Chemical composition and taxonomic structure vertical and seasonal variation of periphyton community in a shallow hypereutrophic reservoir (Garças Reservoir, São Paulo, Brazil)

Variação vertical e sazonal da composição química e estrutura da comunidade perifítica em reservatório raso hipereutrófico (Lago das Garças, São Paulo, Brasil)

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Abstract: Vertical and seasonal evaluation of the chemical composition, biomass and taxonomic classes of the periphyton community were studied in a shallow hypereutrophic reservoir. Water physical and chemical characteristics, as well as biological features of periphyton were studied at 5 depths (subsurface, 1 m, 2 m, 3 m and bottom) during the dry (July) and rainy (January) periods. Periphyton growing on glass microscope slides placed at different depths was sampled after 28 days colonization. Periphyton attributes studied were chlorophyll-*a*, dry mass, ash free dry mass, chemical composition and algal taxonomic classes. Compared to the rainy period, the dry one was characterized by lower resistance to mixing, homogeneous $P\text{-}PO_4$ and $N\text{-}NH_4$ concentration vertical profile, greater optical depth and smaller total phytoplankton biomass. Periphyton showed the smallest biomass and algal growth, and absolute dominance of Cyanobacteria during the rainy period, when the Cyanobacteria bloom was most intense. Unlike the dry period, the smallest bloom intensity allowed the greatest light penetration, favoring the increase of photosynthetic biomass, the growth of algae and the dominance of Bacillariophyceae at the surface and Cyanobacteria at all other depths. Periphyton chemical composition reflected the environment's nutritional conditions, evidencing the periphyton ability for nutrient retention, independent of the algal biomass amount, and that such a condition is more evident mainly concerning the P contents. Molar N:P ratio indicated that the periphyton community was P-limited at all depths and climatic periods studied. Finally, biomass and periphyton community algal taxonomic classes' structure varied both in seasonal and vertical scale, the Cyanobacteria bloom intensity being the controlling factor towards the periphyton biomass increase, whereas the nutrient status and the P contents of periphyton were conditioned to the nutrients' availability in the water column.

Keywords: chemical composition, Cyanobacteria bloom, periphyton, structure, hipereutrophic reservoir.

Resumo: Avaliação em escala vertical e sazonal da composição química, biomassa e estrutura de classes da comunidade perifítica em reservatório hipereutrófico raso. Foram analisadas variáveis físicas, químicas e biológicas da água em cinco profundidades (subsuperfície, 1 m, 2 m, 3 m e fundo) nos períodos seco (julho) e chuvoso (janeiro). O perifíton desenvolvido em lâminas de vidro distribuídas em cada profundidade foi amostrado após 28 dias de colonização. Os atributos do perifíton analisados foram: clorofila-*a*, massa seca, massa seca livre de cinzas, composição química e classes taxonômicas das algas. Em relação ao chuvoso, o período seco caracterizou-se por menor resistência à mistura, perfil vertical homogêneo das concentrações de $P\text{-}PO_4$ e $N\text{-}NH_4$, maior profundidade óptica e menor biomassa do fitoplâncton. O perifíton apresentou a menor biomassa, menor crescimento algal e dominância absoluta de Cyanobacteria no período chuvoso, quando a floração de Cyanobacteria foi mais intensa. Diferente no período seco, a menor intensidade da floração permitiu a maior penetração de luz, favorecendo o aumento de biomassa e do crescimento algal e a dominância de Bacillariophyceae na superfície e de Cyanobacteria nos demais estratos. A composição química do perifíton refletiu as condições nutricionais do meio, evidenciando a capacidade de retenção de nutrientes do perifíton, independente da quantidade de biomassa algal, principalmente em relação ao conteúdo de P. A razão molar N:P indicou uma comunidade perifítica P-limitada em todas as profundidades e períodos climáticos. Finalmente, a biomassa e a estrutura de classes taxonômicas da comunidade perifítica variaram em escala sazonal e vertical, sendo a intensidade da floração de Cyanobacteria o fator controlador do incremento da biomassa perifítica, enquanto que o 'status' dos nutrientes e o conteúdo de P foram associados à disponibilidade de nutrientes na coluna d'água.

Palavras-chave: composição química, estrutura, floração de Cyanobacteria, perifíton, reservatório hipereutrófico.

1. Introduction

Periphyton is a very important primary producer in lentic systems, participating in the nutrient cycle, energy fluxes and in the food web, besides serving as a microhabitat for many organisms (Vadeboncoeur and Steinman, 2002; Stevenson, 1996). Periphyton's ecological role becomes even more important in shallow ecosystems, where there is a dominance of soil-water interfaces (Wetzel, 1990; Dodds, 2003). Despite the important role of periphyton in the functioning of ecosystems, a scarcity of their studies prevails worldwide, including in Brazil (Huszar et al., 2005).

At the ecosystem level, habitat heterogeneity has a strong influence on the structure and functioning of periphyton (Vadeboncoeur and Steinman, 2002). Consequently, studies at different scales are necessary to better understand that community dynamics. Study at a horizontal scale (Kahlert and Peterson, 2002) and, more recently, at a vertical study (Kralj et al., 2006; Hill and Fanta, 2008) led to specific responses of the structure and functioning of the periphytic community depending on the scale considered. Depth at which substratum is placed in the system modifies the community structure depending on the temperature and light (Kralj et al., 2006), as well as on differences in the wave action and grazing impact (O'Reilly, 2006). Specifically for Brazil, Lobo et al. (1990) reported similar characteristics for the periphyton in different lotic systems at the vertical scale.

Information on the periphytic community vertical distribution may help in the prediction of algal responses during re-oligotrophication processes, which deeply modify the ecosystem dynamics and, consequently, the periphyton-phytoplankton relationships (Liboriussen and Jeppensen, 2006). Knowledge of the temporal and spatial variability of biomass, nutrient contents and species composition of the periphytic community may help in the prediction of the functional changes of ecosystems resulting from recovery processes, particularly of the Garças Reservoir.

Present study aimed at investigating the biomass variation, the algal taxonomic classes and the chemical composition of the periphytic community at vertical and seasonal scales, aiming at identifying the main environmental factor(s) that would regulate such variability.

2. Material and Methods

2.1. Study area

Garças Reservoir (23° 38' S and 46° 37' W) is located in the Parque Estadual das Fontes do Ipiranga (PEFI), a preservation area for Atlantic Forest remnants within the urban area of the city of São Paulo (Figure 1). It is a shallow reservoir (Z_{max} 4.7 m; Z_{med} 2.1 m; area 88,156 m²) classified hypereutrophic (Bicudo et al., 2002a,b; Bicudo et al., 2006).

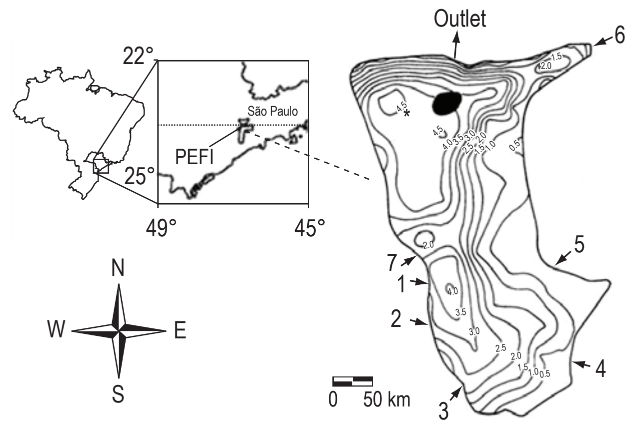

Figure 1. Location and bathymetric map of Garças Reservoir with location of inflows (numbered arrows), outlet and sampling station (*) (Bicudo et al., 2002a).

2.2. Experimental design

The experimental apparatus was placed at the deepest part of the pelagic region of Garças Reservoir 1 m apart from each other, and was made of 5 wood supports with regular glass microscope slides used as substratum. Colonization exposure time was 28 days during both the dry (July 2006) and rainy (January 2007) periods.

Climate data were provided by the Meteorological Station of the CIENTEC, Centro de Ciência e Tecnologia of the Universidade de São Paulo. Variables studied were air temperature, solar radiation, wind speed and rain precipitation.

Samplings of limnological features were done at 5 different depths (subsurface, 1, 2, 3 m and bottom) using a van Dorn sampler. Samples were immediately placed in Styrofoam boxes containing ice and taken to the Aquatic Ecology Laboratory of the Instituto de Botânica for analyses. Abiotic variables studied were: water temperature (Horiba multiprobe), electric conductivity (conductivimeter Digimed), sub-aquatic radiation (Li-Cor probe, model LI-205), alkalinity (Golterman and Clymo, 1971), dissolved oxygen (Golterman et al., 1978), pH (pHmeter Jenway), dissolved inorganic carbon forms, $N\text{-}NO_2$ and $N\text{-}NO_3$ (Mackereth et al., 1978), $N\text{-}NH_4$ (Solorzano, 1969), $P\text{-}PO_4$ and total dissolved P (Strickland and Parsons, 1965). On the sampling day, water samples were filtered under low pressure (<0.3 atm) through Whatman GF/F membrane filters for analyses of dissolved nutrients. Unfiltered water samples were used for total nitrogen (TN) and total phosphorus (TP) determinations (Valderrama, 1981) within at most 30 days from collecting date.

Thermal profile was obtained at every 10 cm depth and the relative thermal resistance (RTR) to mixing was calculated according to Dadon (1995).

Phytoplankton chlorophyll-*a* extraction (corrected for phaeophytin) was performed by using ethanol (90%), according to Sartory and Grobblelaar (1984).

Periphyton colonized glass microscope slides were collected at random. Periphytic material was removed from the substrate by scrapping with a razor blade and distilled or ultrapure water gentle jets. The following periphytic community attributes were studied: chlorophyll-*a* (Marker et al., 1980; Sartory and Grobbelaar, 1984), dry mass and ash free dry mass (APHA, 1989), total N contents (Umbreit et al., 1964) and total P contents (Andersen, 1976; Pompêo and Moschini-Carlos, 2003). To quantify periphytic algae, samples were fixed and preserved with 4% formaldehyde solution and studied under a Zeiss binocular microscope. For quantitative study, samples were fixed with 0.5% acetic lugol solution and stored in total darkness at room temperature until time of counting. Quantification followed Utermöhl method and was performed under an inverted Zeiss (400x) microscope. Counting limit was established according to the most common species rarefaction curve, until reaching 100 individuals in total (Bicudo, 1990).

Dominant classes were those whose densities were greater than 50% of sample total density and abundant classes were the ones greater than the sample average density.

Univariate descriptive and exploratory analyses were conducted by using the MINITAB 14.1. Arithmetic average was used for central deviation measurement and standard error, standard deviation and Pearson variation coefficient for dispersion measurement. Mean value comparison of the periphytic community attributes among different depths were made by variance analysis (one-way ANOVA) using MINITAB 14.1 for Windows. Integrated analysis of abiotic and biological data was performed by using Canonic Correspondence Analysis (CCA) with abiotic data transformed by log (x + 1) and by biological data were transformed ranging $[(X - X_{min}) / (X_{max} - X_{min})]$. PC-ORD version 4.0 for Windows (McCune and Mefford, 1999) was used for the analysis.

3. Results

3.1. Climate

Comparison of dry (July) and rainy (January) periods showed that during the dry period average monthly air temperature was 16.9 °C and during the latter period it was 22.2 °C. During the dry period, solar radiation varied from 2.5 to 16 $MJ.m^{-2}$, whereas during the rainy one from 5.8 to 23.3 $MJ.m^{-2}$. Rain precipitation varied between 0 and 32.2 mm (monthly average 2.7 mm) during the dry period and between 0 and 25.6 mm (monthly average 4.1 mm) during the rainy one.

3.2. Limnological characteristics

Water thermal profile presented a trend towards heterogeneity during the dry period, showing 1.7 °C temperature difference between surface and bottom of reservoir; RTR was greater between 1 and 2 m depth (20.7); and Z_{mix} went up to 2 m deep in the reservoir (Figure 2). During the rainy period, stratification was more pronounced, temperature difference between surface and bottom of reservoir was 3.8

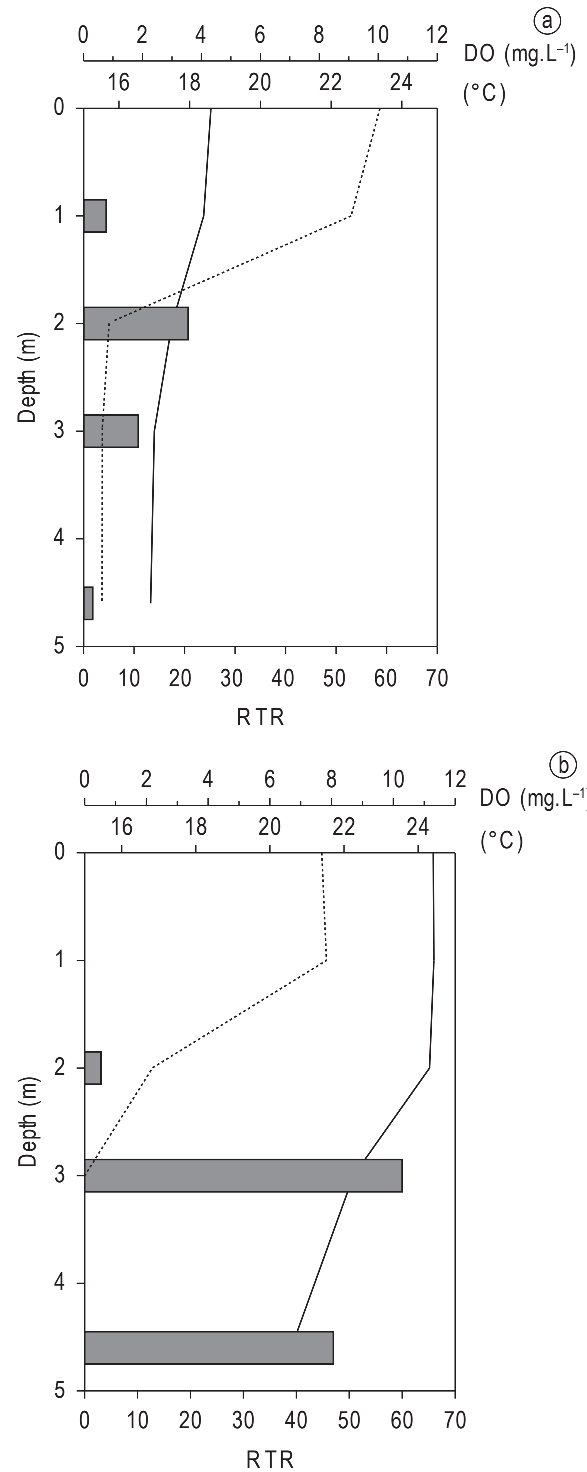

Figure 2. Vertical profile of mean values (n = 2) for temperature (——), dissolved oxygen (----) and relative thermal resistance (RTR ▬) at Garças Reservoir during the a) dry a) and b) rainy period.

°C, RTR (60) was maxima between 2 and 3 m, and Z_{mix} went up to 2 m deep.

A DO clinograd profile was observed during both study periods (Figure 2), the greatest values detected during the dry one. Despite of the low DO values below 2 m deep, complete anoxic conditions were observed during the rainy period.

Vertical distribution of the electric conductivity was heterogeneous in both climatic periods, but the values were from 6 to 16 times greater in the rainy period than in the dry one.

During the two climatic periods studied, sub-aquatic radiation was only detected up to 1 m deep and it was 7-fold greater during the rainy than in the dry period (Figure 3). Water transparency measured with the Secchi disc was 0.6 m during the dry period and 0.25 m during the rainy one.

Phytoplankton chlorophyll-*a* was always greater at the reservoir surface, being 3-fold greater during the rainy than in the dry period (Figure 3). Decrease of the amount of chlorophyll-*a* was measured towards the bottom of reservoir during the two periods studied.

Concerning total and dissolved nutrients concentrations, vertical distribution of $P\text{-}PO_4$ and TP tended to a greater heterogeneity during the rainy period, the greatest values being measured at the bottom of reservoir (Figure 3). TP concentration at the reservoir bottom was 9-fold greater during the rainy than in the dry period. Considering the N series, maximum $N\text{-}NO_3$ concentration was measured in the more superficial layers of reservoir during the dry period, whereas that of $N\text{-}NH_4$ was detected in the lower ones during the rainy period, mainly at the reservoir bottom. TN tended, however, to decrease from surface to reservoir bottom during both periods.

3.3. Periphyton community

Chlorophyll-*a*, AFDW and periphytic algae total density vertical distribution was very much heterogeneous during both dry and rainy periods (Figure 4). Values for all three attributes decreased from surface to reservoir bottom.

Comparison of periphyton chlorophyll-*a* concentration values between the two climatic periods studied showed that the greatest biomass increment occurred during the dry one, mainly at the surface of reservoir, the average value being 3 times greater than in the rainy period (Figure 4). During both periods, community living at the reservoir surface presented the greatest values, significantly different from all other depths of reservoir (Table 1).

During the dry period, periphyton showed the greatest increase of AFDW at the surface, which was significantly different from all other depths of reservoir (Figure 4, Table 1). During the rainy period, it was registered the greatest increase of periphyton AFDW at the surface and reservoir 1 m depth, which did not shown any significant difference, but differed from all other depths (Figure 4, Table 1). A 5.6-fold increase of AFDW values was observed at 1 m depth during the rainy period compared to the dry one.

Periphytic algae total density showed its greatest growth at the surface during the dry period (Figure 4). Algal growth was very much less below the surface, except for at 1 m depth during the rainy period whose total density increase was approximately 10 times greater than in the dry one.

Considering the temporal and spatial scale, algal classes that contributed most to the periphyton community structure were Bacillariophyceae and Cyanobacteria (Figure 5). During the dry period, however, Bacillariophyceae were dominant at the surface (92%) and Cyanophyceae at 2 m and 3 m deep, whereas at 1 m and bottom Bacillariophyceae, Chlorophyceae and Cyanophyceae were abundant (respectively, 21-37%, 17-13% and 38-26%). In contrast, during the rainy period Cyanobacteria were dominant at all depths (50-78%), followed by Bacillariophyceae (4-33%) and Chlorophyceae (8-16%).

Periphyton P contents (%AFDW) presented a heterogeneous vertical variation during both the dry and the rainy period, with the community growing at the bottom of reservoir significantly different from that of the remaining layers (Figure 6, Table 1). Consequently, the greatest periphyton %P was registered at the reservoir bottom during both climatic periods.

Periphyton N contents did not show significant vertical variation during the dry period, whereas during the rainy one a heterogeneous distribution (Figure 6, Table 1) was detected. Periphyton growing at the reservoir upper layers (subsurface, 1 and 2 m) during the rainy period was significantly different from that of the deeper ones (3 m and bottom). Consequently, %N vertical distribution was homogeneous during the dry period and heterogeneous during the rainy one, with a trend towards its greatest concentrations at the deeper reservoir layers.

Considering the Redfield N:P molar ratio, the periphyton community was P-limited at all depths and months, except for the bottom of reservoir during the rainy period whose value was closest to the optimal one. It was noticed that the P-limiting condition tended to decrease along the water column during all months sampled (Figure 7).

3.4. Integrated analysis of abiotic and biotic variables

Canonical Correspondence Analysis (CCA) was carried out considering five environmental variables and algal classes' attributes and three periphyton community attributes (Figure 8, Tables 1 and 2). Eigenvalues for axis 1 ($\lambda = 0.357$) and 2 ($\lambda = 0.144$) explained 77.2% of data variability. The great Pearson correlation species-environment for axis 1 ($r = 0.993$) and 2 ($r = 0.983$) indicated strong relationship between species distribution and environment variables. Monte Carlo permutation test demonstrated that correla-

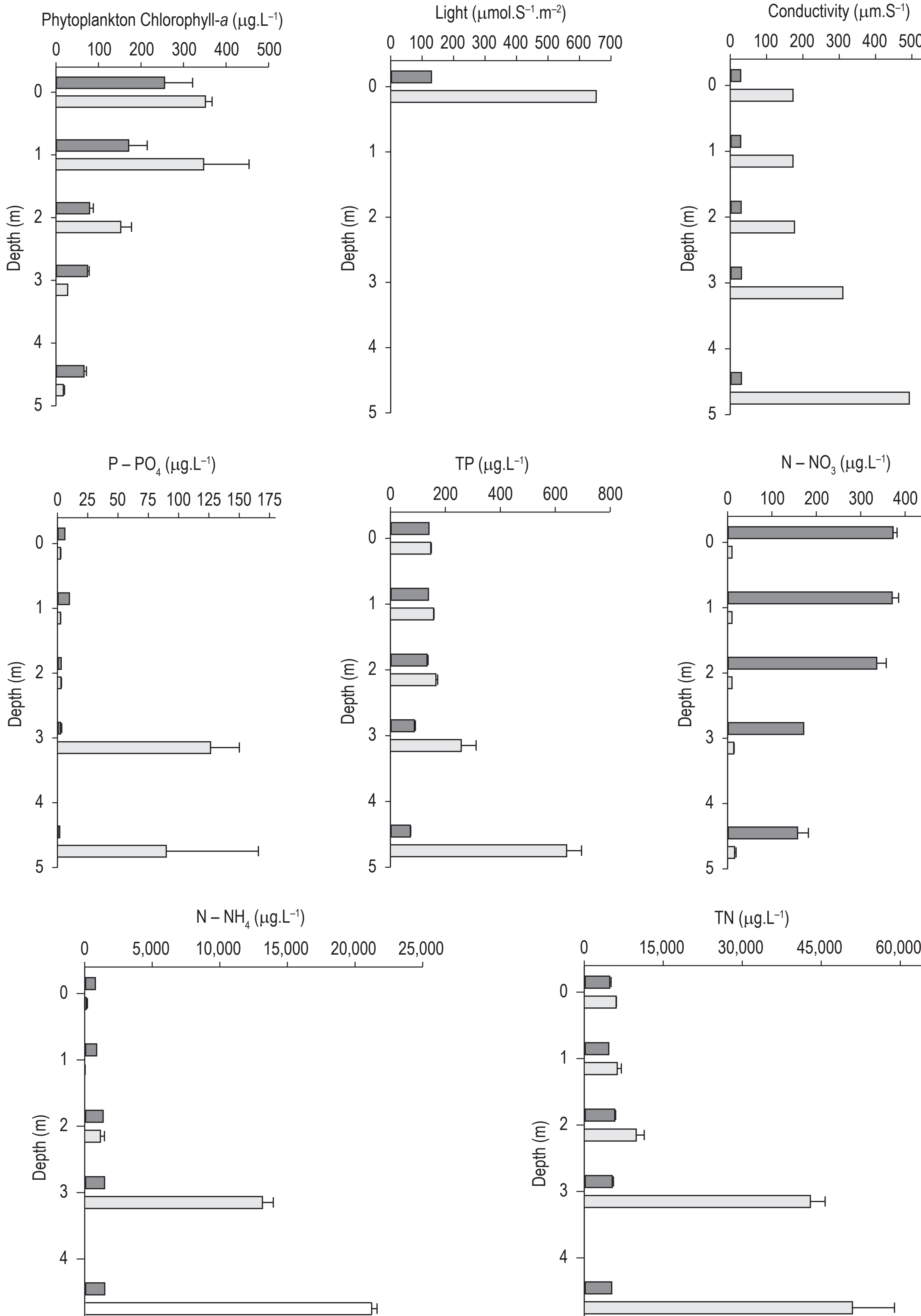

Figure 3. Vertical profile of mean values (n = 2, SD) of abiotic variables at Garças Reservoir during the dry (▒) and rainy period (□).

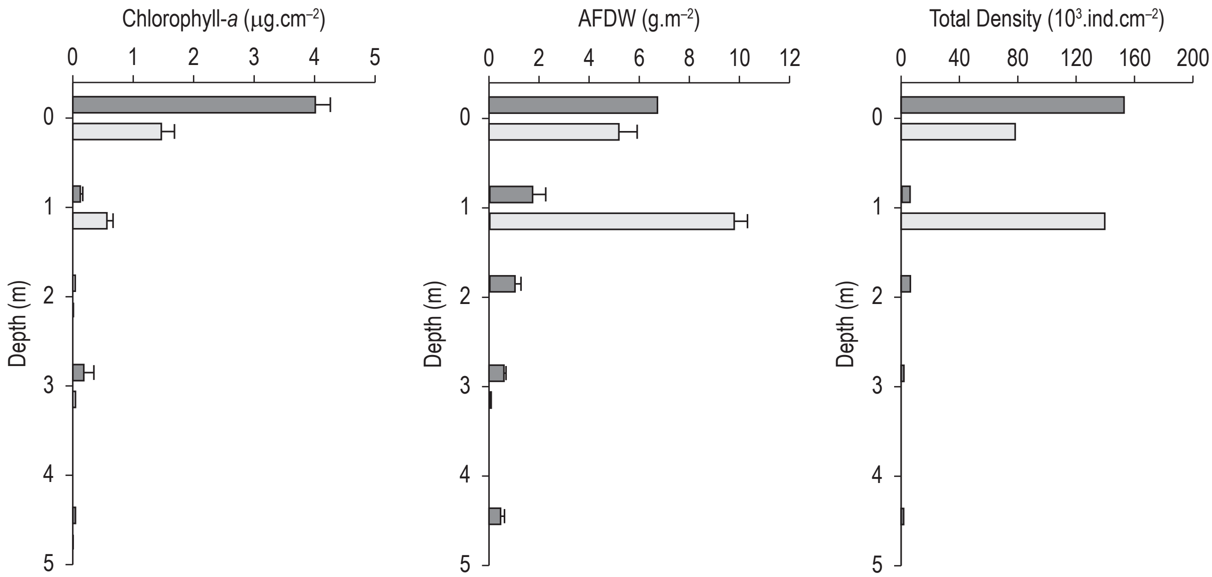

Figure 4. Average vertical variation (n = 2, SD) of chlorophyll-*a*, ash free dry weight (AFDW) and total density of periphytic community algae at Garças Reservoir during the dry (■) and rainy period (□).

Table 1. One-way ANOVA results assessing vertical variation in periphyton biomass (chlorophyll-*a* and AFDW), total density and chemical composition during dry and rainy periods. Bold face values are statistically significant (α = 0.05) and regular print represent statistic difference between reservoir layers through Tukey Test. Same letters indicate attributes without significant difference and, the different letters indicate attributes with difference significant.

		F	p	Surface	1 m	2 m	3 m	Bottom
Chlorophyll-*a*	Dry	242.24	0.000	a	b	b	b	b
	Rainy	67.21	0.000	a	b	c	c	c
AFDM	Dry	187.7	0.000	a	b	c	c	c
	Rainy	1600	0.000	a	b	c	d	e
%N	Dry	0.59	0.679	a	a	a	a	a
	Rainy	6.27	0.009	a	a	b	c	c
%P	Dry	4.39	0.020	a	a	a	a	b
	Rainy	4.84	0.020	a	a	a	b	b

tion between periphytic algal classes and nutritional conditions were statistically significant for axes 1 and 2 (p = 0.01 and 0.07, respectively).

Canonical coefficient for axis 1 showed that phytoplankton chlorophyll-*a* values and temperature were the leading limnological variables for that axis ordination (Table 2). Limnological variables correlated with CCA axis 1 described the spatial scale, from the more superficial layers with greater light availability and high chlorophyll-*a* values at the positive side of the axis to the lower layers with greater nutrient availability at the negative side.

Algal classes, total density and periphyton chlorophyll-*a* were closely associated to the more superficial layers during the dry and the rainy periods (Figure 8, Table 3). On the other hand, %N and %P were more closely associated with the reservoir lower layers also during the two climatic periods. This axis described the spatial variation of periphytic algal community.

Environmental variables correlated with axis 2 described a sub-aquatic radiation availability gradient (Figure 8, Table 3). From all variables included in the CCA, sub-aquatic radiation was positively correlated and temperature negatively correlated with axis 2. The greatest positive score was that of the surface during the dry period that presented greatest affinity to the Bacillariophyceae and periphyton photosynthetic biomass. At the negative side of the same axis, scores from the 1 m depth during the rainy period were the greatest, more closely associated with the Cyanobacteria, whereas the surface showed greater affinity to AFDW, Chlorophyceae and Euglenophyceae.

4. Discussion

According to Bicudo et al. (2007), Garças Reservoir is under Degraded State Equilibrium, in which the stratification process is permanent and maintained by the

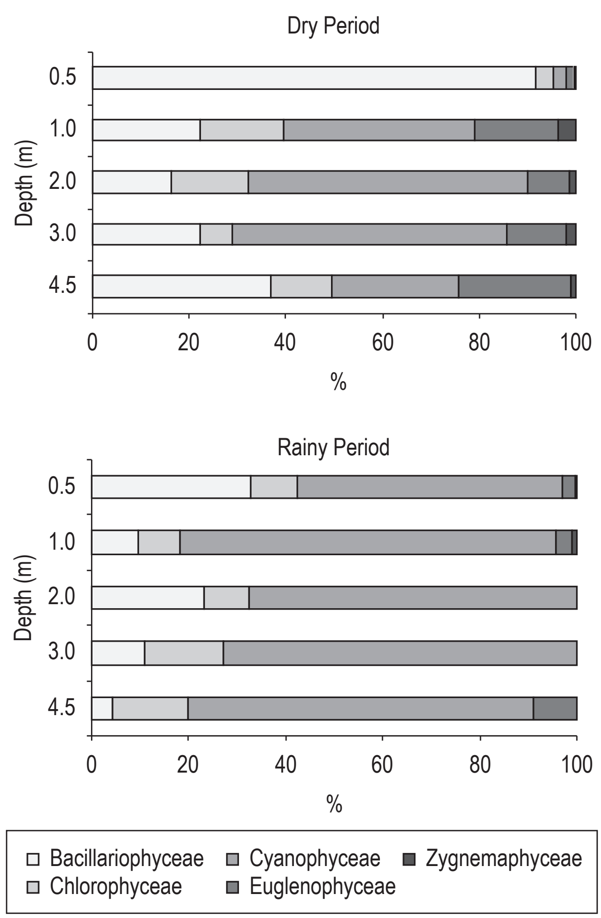

Figure 5. Vertical variation of the periphyton main algal classes relative abundance at Garças Reservoir during the dry and rainy period.

Cyanobacteria multi-species bloom. For the latter authors (Bicudo et al., 2007), increase in the reservoir nutrient concentration, mainly N and P, was first driven by allochthonous loads and presently by internal (autochthonous) ecological processes.

During the present study, lesser resistance to mixing, homogeneous P-PO_4 and N-NH_4 concentration vertical profile, greater optical depth and smaller phytoplankton biomass characterized the dry period. In contrast, concentration of dissolved and total nutrients showed a heterogeneous profile, optical depth was less and phytoplankton biomass was greater during the rainy period. Considering nutrients, greater availability in the water was detected during the rainy period.

Bicudo et al. (2007) reported that the cyanobacterial bloom plays an important role as an integrating factor in the ecosystem self-stabilizing state. In the present study, it was observed that the two climatic periods differed from each other in the intensity of the cyanobacterial bloom, which was more intense during the rainy period than in the dry one. In short, the Garças Reservoir limnological condition identified a less intense bloom during the dry period and a more intense one during the rainy period.

Periphyton photosynthetic biomass vertical distribution was very homogeneous during the two climatic periods, thus reflecting the permanent stratification process of the ecosystem. Periphytic community developing at the surface of reservoir presented the greatest increase of photosynthetic biomass, where light availability was greater, particularly during the dry period. CCA showed association of the dry period surface to the greater sub-aquatic

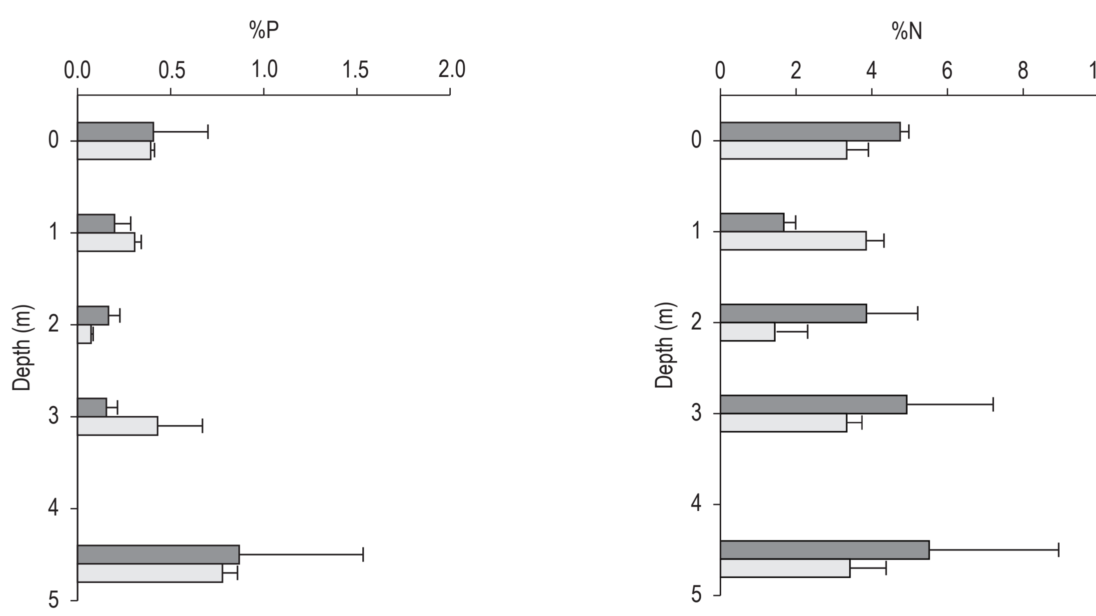

Figure 6. Vertical mean variation (n = 3, SE) of P and N contents (%AFDW) of the periphytic community at Garças Reservoir during the dry ( ) and rainy period ( ).

radiation availability and, more intimately to the greater photosynthetic biomass. Furthermore, periphyton biomass was not associated to the increase of nutrient availability. Consequently, bloom intensity was the key factor in controlling periphyton photosynthetic biomass in the present study, since the bloom intensity reduced light availability and, consequently, growth of periphyton.

Negative effect of phytoplankton on periphyton in enriched systems due to light limitation was reported in several studies (e.g. Hansson, 1988; Havens et al., 1996). In Amazonian lotic systems, Putz (1997) noticed that periphyton productivity was greater in clear water rivers than in dark ones, where light penetration was a limiting factor. For Liboriussen and Jeppesen (2006), in mesotrophic lakes there is an optimal combination of light availability and nutrients for the development of periphyton, and that in oligotrophic lakes the limiting factor was the nutrient availability, whereas in the eutrophic ones light availability would be the limiting factor.

Vercellino (2001) found strong evidence that physical disturbances would control growth of periphyton biomass in the Garças Reservoir. Such findings were contrary to those in the present study, but the two studies were conducted under distinct limnological conditions. Bicudo et al. (2006) identified three distinct limnological phases in the Garças Reservoir after a long-term study. The study of Vercellino (2001) was carried out during phase 2 that was characterized by low PSR availability due to the high P absorption rates by the macrophytes. Present study, on the other hand, was carried out during phase 3 that was characterized by the Cyanobacteria multi-species permanent bloom and the Degraded State Equilibrium (Bicudo et al., 2007).

At a temporal scale, present study located the greatest photosynthetic biomass accumulation and total periphyton density during the dry period. Similar situation was detected by Vercellino (2001). Despite of the distinct limnological phases, both studies indicated the dry period as the most favorable one for the periphyton algal growth in the Garças Reservoir.

Periphytic community developing in the upper layers of reservoir presented high algal growth and increase of organic matter mainly during the dry period. Thus, the lower bloom intensity also favored periphyton growth. However, during the rainy period occurrence of high AFDW and algal density were observed at 1 m depth, when thermal and chemical stratification were very evident indicating the influence of thermal stratification on the periphyton growth. Kralj et al. (2006) verified that, besides light availability, stability of thermocline also affected periphyton vertical distribution.

Unlike from biomass and algal density, a greater P content was observed in the periphyton growing close to the reservoir sediment during both the dry and rainy periods. According to Bicudo et al. (2007), anoxic sediments of Garças Reservoir act as a P reservoir. Furthermore, periphyton associated with sediments has better access to nutrients (Hansson, 1988). In the tropics, experimental studies demonstrated that periphyton P contents increase with increasing P availability in the environment (Ferragut, 1999, 2004; Fermino, 2006). Consequently, results of P contents pointed for P storage in the periphyton under conditions of the high P availability independent of the algal biomass.

Periphyton organic matter N contents showed vertical variation only during the rainy period. However, N availability in the Garças Reservoir water column is very high, differing only in its ionic form (Crossetti, 2006). Thus, vertical distribution of N contents in the periphyton coincided with the more homogeneous profile of total and dissolved nutrients in the water column during the dry period and the more heterogeneous profile during the rainy period.

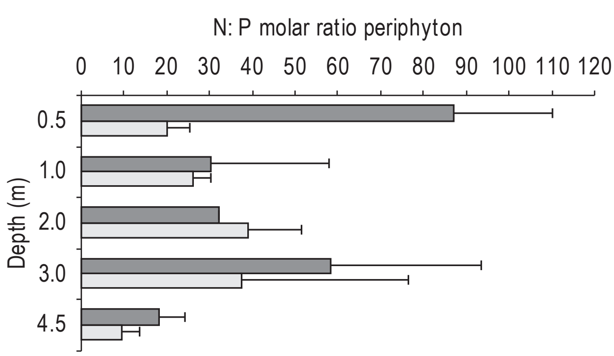

Figure 7. Periphyton mean N:P molar ratio (n = 3, SE) at Garças Reservoir during the dry (▩) and rainy period (▢).

Table 2. Canonical coefficient and intra-set correlation of environmental variables for axes 1 and 2.

Variable	Code	Correlation with ordination axis		Canonical coefficient	
		Axis 1	Axis 2	Axis 1	Axis 2
Phytoplankton chlorophyll-*a*	Chlo-Ph	0.966	–0.151	1.904	2.006
Total N	TN	–0.709	0.051	0.236	2.149
Total P	TP	–0.354	0.045	0.368	–0.464
Sub-aquatic radiation	Rad	0.595	0.439	–0.212	0.482
Temperature	Temp	0.269	–0.448	–0.577	–1.968

Based on the Redfield ratio, the periphyton community was considered P-limited for most samples, except for the bottom ones during the dry period. Preliminary studies carried out for the P when the N:P ratio is greater than 32. Despite highly P-limited in most layers, periphyton acted as a P storage reservoir at the bottom of the Garças Reservoir.

Presently, chemical composition of periphyton was completely separated from the algal biomass, a fact clearly pointed out in the CCA. In temperate lakes of different trophic levels, Kahlert and Pettersson (2002) showed that the nutrient status was not coupled to the algal biomass using different substrata. Hill and Fanta (2008) reported that P plays a secondary role under highly limiting light conditions, but it may play a primary role on the periphyton growth, even under irradiance subsaturation condition.

Considering the periphyton algal classes' structure vertical distribution, dominance of Cyanobacteria was noticed in the community growing on all reservoir layers during the rainy period (intense bloom). Cyanobacteria possess several competitive advantages such as, for example, their capability of fixing atmospheric N_2 (Paerl, 1988), P storage (Oliver and Ganf, 2000) and most of their members' ability to mobilize organic phosphates, thus promoting great competitive advantage under P-limiting condition (Paerl, 1988). Moreover, members of Cyanobacteria may dominate under low light availability condition (Shapiro, 1990), the latter possibly the feature that warranted their success in the periphyton during the rainy period (intense bloom).

During the dry period, on the contrary, bloom intensity was less, light availability was greater and the vertical distribution of the algal classes was heterogeneous.

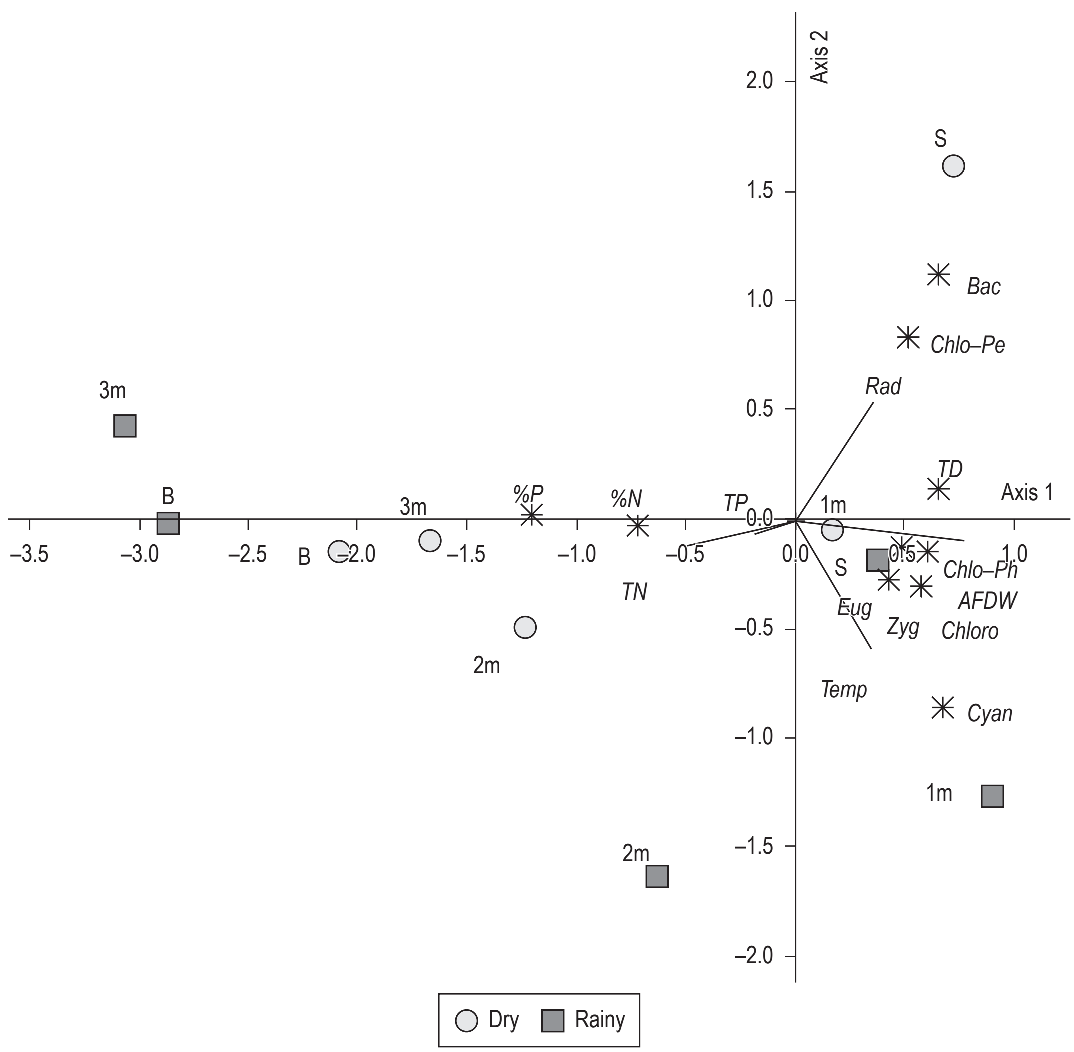

Figure 8. CCA ordination diagram considering 5 depths of Garças Reservoir during both dry and rainy periods produced from 4 environmental variables and 10 attributes of the periphyton community. Codes: sample units measurements indicate water column depth; for vector's abbreviations: Rad = sub-aquatic radiation, TN = total nitrogen, TP = total phosphorus, temp = temperature, Chlo-Ph = phytoplankton chlorophyll-*a*). Codes for the biological variables are in Table 3.

Table 3. Correlations of Pearson (r) with the axes 1 and 2 of ACC and their respective codes.

Periphyton	Code	Axis 1	Axis 2
Bacillariophyceae	Bac	0.505	0.685
Chlorophyceae	Chloro	0.750	–0.103
Cyanophyceae	Cyan	0.570	–0.396
Euglenophyceae	Eug	0.780	–0.083
Zygnemaphyceae	Zyg	0.716	0.029
% P	%P	–0.305	0.386
% N	%N	0.242	0.288
Chlorophyll-*a*	Chlo-Pe	0.569	0.657
AFDW	AFDW	0.802	0.057
Total density	TD	0.757	0.253

Periphyton developing at the surface of reservoir was dominated by Bacillariophyceae, whereas in all other depths Cyanobacteria were just abundant, particularly at 2 m and 3 m deep. Consequently, modification in the Cyanobacteria bloom intensity was enough to modify the periphyton taxonomic classes.

Summarizing, in this study the periphytic community in a hypereutrophic system presented the smallest photosynthetic biomass, the smallest algal growth and the absolute dominance of Cyanobacteria during the rainy period, when the bloom was more intense. On the other hand, during the dry period the lesser bloom intensity allowed greater light penetration, favoring photosynthetic biomass increase, algal growth and dominance of Bacillariophyceae at the surface and of Cyanobacteria at all other depths of reservoir. Chemical composition of periphyton reflected the environment nutritional conditions, evidencing the nutrient retention capability by the periphyton, independent of the amount of algal biomass. Despite the high nutrient availability in the hypereutrophic system, molar N:P ratio indicated that the periphyton community was P-limited at all reservoir depths and climatic periods.

Considering the Degraded State Equilibrium in the hypereutrophic Garças Reservoir, Cyanobacteria bloom intensity was the key environmental factor to regulate biomass modifications and structure of algal classes, acting both in vertical and temporal scale. However, nutrient status and the N and P of periphyton content were primarily driven by the nutrient availability in the water column and secondarily by the temporal scale.

Acknowledgements

To FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo) for fellowship given to MB (Grant nº 06/59342-4) and to CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) for fellowship given to CEMB (Grant nº 303876/2004-2).

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Received: 08 August 2008
Accepted: 03 February 2009