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Vertical distribution of phytoplankton functional groups in a tropical shallow lake: driving forces on a diel scale

Distribuição vertical de grupos funcionais fitoplanctônicos em um lago tropical raso: forças direcionadoras em escala nictemeral

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Abstract: Aim: This study analyzed the vertical distribution of phytoplankton functional groups in two diel cycles in a warm monomictic shallow tropical lake; **Methods:** Sampling of the abiotic variables, phytoplankton and zooplankton communities was performed at intervals of 3 hours over 24 hours in vertical profiles, in the stratification (February) and circulation (July) periods; **Results:** The high thermal stability and the partial atelomixis favored the coexistence of functional groups that are sensitive to destratification, N_A and F, composed by desmids and Chlorophyceae coccoids, and groups S2 and Lo, which persisted during the circulation, and were composed by filamentous cyanobacteria which do not fix N_2 and dinoflagellates, respectively. The discontinuity in the vertical distribution of the functional groups, with dominance of N_A and F in the epilimnion and R and Lo in the metalimnion and hypolimnion, was characteristic of the stratification, and differences between the daytime and nighttime periods were not significant. **Conclusions:** The reduction of 80% of the biomass of the NA group during the mixing period indicates the influence of thermal stability and partial atelomixis as determinant factors in the compartmentalization of functional groups, restricting daytime vertical migration (DVM) and loss by sedimentation during the stratification period.

Keywords: partial atelomixis, daytime variations, stability, functional groups.

Resumo: Objetivo: Analisar a distribuição vertical dos grupos funcionais fitoplanctônicos em dois ciclos nictemerais em um lago tropical monomítico raso; **Métodos:** As amostragens das variáveis abióticas, comunidades fitoplanctônica e zooplanctônica foram realizadas a intervalos de 3 horas ao longo de 24 horas em perfis verticais, nos períodos de estratificação (fevereiro) e de circulação (julho); **Resultados:** A elevada estabilidade térmica e a atelomixia parcial favoreceram a coexistência de grupos funcionais sensíveis a desestratificação N_A e F, compostos por desmidias e clorofícias cocoides e pelos grupos S2 e Lo, persistentes durante a circulação, e compostos por cianobactérias filamentosas não fixadoras de N_2 e dinoflagelados, respectivamente. A descontinuidade na distribuição vertical dos grupos funcionais com dominância de N_A e F no epilímnio e de R e Lo no metalímnio e hipolímnio foi característica da estratificação, e diferenças entre períodos diurno e noturno não foram significativas. **Conclusões:** A redução em até 80% da biomassa do grupo NA durante a circulação indica a influência da estabilidade térmica e atelomixia parcial como fatores determinantes na compartimentalização dos grupos funcionais, restringindo a migração vertical diurna (MVD) e a perda por sedimentação durante a estratificação.

Palavras-chave: atelomixia parcial, variações diurnas, estabilidade, grupos funcionais.

1. Introduction

The daytime variations in the vertical position of the phytoplankton reflect the influence of ecophysiological factors such as the presence of structures such as aerotopes, biotic relationships such as predation and herbivory (Elser and Goldman, 1990; Reynolds, 2006), and environmental factors such as the availability of light and nutrients, wind-induced mixing, and thermal stratification (Frempong, 1981; Reynolds, 2006).

The dynamics of circulation and stratification of a water body, including seasonal and daytime patterns, is the main factor regulating the distribution of abiotic variables and organisms in the water column, as demonstrated for Carioca Lake (Barbosa and Tundisi, 1989; Barbosa and Padisák, 2002). Daytime turbulent mixing restricted to the epilimnetic layer (partial atelomixis) is characteristic of tropical water bodies, where a permanent thermocline may be established (Lewis Junior, 1977). The high incidence of desmids in the epilimnion of tropical lakes was emphasized by Reynolds et al. (2002) and Barbosa and Padisák (2002) as a consequence of partial atelomixis.

Several studies have indicated the determinant role of partial atelomixis in low-latitude lakes in the maintenance of epilimnetic maxima of species of different phylogenetic and functional origins (Tavera and Martínez-Almeida, 2005; Lopes et al., 2005; Becker et al., 2008; Souza et al., 2008). In the present study, was hypothesized that the diel thermal structure (partial atelomixis) of Carioca Lake regulates the vertical position of phytoplankton organisms.

2. Material and Methods

2.1. Study area

The Rio Doce State Park is located in the middle section of the Rio Doce basin, in the state of Minas Gerais (19° 29’ 24”-19° 48’ 18” S and 42° 28’ 18”-42° 38’ 30” W) and includes a considerable part of the lake system of the middle Rio Doce, which comprises approximately 9.8% of the total area of the park. Carioca Lake (19° 45’ S and 42° 37’ W) is a mesotrophic and warm monomictic natural lake, with a short period of circulation during the winter (May-August) and stable thermal stratification in the summer (Henry and Barbosa, 1989). The lake is relatively small, shallow, and round, with a surface area of 142,340 m^2, a volume of 671.2×10^3 m^3, and a shoreline development of 1.28 m (Bezerra-Neto et al., 2010).

2.2. Sampling and data analyses

The study was based on samples collected in the periods of thermal stratification (February, 2000) and destratification (July, 2000) in the deepest point (Zmax = 11.8 m) of the limnetic region of Carioca Lake, at intervals of 3 hours, during 24 hours. Samples of phytoplankton were collected with a van Dorn bottle at the subsurface (100% of incident light), Secchi depth (10% of incident light), three times the Secchi depth (1% of incident light), and the aphotic zone (Cole, 1994).

Data for precipitation (mm), air temperature (°C), and wind speed (m/s) were provided by a meteorological station located at Ipatinga, 10 km distant from the Rio Doce State Park.

Vertical profiles of water temperature, dissolved oxygen, pH, and electrical conductivity were measured in situ using a Horiba multi-probe sensor, model U-22, at intervals of 0.5 m from the surface to the bottom of the lake ($Z_{máx}$ = 11.8 m).

The strata in the stratified period (epilimnion, metalimnion and hypolimnion) were defined from the thermal profile, using differences of 0.6 °C, with the Z_{mix} considered as equivalent to the epilimnion. The thermocline was identified as the largest difference (°C) between one meter and the next lower meter in the thermal profile.

Transparency (m) was estimated with a Secchi disk, and the euphotic zone (Z_{eu}) was calculated as three times the Secchi disk extinction depth (Cole, 1994). The vertical light attenuation coefficient (k) was calculated using the equation $k = 1.7 \times ZDS^{-1}$ (Poole and Atkins, 1929). The ratio of the euphotic zone (Z_{eu}) to Z_{mix} was used as an index of light availability in the mixing zone (Jensen et al., 1994).

The heat content was calculated according to Cole (1994), expressed in $cal.cm^{-2}$. The stability (s) was determined according to the equation of Idso (1973), and thermal exchanges were calculated from the values of heat content ($cal.cm^{-2}$), deducting the values among times, converting them into percentages (%).

The ammonium concentrations were measuredaccording to Koroleff (1976), total nitrogen, nitrate and nitrite according to Mackereth et al. (1978), and reactive soluble phosphorus and total phosphorus according to Golterman et al. (1978). Chlorophyll-*a* was determined by the method of Lorenzen (1967). The trophic state was calculated by the index of Toledo et al. (1983) and the limiting nutrients according to Redfield (1958).

Samples for taxonomic determinations were collected a plankton net of 20 µm mesh, and were preserved in a 4% formaldehyde solution.

The samples of phytoplankton were fixed with neutral lugol solution. The quantitative analyses followed Utermöhl (1958), counting 400 individuals of the most frequent species (Lund et al., 1958). The density of the organisms was calculated according to Villafañe and Reid (1995), and expressed as individuals.mL^{-1}.

The biovolume (mm^3.L^{-1}) was estimated from the geometric shapes that were closest to the cell shape, individually or combined (Sun and Liu, 2003; Hillebrand et al., 1999), from the mean values of the measurements of 20 to 30 individuals. The biovolume was expressed in units of fresh weight, where 1 mm^3.L^{-1} = 1 mg.L^{-1} (Wetzel and Likens, 1991).

Zooplankton community samples were obtained by filtering 10 L of water collected with a Van Dorn bottle in a plankton net of 68 µm, stained with rose Bengal, fixed with 4% formalin, with pH corrected to 7.0 with borax (Haney and Hall, 1973). The organisms were counted in a Sedgwick-Rafter chamber (1.0 mL) with a minimum of 250 individuals per sample, and a variation coefficient of 0.20 or less (McCauley, 1984). Nauplii, copepodids and adults were counted separately.

Phytoplankton taxa were classified according to the following criteria:

i) Life form of desmids: unicellular nonflagellate with projections (UNFp), unicellular non-flagellate without projections (UNF), and colonial filamentous (CFi);

ii) Size: evaluated from the values of the maximum linear dimension (MLD) (adapted from Sieburth et al., 1978). Class 1: < 10 µm, class 2: between 11 and 20 µm, class 3: between 21 and 50 µm, and class 4: > 50 µm;

iii) Functional groups were defined for species that contributed at least 5% of the mean phytoplankton biomass in each period (Reynolds et al., 2002; Reynolds, 2006; Padisák et al., 2009); and

iv) The dominant phytoplankton functional groups were considered as those with a biomass > 50% of the total of the sample (adapted from Lobo and Leighton, 1986).

The mean depths of the phytoplankton functional groups, dominant zooplankton species, and life habit of desmids i (Pmi) or the depth at which a population i was located in the water column, during the day and the night, were calculated according to Dini et al. (1993). (Equation 1)

$$Pm_i = \frac{(\sum XiZi)}{(\sum Xi)} \quad (1)$$

where:

Xi = relative biovolume (phytoplankton and desmids) and relative density (zooplankton), Zi = depth of sample i.

The phytoplankton functional groups that occurred in at least 80% of the sampling periods were included in the analyses. The existence of daytime vertical migration (DVM) was determined by comparing the daytime and nighttime periods through a two-tailed *t* test for each population.

The Kruskal-Wallis non-parametric analysis was used to compare the variables among depths and hours; and the Spearman correlation to estimate the relationship among the phytoplankton and zooplankton populations. These analyses were performed through the Statistica software version 5.1 (Statsoft). Multivariate descriptive analyses were carried out by applying principal components analyses (PCA) to the abiotic data using a covariance matrix with data transformed by ranging. The programs used were FITOPAC (Shepherd, 1996) to transform data, and PC-ORD, version 3.0 for Windows (McCune and Mefford 1997) for the execution of the analyses.

3. Results

3.1. Chemical and physical scenario

The analyses of the abiotic factors evidenced seasonal differences in the thermal and chemical behavior of the lake. The seasonal dynamics were determined by the stratification pattern, and the diel dynamics by the effect of the atelomixis.

The vertical profile during the stratification period indicated high thermal stability (86.4 g.cm.cm^{-2}), and the occurrence of partial atelomixis was recognized through the "breaking" of micro-stratifications (<6 °C) to 4 m (= epilimnion), favored by the air-temperature reduction during the night (14 °C difference between the daytime and nighttime periods) (Figure 1).

In this period, the surface layers (to 4 m) were more oxygenated, with a clinograde oxygen distribution and anoxia in the hypolimnion. The epilimnetic layer was deficient in nitrogen and phosphate forms (Table 1).

During the mixing period (July), the loss of heat in the surface layers led to almost complete thermal mixing, except for short-term stratifications in the surface layers between 3:00 PM and 12:00 AM (Figure 2). The water column was totally oxygenated (orthograde profile) and with nutrients available. The trophic state depended on the season (oligotrophic during the stratification, and eutrophic during turnover).

The period of stratification coincided with the maximum values of water transparency (1.5 m; n = 9) and the Z_{eu} (5 m; n = 18) exceeded the Z_{mix} (4 m; n = 18), indicating availability of light in this layer (Z_{mix}: Z_{eu} = 1.2). However, the values of

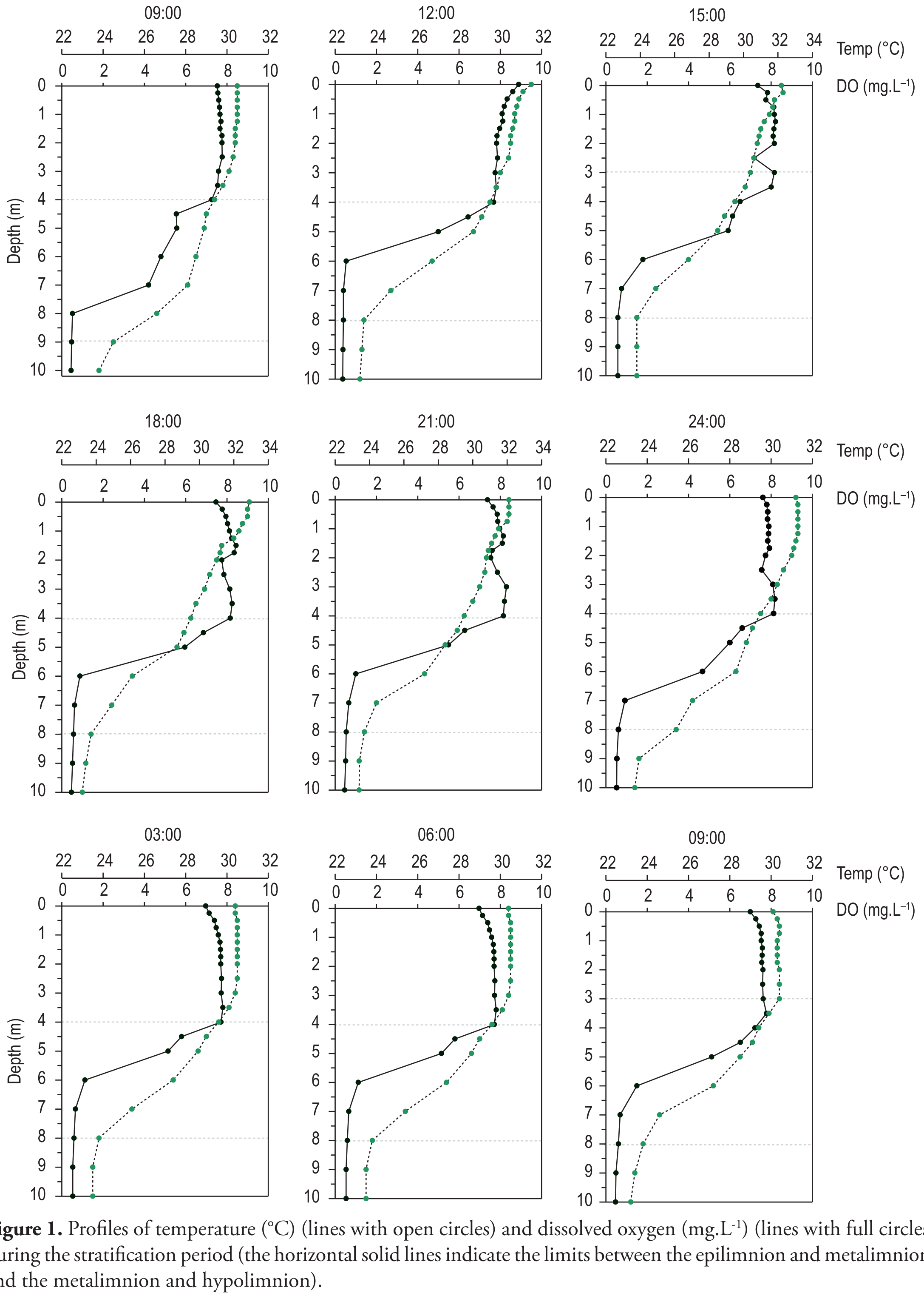

Figure 1. Profiles of temperature (°C) (lines with open circles) and dissolved oxygen (mg.L^{-1}) (lines with full circles) during the stratification period (the horizontal solid lines indicate the limits between the epilimnion and metalimnion, and the metalimnion and hypolimnion).

Table 1. Summary of the physical and chemical variables (means and range of variation) of Carioca Lake during the stratification period (February) and mixing period (July) (total number of samples in the two periods = 72).

Variables	Stratification (February)			Mixing (July)	
	Zeu	Zaph		Zeu	Zaph
	Epilimnion (0-4 m) (n=18)	Metalimnion (4-8m) (n=9)	Hypolimnion (8-11,8 m) (n=9)	Camada até 4m (n=18)	Entre 4 e 8m (n=18)
pH	5.9 (6.2-6.8)	5.7	5.7	6.3 (6-6.9)	5.7 (5.4 – 6.2)
Electrical conductivity (µS.cm^{-1})	28.0	27.0	105.0	24.6 (24.0-25.0)	24.7 (24.0-25.0)
Total phosphorus (µg.L^{-1})	14.2 (9.9-20.3)	20.3	40.1	30.2 (24.9-36.5)	28.6 (20.5-32.7)
Total nitrogen (µg.L^{-1})	156 (448-793)	534.4	2320	609 (1082-1978.5)	687 (1250-2058)
PO_4-P (µg.L^{-1})	3.3 (0.3-12)	2.2	1.9	3.4 (1.7-5.9)	3.4 (3.1-5)
NH_4^+-N (µg.L^{-1})	8.4 (20.2-62.7)	13.2	716.6	71.6 (18.5-137)	86.7 (46-137.2)
NO_3-N (µg.L^{-1})	7.1 (0.6 – 12.3)	11.6	14.3	7.4 (1.8-13.7)	8.6 (1.3-29.9)
NO_2-N (µg.L^{-1})	1.4 (0.3-6.2)	3.4	5.4	1.1 (0.5-3.1)	0.9 (0.3-2.1)
Ration C:N:P molar	99:06:0.5	90:07:0.6	94:33:1.2	86:13:1	84:21:0.9

the light attenuation coefficient were high (between 1 and 3 m).

Differences in the heat content between the daytime and nighttime periods (during the rainy and dry seasons) were not observed, indicating a predisposition to a conservative behavior on the diel scale. During the stratification, the thermal exchanges occurred in the entire water column, and the thermocline was not an obstacle. In general, only 1% of the total heat was exchanged during the stratification, with reduction during the circulation period (< 0.5%) (Figure 3).

PCA using 13 abiotic variables explained 77.5% of the data variability on the first two ordination axes (Figure 4), with the samples grouped independently of the hour and as a function of the depth, mainly during the stratification. The variables contributing most to the ordination of axis 1 were: Dissolved oxygen (r = 0.4), total nitrogen (r = -0.3), free CO_2 (r = -0.4), N-NH_4 (r = -0.3), electrical conductivity (r = -0.4) and HCO_3 (r = -0.4), respectively. For axis 2, temperature (r = -0.8) and total phosphate (r=0.3) showed the highest correlations (Figure 4).

The samples from the stratification period (subsurface, 10% and 1% of incident light) grouped on the negative side of axis 2, associated with high temperatures. The samples from the aphotic zone grouped on the negative side of axis 1. The samples associated with the mixing period (subsurface, 10% and 1% of incident light and aphotic zone) grouped on the positive side of axis 2, positively correlated with the high values of total phosphorus (r = -0.3).

3.2. Daytime pattern of the plankton communities

In the two periods, 86 phytoplankton taxa wee identified, members of 8 classes, 20 families and 39 genera. Of this total, 15 described species were accommodated in 6 functional groups (Table 2).

The total biomass differed among depths, mainly between subsurface and hypolimnion (H = 11.0; p = 0.00). The maximum value was identified at 6:00 PM (82.6 mg.L^{-1}), associated with functional group R (mainly *Oscillatoria* sp.) in the hypolimnion.

During the stratified period, the groups N_A, R, L_0 and F, composed by small desmids (< 10 µm), filamentous cyanobacteria, dinoflagellates and colonial green algae, respectively, were the most numeroud (Table 2). During the mixing period, coinciding with the increase of the trophic state and reduction of thermal stability (7.7 g.cm.cm^{-2}), groups S_1 (*Pseudanabaena galeata* Böchner) and Lo (*Gymnodinium* spp.) were dominant.

In stratification, three trends in the vertical profile were identified: 1) Epilimnion: high values of biomass of the functional group NA (46% of the total), with MDL between 5 and 10 µm, coexisting with group F (13% of the total), with MDL between 20.1 and 64 µm; 2) Metalimnion: Functional group Lo (48%), with a discontinuous distribution in hours, and MDL between 20.1 and 64 µm; and 3) Hypolimnion: higher biomasses of functional group R (> 90%), with MDL > 64.1 µm (Table 2).

Groups NA and R were the only ones observed in all sampling times, and no differences between daytime and nighttime were identified for any of the functional groups. The biomass of group NA differed significantly between the epilimnion

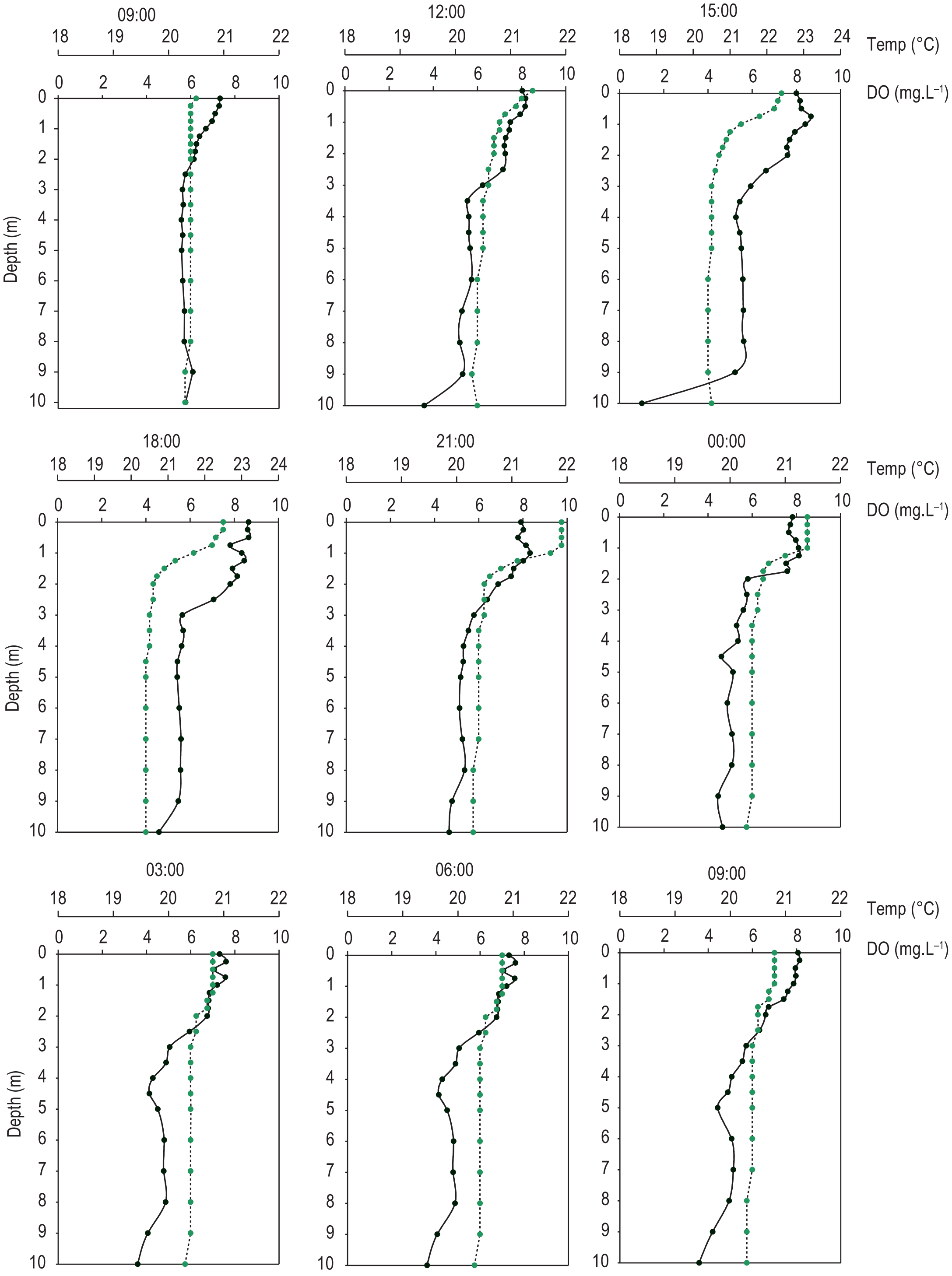

Figure 2. Profiles of temperature (°C) (lines with open circles) and dissolved oxygen (mg.L^{-1}) (lines with full circles) (solid lines) during the mixing period (July).

and hypolimnion (Kruskal–Wallis H = 10.9, p = 0.00, n=72) with reductions in the density and biomass as the depth increased. The metalimnion and hypolimnion were the preferential habitat of group R, with significant differences between the epilimnion and hypolimnion (Kruskal–Wallis H = 10.9, p = 0.00, n = 72), and the highest densities and biomasses below 4 m.

For the zooplankton community, the omnivorous cyclopoid copepod *Thermocyclops minutus* (Lowndes, 1934) was dominant during the stratification and in the turnover (values above 80%) in each depth sampled, despite the high richness and

Table 2. Dominant phytoplankton taxa (%, contribution to total biomass), class size, and their functional groups identified in Carioca Lake during the 24-hours cycle in the stratification (February) and mixing periods (July).

Stratification period	Taxon	Ocorrence (%)	Class size	Functional group
Epilimnion (n = 18)	*Coelastrum sphaericum; Botryococcus* sp.	13 ± 13*	III	F
	Cosmarium asphaerosporum var. *strigosum, C. bioculatum Staurastrum taylorii, S. tetracerum* var. *tetracerum f. tetracerum and Staurodesmus crassus*	46 ± 0,12*	I	N_A
	Peridinium spp.; *Gymnodinium* spp.	36 ± 12*	III	L_0
Metalimnion (n = 9)	*Coelastrum sphaericum* Näg.; *Botryococcus* sp.	9,9*	II; III	F
	C. asphaerosporum var. *strigosum*, *C. bioculatum Staurastrum taylorii, S. tetracerum* var. *tetracerum f. tetracerum* and *Staurodesmus crassus*	34*	I	N_A
	Peridinium spp.; *Gymnodinium* spp.	48*	III	L_0
Hypolimnion (n = 9)	*Pseudanabaena galeata*	98 (9-15 h)	III	R
	Oscilatoria spp.	96 (18-21 h)	IV	R
Mixing period				
0-4 m (n = 18)	*Coelastrum sphaericum*	6.8 ± 4*	III	F
	Pseudanabaena galeata	85 ± 5*	III	S_1
Between 4 e 8m (n = 18)	*Gymnodinium* spp.	85*	III	L_0

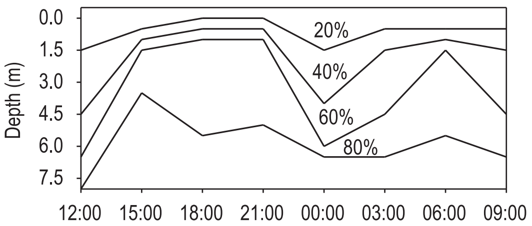

Figure 3. Daytime variation of the thermal exchanges in Carioca Lake during the stratification period (February).

densities of rotifers present (values < 10%). During the stratification, *T. minutus* was dominant between the epilimnion and metalimnion (86% of the total density during the period).

The analyses of the DVM for *T. minutus* (adults and nauplii) indicated that the species did not show typical migratory behavior. Groups R and N_A showed no significant changes in vertical distribution between daytime and nighttime (Figure 5). The habitat overlap between *T. minutus* (adults and nauplii) and group N_A was confirmed through positive correlations ($r = 0.5$, $p \geq 0.05$, $n = 72$).

The classification of the life habit of the desmids indicated a dominance of unicellular non-flagellates (UNF), except *Teilingia granulata* (Roy & Biss.) Bourr. and *Spondylosium panduriforme* (Heim.) Teil. (filamentous). Such differences in the life habit were determinant for the vertical distribution, as indicated by DVM analyses (Figure 6): the filamentous forms were slightly more sensitive to sinking, due to their larger size (MDL between 24 and 30 μm) and greater volume (values between 680 and 1840 μm^3) compared to unicellular forms. The differences between daytime and nighttime periods were not significant, indicating the efficiency of the thermal stability and partial atelomixis in reducing losses of desmids through sinking.

During the turnover, associations adapted to stratified environments and with differentiations of resources in the vertical profile (N_A, F, R) were replaced by species that are tolerant of shade and completely mixed, shallow environments (group S1). Thus, functional group S_1 (*Pseudonabaena galeata*) was dominant in the layer between 0 and 4.5 m (comprising 85% of the total biomass; n = 72); and the Lo group, comprising 85% of the total biomass, predominated between 4.5 and 7 m.

4. Discussion

The composition and vertical structure of the phytoplankton proved to be dependent on the physical contrasts, directly influenced by the thermal structure on both the seasonal and diel scales. This influence of the thermal regimen on the functional groups is evidenced in tropical and subtropical regions, where thermal stratification is lasting and the partial atelomixis exerts a selective force on the functional groups in the 24-hours cycle (Barbosa and Padisák, 2002; Becker et al., 2008).

During the stratification, the main functional groups present in the epilimnion were composed by non-mobile Chlorophyceae, colonial forms with high MDL and mucilaginous sheaths (group F),

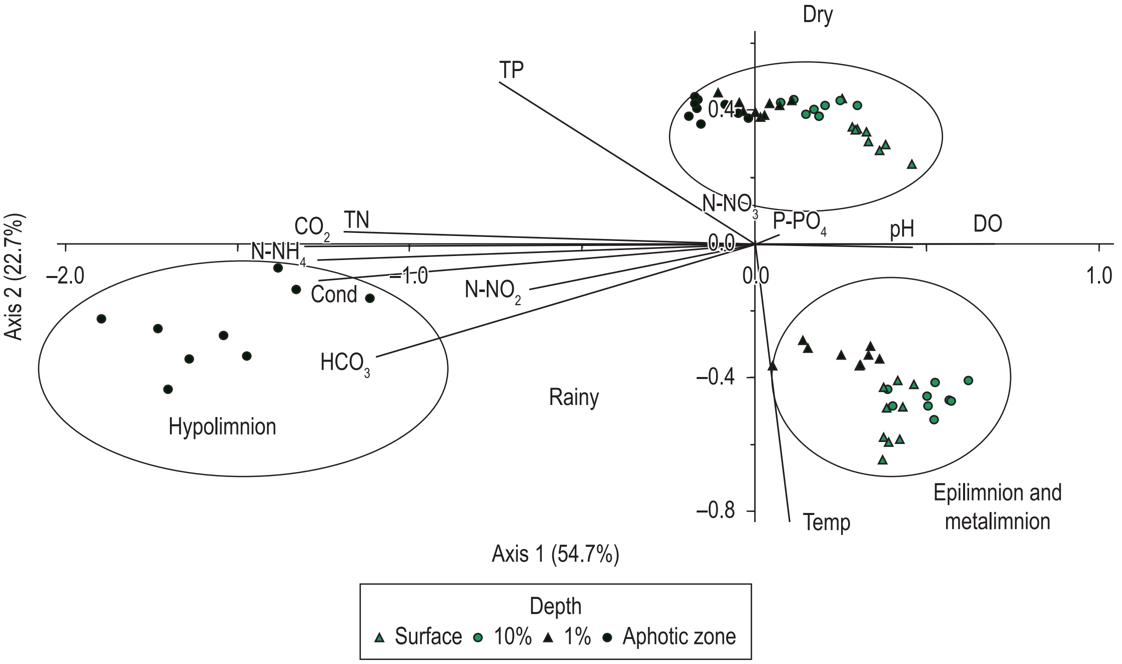

Figure 4. PCA ordination diagram of the sampling units for the abiotic variables in Carioca Lake, emphasizing the depths.

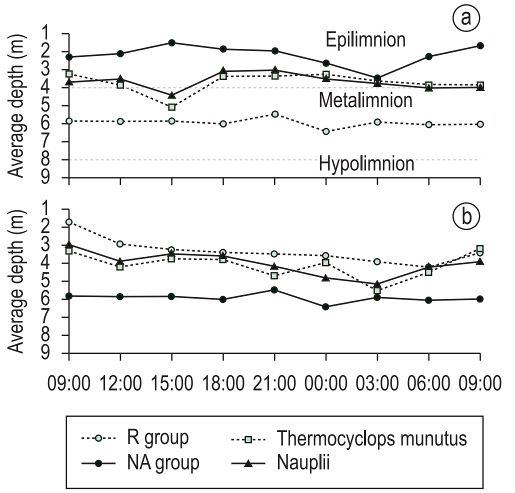

Figure 5. Diel variation of the mean depths of phytoplankton functional groups and *Thermocyclops minutus* (Lowndes, 1934) during the stratification (a) and turnover (b) seasons. Absence of statistical differences between daytime and nighttime periods.

and non-mobile forms with small MDL (>5 µm) and occasional mucilaginous sheaths (group NA), adapted to clear, stratified, nutrient-poor lakes (Reynolds et al., 2002; Padisák et al., 2009). The action of atelomixis as a determinant factor in the maintenance of the desmids (group NA) (Tavera and Martínez-Almeida, 2005; Souza et al., 2008) and the Chlorophyceae coccoids (group F) in the epilimnion (Becker et al., 2008) was identified.

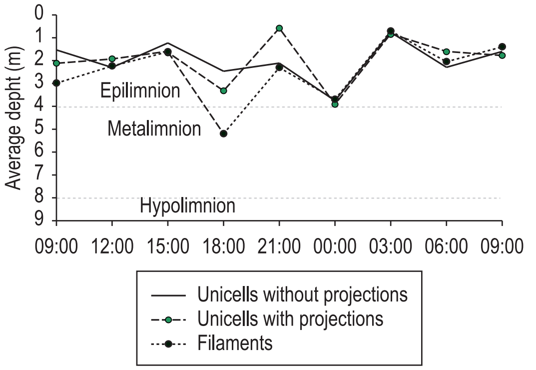

Figure 6. Diel variation of the mean depth of the strategies adopted by the desmids during the stratification season. Absence of statistical differences between daytime and nighttime periods.

In temperate environments, desmids seldom comprise a significant part of the phytoplankton biomass (Yung et al., 1986). These species do not remain permanently in the epilimnion of stratified tropical lakes, a function only associated with the resistance of cells to sinking (Reynolds et al., 2002; Padisák et al., 2003).

Small-sized species (10 µm) with a volume less than 1000 µm^3 (O´Farrel et al., 2007) are generally identified as efficient in light-limited lakes. The high attenuation of light produced by high concentrations of dissolved organic carbon and colored organic matter (Bezerra-Neto et al., 2006), together with the nutrient limitation in the epilimnion, potentially select for small-sized species (>10 µm), with longer residence times in the Z_{eu}, indicating that size differences may act as a selective factor, attenuating losses by sedimentation.

Functional group N_A, typical of low latitudes, is composed by small-sized desmids (Souza et al., 2008; Pádisak et al., 2009). In these regions, the lower viscosity increases the sinking velocity, which is also increased in conditions of limitation by light and nutrients (Peperzak et al., 2003). Thus, the partial atelomixis and the small sizes of the species (MDL < 10 µm) appear to be ecologically important for the maintenance of the maximum biomass.

Group R, adapted to the metalimnion and hypolimnion of oligo-mesotrophic lakes and to shading, form maximum population layers (Padisák et al., 2009) in stratified lakes such as Carioca, where metalimnetic and hypolimnetic populations of cyanobacteria had been identified for at least three decades (Reynolds et al., 1983; Barbosa and Padisák, 2002; Padisák et al., 2003), coincident with the chlorophyll-*a* maxima. The predominance of elongated forms with high surface:volume ratios (Reynolds, 1997) reflects the, advantage of this shape in absorbing light energy, even in near-limiting conditions.

Species from the Lo group often dominate the phytoplankton community in water bodies that are thermally stratified, with vertically separated resources (Reynolds, 2006). The flagellates are considered as good indicators of the concentrations of organic matter and dissolved organic carbon (Grigorszky et al., 2003), conditions observed in Carioca Lake.

Besides the thermal structure, the daytime vertical distribution of the functional groups and phytoplankton classes of size also may be influenced by the presence of more efficient herbivores (Rangel et al., 2009). In Carioca Lake, the overlapping of microhabitats between copepod nauplii, copepodids and adults may occur because of the differentiation of resources and feeding habits; since nauplii are rather bacteriophagous (Sherr and Sherr, 1987) and copepodids and adults of *T. minutus* are omnivorous (Matsumura-Tundisi, 1997). The raptorial habit allows these copepods to manipulate larger particles (>50 nm), including cyanobacteria (Rietzler and Espíndola, 1998; Maia-Barbosa et al., 2003). Despite their broad feeding habits, in the present study the analysis indicated positive correlations and habitat overlapping of *T. minutus* with group NA, and this factor is not indicative of herbivory.

In Carioca Lake, the virtual absence of vertebrate predators of zooplankton may be the main reason that no migration in the zooplankton community is observed (Bezerra-Neto et al., 2009).

In summary, the functional groups were influenced by the thermal regimen on both the seasonal and diel scales. The results show that the thermal stratification and partial atelomixis are operating forces influencing the vertical distribution of phytoplankton. The absence of MVD confirms this factor, indicating reduction of losses by sedimentation of the functional groups NA and F. During the period of circulation, the reduction in up to 80% of the relative biomass of group NA indicates the importance of the stratification regimen and the partial atelomixis in maintaining the epilimnetic maximum. The restriction of vertical mixing to the epilimnion plays a key role in the survival of groups NA and F.

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