when it gradually increased towards the bottom. EC values were much lower in the Embu-Guaçu sampling stations, especially in EG1. As expected, Zmax increased towards the dam direction, ranging from 3.0 to 9.2 m (Table S1). All analysed variables in all sampling stations along the Guarapiranga reservoir longitudinal axis are included in Table S1.

Cluster analysis suggested the presence of heterogeneity along the Guarapiranga reservoir longitudinal axis based on water quality (Fig. 3). Three clear compartments were formed: 1) the Embu-Guaçu region (EG1, EG2 and EG3); 2) the Parelheiros region (P1 and P2); and 3) the lower part of the reservoir, which will be



Figure 3. Hierarchical cluster dendrogram (Euclidean distance and Ward's linkage method) based on the water quality variables in the nine sampling stations along the Guarapiranga reservoir longitudinal axis. *Análisis de conglomerados jerárquico (distancia euclidiana y método de vinculación de Ward) basado en las variables de calidad del agua en las nueve estaciones de muestreo a lo largo del eje longitudinal del embalse Guarapiranga.*

called the dam region (dam, C1, C2 and EM). In this last compartment, the dam sampling point was segregated from the others. According to multiple discriminant analysis, the three compartments formed by the cluster analysis based on water quality were different from each other (p < 0.05).

Figure 4 shows the variables that displayed clearer trends along the sampling stations and among the compartments. A decrease in water quality (TSI) in the dam region in the epilimnetic zone was observed (Fig. 4a). The EC, TIN and TP values in the epilimnetic layers showed clear gradients, with lower values in the Embu-Guaçu region, intermediate values in the dam region and higher values in the Parelheiros region (Fig. 4b, Fig. 4c and Fig. 4d). The DO concentrations were much lower in the Parelheiros region compared with the rest of the reservoir (Fig. 4e), and the SRSi concentrations were higher in the Embu-Guaçu region, especially in EG1 (Fig. 4f).

Phytoplankton community: composition, biomass and horizontal heterogeneity

The phytoplankton richness totalled 65 species, and 26 species were considered descriptors (Table 1). Phytoplankton biomass ranged from 7.8 (EG1) to 94.8 mg/l (dam region) (Fig. 5). Phytoplankton composition varied along the sampling stations (Table 1, Fig. 6). R-strategist centric diatoms Urosolenia eriensis and Cyclotella meneghiniana were most prominent in the mesotrophic Embu-Guacu region, which displayed higher SRSi concentrations. In particular, U. eriensis was present only in the Embu-Guacu region. C-strategist species such as Aphanocapsa delicatissima, Cryptomonas curvata and Acanthosphaera zachariasi were dominant in the Parelheiros region, which was characterised by higher nutrient availability and lower DO concentrations. However, S-strategist species were also important in Parelheiros; Peridinium gatunense and Eudorina illinoisensis contributed significantly to the total biomass. In the dam region, C-strategists (e.g., Aphanocapsa delicatissima) and S-strategists (e.g., Dolichospermum spiroides, Eudorina illinoisensis and Gymnodinium fuscum) tended to co-dominate, except in C1. In C1, S-strategist filamentous, N₂-fixing cyanobacteria (Dolichospermum spiroides) and large, ellipsoidal dinoflagellates (*Peridinium ga-tunense*) were the most prominent species.

The cluster analysis based on phytoplankton descriptor species biomass resulted in three compartments: 1) EG1, EG2, EG3, C1; 2) P1, P2, C2, EM; and 3) the dam region (Fig. 7a). These compartments did not overlap as in the compartments formed by the water quality variables (Fig. 3). Moreover, sampling stations within each compartment were not close geographically and did not present similar environmental characteristics. Cluster analysis based on phytoplankton CSR-strategist biomass formed three different compartments: 1) the Embu-Guaçu region (EG1, EG2, EG3); 2) P1, EM, P2, C1, C2; and 3) the dam region (Fig. 7b). CSR-strategist biomass segregated the mesotrophic Embu-Guacu region from the rest of the reservoir and isolated the dam sampling station. According to the discriminant analysis, none of the phytoplankton data clusters formed compartments distinct from each other.



Figure 4. a) Trophic State Index (TSI; O: oligotrophic; M: mesotrophic; E: eutrophic), b) electric conductivity (EC), c) total inorganic nitrogen (TIN), d) total phosphorous (TP), e) dissolved oxygen (DO) and (f) soluble reactive silica (SRSi) values in the nine sampling stations along the Guarapiranga reservoir longitudinal axis. Sampling stations are grouped into the compartments revealed by the hierarchical cluster analysis based on water quality (Figure 3). a) *Índice de Estado Trófico (TSI; O: oligotrófico, M: mesotrófico, E: eutrófico), b) conductividad eléctrica (EC), c) nitrógeno inorgánico total (TIN), d), fósforo total (TP), e) oxígeno disuelto (DO) y f) silica reactiva soluble (SRSi) en las nueve estaciones de muestreo a lo largo del eje longitudinal del embalse Guarapiranga. Las estaciones de muestreo se agrupan según los compartimientos encontrados en el análisis de conglomerados jerárquico basado en la calidad del agua (Figura 3).*



Figure 5. Phytoplankton biomass and zooplankton total density in the nine sampling stations along the Guarapiranga reservoir longitudinal axis. *Biomasa del fitoplancton y densidad del* zooplancton en las nueve estaciones de muestreo a lo largo del eje longitudinal del embalse Guarapiranga.

For both individual species and CSR-strategists, the two main compartments (1 and 2) formed by the cluster analysis were not different from each other (p > 0.05). In these cases, the third compartment (dam region) could not be included in the discriminant analysis because there was only one sampling station in this compartment. Accordingly, the phytoplankton community did not exhibit horizontal heterogeneity along the Guarapiranga reservoir longitudinal axis.

Zooplankton community: composition, density and horizontal heterogeneity

Zooplankton richness totalled 39 species and its density ranged from 77.5 (EG1) to 1241.6 org/l (dam region); it exhibited a similar trend to the phytoplankton community along the sampling stations (Fig. 5). A positive correlation between phytoplankton biomass and zooplankton density was found by Spearman's rank correlation coefficient ($r_s = 0.73$; p < 0.05). This correlation is a good reflection of the close relationship between both communities.

Rotifers were dominant and very abundant in the zooplankton community (Table 2, Fig. 6). In the Embu-Guaçu region, rotifers, mainly *Conochilus unicornis* and *Polyarthra* aff. *vulgaris*, were the most prominent; in the Parelheiros region, these species were replaced by *Kellicottia bostoniensis* and *Filinia opoliensis*. *Polyarthra* aff. *vulgaris*, *Keratella tropica* and *K. cochlearis* were very important in the dam region, especially in the dam sampling station. The contribution of copepods to the total density was only significant in P1 (Fig. 6b). In particular, cyclopoid copepods *Eucyclops subciliatus* and *Mycrocyclops anceps* were only found in the Embu-guaçu region (Table 2). Conversely, the cyclopoid copepod *Thermocyclops decipiens* was found in all sampling stations, especially in the Parelheiros region (P1 and P2). Cladoceran abundance was very low in all sampling stations (Fig. 6b), with *Bosminopsis deitersi*, *Bosmina longirostri* and *Moina minuta* as the main representative species.

The cluster analysis based on zooplankton species density formed three groups: 1) EG1, EG2, EG3, C1, C2, EM; 2) P1, P2; and 3) the dam region (Fig. 7c). Although this arrangement segregated the dam sampling station and the Parelheiros region from the rest of the reservoir, a large and heterogenetic group was formed with the remaining sampling stations that included locations with distinct environmental characteristics (e.g., the Embu-Guaçu region and central sampling stations). However, based on the zooplankton community, the two main compartments (1 and 2) were different from each other according to the discriminant analysis (p = 0.0006). The third compartment (the dam region) could not be included in the discriminant analysis because there was only one sampling station in this compartment. Accordingly, the zooplankton community exhibited horizontal heterogeneity along the Guarapiranga reservoir longitudinal axis. However, the pattern did not follow the same compartments observed in the water quality variables.

DISCUSSION

Previous studies have revealed that the Guarapiranga reservoir exhibits spatial heterogeneity along the longitudinal axis for several variables, such as water quality, trophic status (Cardoso-Silva, 2008), metals in sediment (Padial, 2008) and aquatic macrophyte distribution (Rodrigues, 2011). Except for Domingos (1993), who investigated the distribution of the zooplankton community in the Guarapiranga reservoir, little is known about the distribution of planktonic organisms in this reservoir. Our sampling showed a tendency of compartmentalisation along the longitudinal axis of the Guarapiranga reservoir, especially when based on water quality (physical, chemical and biological data). Guarapiranga reservoir's compartments were not well defined, as proposed by Kimmel et al. (1990). Riverine, transition and lacustrine zones within a reservoir are not discrete and invariable entities; they are a result of the combined effects of a number of overlapping gradients (Kimmel et al., 1990), such as nutrient input from sewage water and agriculture, tributary water quality, algaecide treatment and retention time. These factors will be discussed further in this section.

One of the main factors influencing the process of temporal and spatial compartmentalisation in reservoirs is water retention time (Straskraba *et al.*, 1993). The long retention time of the Guarapiranga reservoir (185 days, Carvalho *et al.*, 2007) is one of the possible factors promoting the compartmentalisation of the reservoir in zones exhibiting different water quality characteristics. However, long retention time does not promote direct advective effects of water renewal on phytoplankton abundance (Kimmel *et al.*, 1990), thus interfering in the formation of clear compartments based on phytoplankton biomass.

Although a 24 h-cycle study was not conducted to verify stratification patterns in the Guarapiranga reservoir, it is known that most reservoirs in São Paulo state, including Guarapiranga, are polymictic due to their shallowness and continuous wind action (Arcifa et al., 1981; Matsumura-Tundisi et al., 1981: Takino & Maier. 1981). In our study, mixing was more frequent than stratification in the sampling stations, indicating polymixis in the Guarapiranga reservoir. The mixing pattern also has a strong influence on the compartmentalisation of reservoirs because it affects the metabolism and structure of the ecosystem, not only in the vertical but also in the longitudinal axis (Nogueira et al., 1999). In this sense, the influence of Guarapiranga's mixing pattern on the ecosystem metabolism can be demonstrated by the vertical distribution of several chemical variables, such as DO and pH, which followed the same pattern as temperature.

In general, reservoir branches, when present, contribute to the system heterogeneity (Nogueira, 2001). Thus, reservoir branches may exhibit different features from the main axis of the reservoir, reflecting the water quality of the tribu-



Figure 6. A) Relative biomass of phytoplankton CSR-strategists along the sampling stations in the Guarapiranga reservoir. B) Relative density of the main zooplankton groups found in the nine sampling stations in the Guarapiranga reservoir longitudinal axis. *A) Biomasa relativa del fitoplancton con estrategias CRS a lo largo de las estaciones de muestreo en Guarapiranga. B) Densidad relativa de los principales grupos de zooplancton que se encuentran en las nueve estaciones de muestreo en el eje longitudinal del embalse Guarapiranga.*



Figure 7. Hierarchical cluster dendrogram (Ward's method; Manhattan distance) A) of the phytoplankton descriptor species biomass, B) of the phytoplankton CSR strategist biomass and C) of the zooplankton density from the nine sampling stations along the Guarapiranga reservoir longitudinal axis. *Análisis de conglomerados jerárquico (método de Ward, distancia Manhattan) A) de la biomasa de las especies descriptoras del fitoplancton, B) de la biomasa del fitoplancton clasificado según las estrategias CRS y C) de la densidad del zooplancton de las nueve estaciones de muestreo a lo largo del eje longitudinal del embalse Guarapiranga.*

taries. The Embu-Guaçu and Parelheiros regions are Guarapiranga reservoir's branches and are mainly influenced by their tributaries, the Embu-Guaçu River and Parelheiros stream, respectively. The Embu-Guacu River is located in a well-preserved area, without severe human impacts. Accordingly, the Embu-Guacu region exhibited a lower trophic status (mesotrophic) and lower nutrient concentrations (TIN and TP). Although this region exhibited the lowest concentrations of nutrients associated with eutrophication processes, compared with the other regions, nitrogen availability was not likely constraining phytoplankton activity and growth, as phytoplankton can assimilate TIN from the medium in concentrations as low as $56 \,\mu g \cdot l^{-l}$ (Reynolds, 2006). Further, our data revealed that most of the phosphorous was part of the pelagic biomass or was unavailable, as most of the phosphorous was in the TP form (Reynolds, 2006).

In addition, the Embu-Guacu branch has a semifluvial nature with relatively high levels of turbulence and SRSi loading into the reservoir. Silicon plays a regulatory role in the plankton, not as a conventional nutrient, but as a vital skeletal requirement of diatoms that utilise SRSi present in natural waters from a range of 0.7-7 mg \cdot l⁻¹, until this nutrient is depleted to halfsaturation levels of approximately $0.1 \text{ mg} \cdot l^{-1}$ (Reynolds, 2006). In this way, sufficient quantities of SRSi in the Embu-Guaçu region favoured the growth of large and non-motile R-strategist diatoms. In particular, the centric diatom Urosolenia eriensis is characteristic of environments with a low trophic status (Padisák et al., 2009) and was found exclusively in the Embu-Guacu region. This finding is a good reflection of the higher water quality in the upper part of the reservoir under the influence of the Embu-Guacu River.

The Parelheiros branch tributary is the Parelheiros stream, which receives high loads of domestic sewage water from the irregular human settlements in the surroundings (Whately & Cunha, 2006). The poor water quality that enters the Parelheiros region is responsible for the characteristics of this compartment, such as eutrophication, high EC and nutrient concentrations and low DO. Eutrophication and DO depletion are closely related. With nutrient increases in the water column in the Parelheiros region and the subsequent increase in algae biomass, the amount of organic material injected into the water increases as well (Wetzel, 2001). These increased organic loads increase the decomposition rates and, subsequently, the rate of oxygen depletion. In this sense, a low concentration of DO is also an indicator of eutrophication in the water column, causing a number of significant changes in the chemistry and biology of the Parelheiros region.

Particularly for the phytoplankton, water quality conditions in the Parelheiros region favoured the dominance of small-celled, fastgrowing C-phytoplankton species. C-strategists generally have low rates of sinking and are highly susceptible to grazing by zooplankton (Reynolds et al., 2002). The low rates of sinking of phytoplankton C-strategists could have favoured their dominance in P1, the only sampling station where stratification was detected at the time of the sampling. Moreover, the higher abundance of filtering-feeding zooplankton compared with the potentially grazing zooplankton could have also favoured C-strategist growth. Large-celled and colonial, motile S-strategist phytoplankton species and flagellated, motile S-strategist phytoplankton (e.g., Eudorina illinoisensis and Peridinium gatunense) were also important in the Parelheiros region. As these species can adjust their vertical position in the water column, the exploitation of nutrients is considerably enhanced (Raven & Richardson, 1984), enabling their co-dominance with C-strategist phytoplankton species in the Parelheiros region.

Whereas the Embu-Guaçu and Parelheiros regions are located in the uplake riverine zone of the reservoir, the dam region included sampling stations with transitional and lacustrine characteristics, according to the classification of Kimmel *et al.* (1990). The lower part of reservoirs (lacustrine zone) usually present a higher retention time and greater depth, which contribute to the accumulation of elements (Beyruth, 2000), leading to eutrophication due to land use in the surrounding areas of this compartment (human settlement without proper

sewage water treatment and agriculture (Beyruth, 1996)). As expected, our data showed greater depth in the dam region; specifically, in the dam sampling station, greater phytoplankton biomass and zooplankton density was observed. As observed in the Parelheiros region, the ability of flagellated, motile S-strategists phytoplankton (e.g., Dolichospermum spiroides, Eudorina illinoisensis and Gymnodinium fuscum) to adjust their vertical position considerably enhances the opportunities to exploit the nutrient resources available in the dam region's water column (Raven & Richardson, 1984), enabling their co-dominance with C-strategist phytoplankton species in the dam region. During our fieldwork, the environmental agency (SABESP) was adding copper sulphate in the lower part of the reservoir, near sampling station C1. It is possible that this was the cause of the distinct phytoplankton composition in sampling station C1 compared to the other sampling stations. Copper sulphate treatment causes cell lysis and sinking (Jones & Orr, 1994). Therefore, this algaecide acts as an anthropogenic disturbance, opening a gap in the phytoplankton community and promoting the growth of fast-growing survivors in the new environmental conditions (Beyruth, 2000). After treatment and settling of the biomass, the species that remained in the water column were favoured by the abrupt increase in nutrient availability, by the decrease in competition and by the toxic effects of copper on grazers (Beyruth, 2000). However, without reliable data from the environmental agency, it is impossible to know the total extent and the exact frequency of the copper sulphate treatment in the reservoir. Accordingly, it is impossible to know how much the phytoplankton community is being influenced by the algaecide action. Studies on the effects of copper sulphate on the phytoplankton community showed that this algaecide caused remarkable effects on the sequence of dominance (Bevruth, 2000) and abrupt phytoplankton changes in density (Padovesi-Fonseca & Philomeno, 2004) in Brazilian reservoirs. Therefore, it is possible to infer that copper sulphate action is one of the main factors determining the phytoplankton distribution in the Guarapiranga reservoir,

explaining the absence of clear compartments based on phytoplankton biomass.

Phytoplankton consumption by heterotrophs is an important cause of phytoplankton loss (Padisák, 2004) and cannot be neglected in phytoplankton studies. Filter feeding efficiency is determined by the size of the zooplankton population involved and the physical sizes (and other properties such as digestibility) of phytoplankton particles compared with the ability of grazers to consume the given size spectrum (Padisák, 2004). Therefore, the close relationship between phytoplankton and zooplankton communities found in our study might be attributed to ecological interactions such as grazing or competition for nutrients. In a previous study in the Guarapiranga reservoir, Caleffi (2000a) found that zooplankton community structure was driven mainly by the phytoplankton community, especially by its potential as a feeding resource for herbivorous zooplankton.

Rotifers were the most abundant zooplankton for all the sampling stations. These small sized organisms react faster than other zoological groups of freshwater zooplankton to changes in water conditions due to their short developmental cycle; they are considered more sensitive to physical and chemical changes that occur in the environment (Gannon & Stemberger, 1978). They can also develop numerous populations using low quality food resources, such as organic detritus (Mangas & Garcia, 1991). Among rotifer species, the high density of Keratella tropica was associated with lentic characteristics of the environment and was found in high densities in the dam region. Polyarthra aff. vulgaris and Keratella cochlearis, two eurytopic species (Bielanska-Grajner & Gladysz, 2010), were also important for the total density of the zooplankton community in the dam region. Due to its tolerance to a wide range of environmental conditions, P. vulgaris was also present in high densities in the Embu-Guaçu region, a more preserved and less eutrophic area. The genus Collotheca was found only in the Embu-Guaçu region and might be associated with less eutrophic conditions. Conochilus unicornis and C. coenobasis were present in high densities both in the EmbuGuaçu and Parelheiros regions. Therefore, the occurrence of these two species might be more related to lotic conditions than to the trophic status of the environment. *Kellicottia bostoniensis* and *Filinia opoliensis* were found in high densities in the Parelheiros region, confirming their preference for eutrophic environments (Lucinda *et al.*, 2004).

As a general rule, rotifers dominate zooplankton in Brazilian natural and artificial inland waters (Rocha *et al.*, 1995; Nogueira, 2001; Sendacz & Monteiro Jr., 2003). Importantly, in terms of total zooplankton biomass, rotifers can only have a minor contribution due to their small size (Matsumura-Tundisi *et al.*, 1989). However, if the same results were expressed in units of biomass, it is likely that the importance of the copepods, which are larger zooplankton, would be further increased in the community structure.

The copepod cyclopoid *Thermocyclops decipiens* is commonly found in environments with high human impacts, especially mesotrophic and eutrophic environments (Landa *et al.*, 2007), as this species can support a wide variety of environmental conditions. Accordingly, *T. decipiens* was found in high densities in the Parelheiros region, especially in P1. In the Embu-Guaçu region, no single species dominated, most likely due to less eutrophic conditions that do not allow the dominance of species that are more resistant to eutrophic conditions, such as *T. decipiens*.

The presence of suitable phytoplankton, such as small-celled C-strategist species, as food resources could have helped sustain the equilibrium among microcrustacean species, especially cladocerans, in the dam region. Although cladoceran density did not increase in this region, there were several co-occurring species instead of the dominance of a few smaller species, such as Bosminopsis deitersi and Bosmina longirostri, in the dam sampling station. In eutrophic environments with cyanobacteria dominance, rotifers and small microcrustaceans tend to be dominant due to their short life cycle, as they allocate more energy to reproduction than growth (Esteves & Sendacz, 1988; Matsumura-Tundisi & Tundisi, 2005). Matsumura-Tundisi & Tundisi (2005) observed larger zooplankton species and higher species richness associated with chlorophyte dominance in a eutrophic Brazilian reservoir. Accordingly, zooplankton composition and density possibly affected the phytoplankton community structure, as observed in our study.

Other parameters that were not included in our study, such as predation by planktivorous fishes, may have also affected the spatial and temporal distribution of zooplankton species, especially cladocerans (Iglesias *et al.*, 2008). As their population development is slower, cladocerans are more likely to be controlled by a top-down process, while rotifer life histories are strongly influenced by bottom-up mechanisms (Walz, 1997). Copepod populations are intermediate, as they display intermediate growth rates.

Importantly, copper sulphate treatment can also affect zooplankton communities, directly through the toxicity of the algaecide (effects on reproduction) or indirectly through changes in the phytoplankton community. In the Guarapiranga reservoir, Caleffi (2000b) observed lower zooplankton density and species richness associated with intense copper sulphate treatments. The author affirmed that cladocerans were the most affected group in terms of density. Gusmão (2004) confirmed the high sensitivity of cladocerans to copper sulphate toxicity in mesocosm experiments. According to this study, cladocerans are especially affected by indirect effects such as changes in food availability and competition, leading to small-sized species dominance. Moreover, rotifers seem to be less sensitive to copper sulphate effects and are most likely favoured by the competition reduction, as microcrustaceans have their density directly or indirectly reduced by the effects of copper sulphate.

Water quality characteristics and the zooplankton community indicated the presence of compartments in the Guarapiranga reservoir during sampling, whereas the phytoplankton community did not. These different outcomes indicate that the water quality, phytoplankton and zooplankton communities captured different features from the longitudinal axis of Guarapiranga reservoir. Phytoplankton and zooplankton communities in the dam region were altered, directly or indirectly, by the copper sulphate treatment. Therefore, this human intervention was most likely the main force driving the phytoplankton composition and biomass in the reservoir. It is likely that for this reason, the phytoplankton community was not able to capture the reservoir compartmentalisation. Consequently, the zooplankton structure was also affected, although to a lesser extent.

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