



## Is phytoplankton functional classification a suitable tool to investigate spatial heterogeneity in a subtropical shallow lake?

Luciane Oliveira Crossetti<sup>a,\*</sup>, Vanessa Becker<sup>b</sup>, Luciana de Souza Cardoso<sup>c</sup>, Lúcia Ribeiro Rodrigues<sup>d</sup>, Luciana Silva da Costa<sup>d</sup>, David da Motta-Marques<sup>d</sup>

<sup>a</sup> Postgraduate Program in Biology, C2, Universidade do Vale do Rio dos Sinos, São Leopoldo, Brazil

<sup>b</sup> Program in Sanitary Engineering, Universidade Federal do Rio Grande do Norte, Centro de Tecnologia, Departamento de Engenharia Civil, Natal, Brazil

<sup>c</sup> Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

<sup>d</sup> Instituto de Pesquisas Hidráulicas, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

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### ABSTRACT

Functional groups of phytoplankton are widely recognized to vary in response to certain environmental variables, according to their niche preferences. The aim of this study was to evaluate the strength of the relationship between functional traits of phytoplankton and environmental predictors in a spatially heterogeneous large subtropical shallow lake (Mangueira Lake, southern Brazil), analyzing whether phytoplankton functional approach is a suitable tool to investigate spatial heterogeneity. Samples were taken twice a year (summer and winter), for six years (2001–2006) in the subsurface water at north, center and south sampling stations in that large system (90 km long). This biannual frequency enabled us to evaluate the seasonal and spatial changes of functional groups in relation to environmental variations, by means of ordination analysis (PCA and CCA). The integrated analysis of phytoplankton functional groups and abiotic variables evidenced clear and significant spatial and seasonal gradients (Monte Carlo test,  $p=0.01$ ). The seasonal gradient was related to temperature, water-level fluctuations and wind action, leading to spatial heterogeneity of the phytoplankton. The northern part of the lake proved to be dissimilar, with greater availability of soluble reactive phosphorus and higher biomass of phytoplankton. Functional groups related to turbid and mixed environments, such as **MP**, **S1** and **J** were important. Hydrodynamics-related features were the driving forces for structuring the phytoplankton functional groups, which appropriately showed the main tendencies observed in this ecosystem, proving to be an adequate tool to access spatial heterogeneity.

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### Introduction

The physical and chemical variability of coastal shallow lakes is largely dependent on the hydrodynamics and human impacts, and so are their communities (Scheffer, 1998). In these systems and in several others with peculiar features, phytoplankton communities are essential descriptors of the water quality because of their wide phenotypic diversity, short generation time and rapid response to environmental variability (Reynolds et al., 2002). Also, the phytoplankton constitutes the basis of almost all food webs, and regulates energy flow in most fresh waters (Bonilla et al., 2005; Kent et al., 2007). Despite their notable importance, very little is known about the factors that determine the function and structure of

phytoplankton communities in subtropical lakes, although lake area and submerged vegetation have been mentioned as some of the determinants of phytoplankton biodiversity in subtropical shallow lakes (Kruk et al., 2009).

Changes in the water column in lentic systems, related to the water-circulation patterns, are considered one of the main environmental forces that affect phytoplankton dynamics. Turbulence and the availability of growth-limiting resources for algae, such as light and nutrients, are recognized as the most important variables in determining phytoplankton assemblages (Margalef, 1978; Reynolds, 2006) and dissimilar distribution of those resources in spatially heterogeneous environments have been related to heterogeneous arrangement of phytoplankton species and functional groups (Nogueira et al., 1999; Caputo et al., 2008; Rychtecký and Znachor, 2011).

In the past decade, studies on phytoplankton dynamics have proved that morpho-functional grouping of species may be useful for ecological purposes (Dokulil et al., 2007; Padišák et al., 2009). Particularly, the functional-groups approach *sensu* Reynolds et al.

\* Corresponding author at: Programa de Pós Graduação em Biologia, C2, Universidade do Vale do Rio dos Sinos (UNISINOS), Av. Unisinos, nº. 950, Caixa Postal 275, 93022-000 São Leopoldo, RS, Brazil.

E-mail address: [lcrossetti@unisinos.br](mailto:lcrossetti@unisinos.br) (L.O. Crossetti).

(2002) is one of the most widely accepted forms of grouping phytoplankton species (Padisák et al., 2009), although other grouping approaches based on morphology have been recently proposed presenting interesting results (Salmaso and Padisák, 2007; Kruk et al., 2009, 2011). In the functional-groups (FGs) classification, species are grouped by their related morphological (size, length, mucilage, presence of specialized structures) and physiological features (pigment composition, reproductive rates, buoyancy ability, capacity for light absorption and nutrient uptake, susceptibility to grazing, motility, and nutritive habit) (Salmaso and Padisák, 2007). The functional-groups approach has corroborated the predictive potential of the phytoplankton community, and has been extensively validated in pelagic communities of temperate (e.g., Huszar et al., 2003; Leitão et al., 2003; Becker et al., 2010), tropical (e.g., Lopes et al., 2005; Sarmiento et al., 2007; Crossetti and Bicudo, 2008a; Costa et al., 2009), and subtropical (e.g., Fabbro and Duivenvoorden, 2000; Kruk et al., 2002; Bonilla et al., 2005; Becker et al., 2009) regions.

In general, it is widely known that the selection of coexisting phytoplankton species depends on their biogeographical spread and on local conditions such as temperature, light, and nutrient and ion concentrations (Conley et al., 2000). For large shallow lakes, wind-induced mechanisms such as suspended solids, nutrients, and light availability (Carrick et al., 1993; Schelske et al., 1995; Bachmann et al., 1999; Cardoso et al., 2012) are generally found to be dominant factors leading to both spatial and temporal heterogeneity of phytoplankton, either indirectly by affecting the local nutrient concentration and light availability due to resuspended particles, or directly by resuspending algae from the sediment (Scheffer, 1998). If in spatially heterogeneous lentic ecosystems the distribution of planktonic communities might be determined by the irregular supply of resources, in large shallow lakes with spatial heterogeneity hydrodynamic factors tend to be even more important for plankton distribution (Cardoso et al., 2012). Also, ecosystems that are often influenced by water-level variations may show alterations in the phytoplankton structure, as reflected in abiotic conditions such as light and nutrient availability (Crossetti et al., 2007).

Since it is expected that the predictability of phytoplankton functional groups may be closely constrained by environmental patterns, and in order to contribute to the knowledge of phytoplankton structuring in subtropical shallow ecosystems, we

evaluated the strength of the relationship between functional traits of the phytoplankton community and environmental predictors in a spatially heterogeneous large subtropical shallow freshwater ecosystem, Mangueira Lake in southern Brazil. We focused on the question: is phytoplankton functional approach a suitable tool to investigate spatial heterogeneity in a subtropical shallow lake?

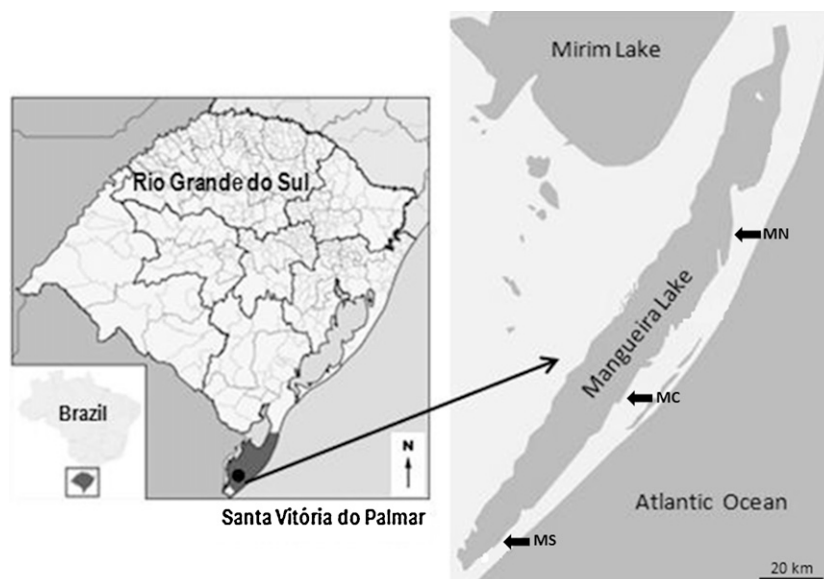
## Methods

### Study area

The Taim Hydrological System (THS) is site 7 of the Long-Term Ecological Research of the Brazilian network (LTER = PELD/CNPq), located in the southern part of the state of Rio Grande do Sul (32°20' and 33°00'S, and 52°20' and 52°45'W). The system area is 2254 km<sup>2</sup>, contains the federal Taim Ecological Station (ESEC – Taim, 33,935 ha), and is situated on a narrow strip of land between the Atlantic Ocean and Mirim Lake (Fig. 1). The region has a subtropical climate (Cfa type; Kottek et al., 2006). The lakes in the THS were formed after the last Post-Glacial Marine Regression (Holocene ~5000 BP) (Tomazelli et al., 2000). The study was carried out in the largest lake of the THS. Mangueira Lake is a large shallow coastal lake ( $Z_{\max}$  = 6 m,  $Z_{\text{mean}}$  = 2.6 m), 90 km long and 3–10 km wide (Fig. 1). It covers a total area of 820 km<sup>2</sup>. The lake's main axis is northeast-southwest, aligned with the prevailing winds (Fragoso et al., 2008). The lake is continuous warm polymictic (no seasonal ice cover, stratifying at most a few hours at a time) (Lewis, 1983), with daily mixture due to intense wind action. The northern and southern extremes of the lake interface extensively with the THS wetlands. The trophic state ranges from oligotrophic to mesotrophic. The mesotrophic conditions occur in the spring and summer when it suffers from a notable water withdrawal to irrigation of rice crops (approximately 2 L ha<sup>-1</sup> s<sup>-1</sup> during 100 days), as well as a high input of nutrients loading from its watershed (Fragoso et al., 2008), determining its hydroperiod, comprised by low-water (generally in summer) and high-water (generally in winter) periods.

### Sampling and abiotic and biological variables

Sampling was carried out twice a year in summer and winter, during 6 years (2001–2006) for biological and abiotic analyses, at



**Fig. 1.** Taim Hydrological System (THS). Legend: MN, North Mangueira Lake; MC, Central Mangueira Lake; MS, South Mangueira Lake.

**Table 1**Mean, interval (minimum and maximum) and standard deviation values of limnological variables ( $n = 12$ ) at the three sampling stations over six years in Mangueira Lake.

	North			Center			South		
	Mean	Interval	sd	Mean	Interval	sd	Mean	Interval	sd
Water temperature ( $^{\circ}\text{C}$ )	18.2	11.2–25.2	4.2	18.1	13.7–17.6	3.9	18.4	19.9–24.7	3.8
Wind speed ( $\text{m s}^{-1}$ )	2.7	0.1–5.8	1.3	3.2	1.2–5.8	1.5	3.2	1.2–5.8	1.4
Dissolved oxygen ( $\text{mg L}^{-1}$ )	9.4	7.7–10.6	0.9	9.8	8.6–12.1	1	10	7.9–11.9	1.1
Conductivity ( $\mu\text{S cm}^{-1}$ )	275	203–332	40.2	264	194–311	39	256	187–332	41.8
pH	8	7.1–8.8	0.5	8	6.8–8.8	0.5	8.1	6.8–8.8	0.5
Transparency (m)	0.6	0.16–1.0	0.2	0.8	0.4–1.1	0.2	1.2	0.42–2.0	0.5
Total suspended solids ( $\text{mg L}^{-1}$ )	27.3	10.0–55.5	13.9	19.5	5.0–30.8	7.5	15.1	1.0–46.0	11.7
$\text{CO}_2$ ( $\text{mg L}^{-1}$ )	4.5	1.0–7.2	2	4.3	2.0–7.1	2	4.4	1.0–7.1	2.2
SRSi ( $\text{mg L}^{-1}$ )	3.4	1.4–6.6	1.7	4	1.4–7.8	2.1	4	1.8–7.8	1
$\text{N-NO}_3^-$ ( $\mu\text{g L}^{-1}$ )	297.1	7.6–550.0	230.7	309.9	3.0–590.0	234.7	321.4	2.1–690.0	254.1
$\text{N-NH}_4^+$ ( $\mu\text{g L}^{-1}$ )	51.6	10.0–149.5	44.4	36.1	8.0–116.6	37.5	43.6	6.0–133.7	37.9
SRP ( $\mu\text{g L}^{-1}$ )	28.3	1.7–157.4	43.1	18.1	2.2–54.1	15.8	23.1	0.0–62.7	21.7
Chlorophyll $a$ ( $\mu\text{g L}^{-1}$ )	12.1	0.3–50.4	14.6	14.8	0.5–63.3	18.9	10.1	0.2–51.8	13.9
Biomass ( $\text{mg L}^{-1}$ )	10.9	0.6–68.4	19.9	4	0.7–13.1	13.1	2.4	0.6–7.2	7.2

three sites in the pelagic zone of Mangueira Lake (north, central and south), at the subsurface of the water column. The samples were analyzed for nutrients (soluble reactive phosphorus – SRP, ammonium –  $\text{N-NH}_4^+$  and  $\text{N-NO}_3^-$ ; Mackeret et al., 1989; soluble reactive silicon – SRSi; APHA, 1992) and total suspended solids (SST; APHA, 1992). Transparency (Secchi disk), water temperature, pH, electrical conductivity and dissolved oxygen (YSI 6920 probe) were measured at all sampling stations. Chlorophyll  $a$  was extracted from GF/F filters into 90% ethanol (Jespersen and Christoffersen, 1987) and measured by the spectrophotometric method (APHA, 1992). Phytoplankton was counted according to Utermöhl (1958); sedimentation time followed Lund et al. (1958). Biomass ( $\text{mg L}^{-1}$ ) was estimated through biovolume. Phytoplankton species were sorted into functional groups (FGs), according to Reynolds et al. (2002) and Padišák et al. (2009).

#### Identification of environmental gradients

Descriptive analysis of data was done using the program Minitab 14 Statistical Software (2003). A Principal Components Analysis was performed to evaluate the overall variation considering all the abiotic variables. The data set was transformed by 'ranging'. For integrated analysis of abiotic and biological data, a canonical correspondence analysis (CCA) was performed. For the CCA the abiotic data were transformed by 'ranging' (Sneath and Sokal, 1973), which reduces the values of a variable to the interval [0, 1] by first subtracting the minimum observed for each variable and then dividing by the range (Legendre and Legendre, 1998). The biological data (phytoplankton functional groups) were transformed by  $\log x + 1$ , respectively. For the CCA, the most important variables indicated by the PCA were chosen, avoiding collinearity. To explain the data variability, the canonical coefficient that represented the importance of the contribution of each environmental variable to the ordination of the axis was used. Also used was the intra-set correlation representing possible correlations between the abiotic variables and their ordination with that axis, but retaining the dependence relationship between biological and abiotic variables. To reinforce the latter, the Pearson and Kendall's correlation ( $r$ ) coefficient was calculated. For all the ordination analyses, the software PC-Ord 6 (McCune and Mefford, 2011) was used.

## Results

#### Physical and chemical variables

Descriptive analyses of abiotic variables are given in Table 1. The three sampling stations in Mangueira Lake were considered significantly different only regarding light availability (transparency

and total suspended solids), where the southern part of the lake tended to be clearer ( $p < 0.05$ ). Regarding climate variables (Table 2), temperature followed the seasonal distribution, while air relative humidity and precipitation did not show any seasonal tendency.

The PCA of environmental data summarized the major variability of Mangueira Lake (Fig. 2). In the PCA diagram, the three axes explained 60.1% of the environmental data variance. Based upon the correlation values,  $\text{N-NO}_3^-$  ( $-0.92$ ) and SRSi ( $-0.74$ ) were the most important variables for the ordination of the first axis (27.6%), while conductivity ( $-0.69$ ) and temperature ( $-0.66$ ) strongly influenced axis 2 (18%), and wind ( $-0.78$ ) influenced axis 3 (14.5%). In an overview, a seasonal pattern and the gradient of nutrients were identified along the first axis, but no spatial tendency was observed in the variations of abiotic parameters.

#### Phytoplankton structure

The mean biomass was highest in the northern part of Mangueira Lake ( $10.9 \text{ mg L}^{-1}$ ), and decreased toward the south (Fig. 3). Concentrations of chlorophyll  $a$  were similar at all sampling points, although the center showed the highest mean value ( $14.8 \mu\text{g L}^{-1}$ ) (Table 1). Regarding biomass and chlorophyll  $a$ , no significant difference was found ( $p > 0.01$ ) among the three sampling sites.

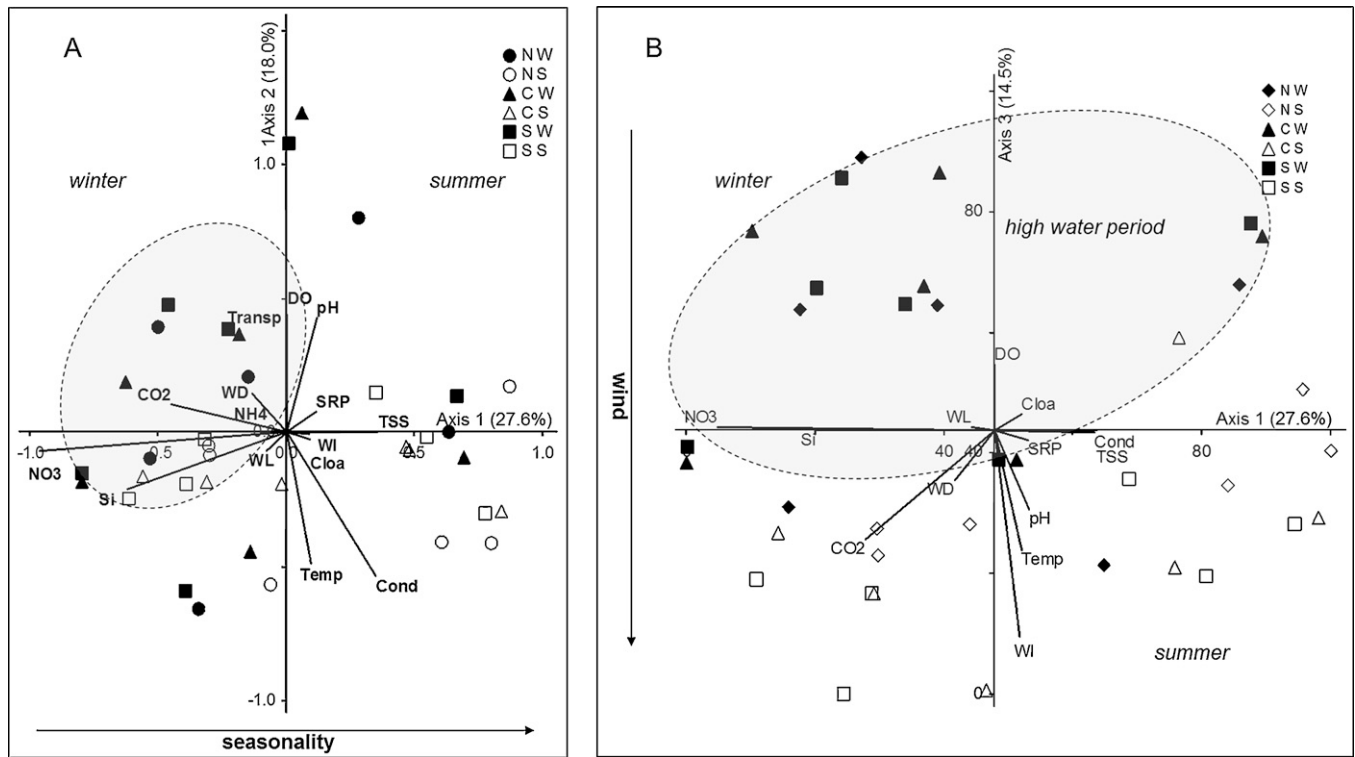
From the total of 20 FGs identified in Mangueira Lake, seven together contributed most to the absolute values of biomass in the northern (84% of total biomass), center (83%) and southern (63%) sampling sites (Table 2).

In an overview, in the northern part, the FGs **M** (mainly represented by *Microcystis aeruginosa*), **MP** (mainly represented by

**Table 2**

Climate variables during the study period in Mangueira Lake.

	Air temperature ( $^{\circ}\text{C}$ )	Air relative humidity (%)	Precipitation (mm)
August 01	11.7	85	0.0
December 01	18.1	81	0.0
August 02	12.1	84	2.0
December 02	18.7	74	0.2
August 03	5.8	77	0.0
December 03	15.0	67	3.6
August 04	15.1	97	2.3
November 04	18.5	93	6.2
May 05	24.2	57	0.0
November 05	24.8	42	0.0
August 06	10.5	81	0.0
November 06	18.3	53	0.0



**Fig. 2.** Ordination diagrams of the first and second axes (A) and first and third axes (B) of the Principal Components Analysis (PCA) for the 15 environmental variables, during winter (solid symbols) and summer (open symbols) in the north (circles), center (triangles) and south (squares) of Mangueira Lake.

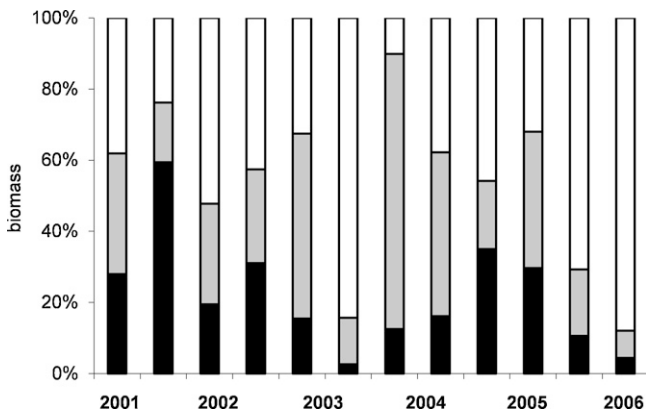
*Tabellaria flocculosa* and **L<sub>0</sub>** (mainly represented by *Radiocystis fernandoi*) contributed most to the total biomass (Fig. 4, Table 3). **K** (mainly represented by *Synechococcus nidulans*), **M** (mainly represented by *M. aeruginosa*), **J** (especially *Coelastrum reticulatum*) and **S1** (mainly represented by *Planktolyngbya contorta*) were the most important assemblages in the center of Mangueira Lake. In the southern part, **S1** (mainly represented by *P. contorta*), **K** (mainly represented by *Aphanocapsa delicatissima*), **L<sub>0</sub>** (represented by *R. fernandoi* and *Snowella lacustris*) and **F** (mainly represented by *Oocystis lacustris*) were the most important phytoplankton groups (Fig. 4, Table 3).

Temporally, with the exception of 2004, the functional groups composition was distributed over a spatial gradient (from the north to the south of the lake). The central point clearly represented a transitional area, containing representatives from both the northern and southern functional groups (Fig. 5).

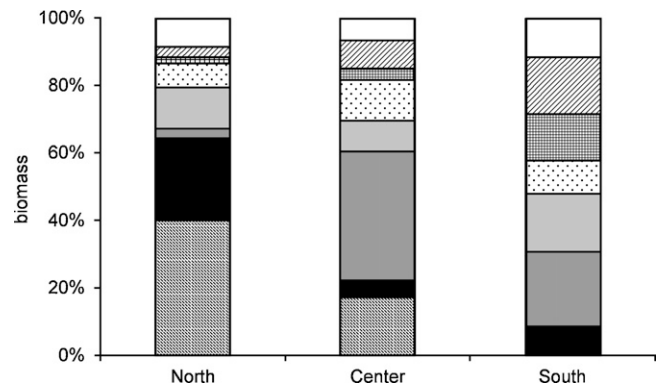
*Integrated analysis*

The CCA results performed with six environmental variables and the seven functional groups with the highest biomass contribution explained 39.3% of the total variation on the first two axes. The eigenvalues for axes 1 and 2 were 0.373 and 0.111. Pearson's correlations of environment-species were high for both axes (0.87 and 0.67), indicating a strong correlation between abiotic variables and the biological distributions. The Monte Carlo test ( $p=0.01$ ) used to determine the significance level of canonical axes demonstrated that the ordination of axes 1 and 2 was statistically significant ( $p < 0.05$ ).

The canonical coefficient indicated that N-NO<sub>3</sub><sup>-</sup> (-1.209) and conductivity (-1.071) were the most important variables for axis 1 ordination; and for axis 2, conductivity (1.028) and temperature (-0.993) were important. Considering the intraset correlations, N-



**Fig. 3.** Relative biomass (%) in the north, center and south of Mangueira Lake. Legend: □, north; ■, center; ■, south.

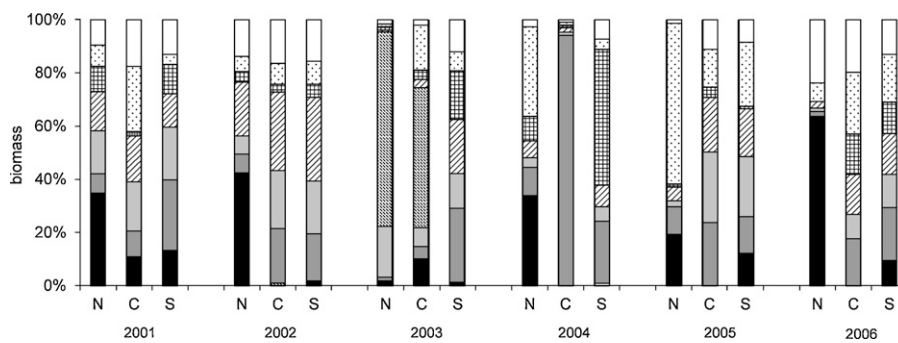


**Fig. 4.** Relative biomass (%) of the main functional group in the north, center and south of Mangueira Lake. Legend: ■, functional group MP; ■, K; □, L<sub>0</sub>; ▨, J; ▤, F; ▩, S1; ▨, M; □, others.



**Table 3**  
Main phytoplankton functional groups (FGs), respective main species and biomass relative contribution (%) in Mangueira Lake.

FGs	Species	North (%)	Center (%)	South (%)
F	<i>Oocystis lacustris</i> Chodat	2	2	9
	<i>Treubaria</i> sp.			4
J	<i>Scenedesmus obtusus</i> Meyen	3		
	<i>Scenedesmus</i> cf. <i>caribeus</i> Komárek	1		
	<i>Coelastrum reticulatum</i> (Dangeard) Senn		4	
K	<i>Pediastrum boryanum</i> (Turpin) Meneghini			3
	<i>Aphanocapsa delicatissima</i> West & West	1	3	8
	<i>Synechococcus nidulans</i> (Pringsheim) Komárek		21	
	<i>Aphanotece smithii</i> Komarková-Legnerová & Cronberg		1	
L <sub>0</sub>	<i>Aphanocapsa conferta</i> (W. West & G.S. West) Komárková-Legnerová & Cronberg			7
	<i>Radiocystis fernandoi</i> Komárek & Komárková-Legnerová	10		6
M	<i>Snowella lacustris</i> (Chodat) Komárek & Hindák	1	4	8
	<i>Microcystis aeruginosa</i> (Kützing) Kützing	40	12	
MP	<i>Gomphonema parvulum</i> (Kützing) Kützing		2	
	<i>Coscinodiscus</i> sp.			4
S1	<i>Tabellaria flocculosa</i> (Roth) Kützing	23	28	
	<i>Planktolyngbya contorta</i> (Lemmermann) Anagnostidis & Komárek	2	6	14



**Fig. 5.** Relative biomass (%) of the main functional group over six years in the north, center and south of Mangueira Lake. Legend: ■, functional group MP; ■, K; ■, L<sub>0</sub>; ■, J; ■, F; ■, S1; ■, M; □, others.

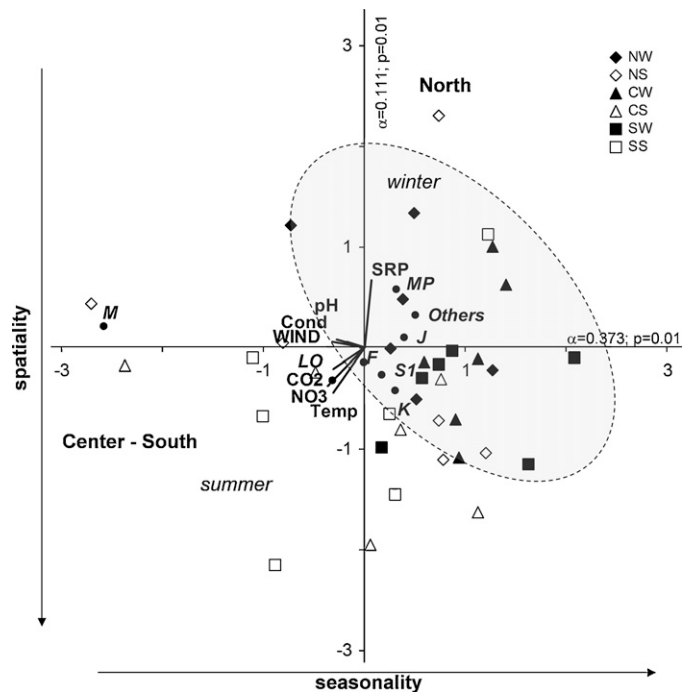
NO<sub>3</sub><sup>-</sup> (-0.403) and pH (-0.351) were the most important for the ordination of axis 1, and SRP (0.482) and temperature (-0.321) accounted for the axis 2 ordination.

The ordination diagram (Fig. 6) showed on the positive side of axis 1, the FGs K, MP, F, S1, F, J and others more associated with the sample units of winter and the high-water period, and consequent lower temperature, N-NO<sub>3</sub><sup>-</sup> levels, conductivity and pH. On the negative side of axis 1, the FGs M and L<sub>0</sub> were associated with the higher values of these abiotic variables and with the low-water period sampling units. Considering axis 2 ordination, on its positive side, especially MP and J were associated with the higher values of SRP, mainly, and with the sample units in the north. On its negative side, the majority of the codons were ordinated to the higher values of temperature and N-NO<sub>3</sub><sup>-</sup> and to the sample units of center and south Mangueira Lake.

Regarding the main trends shown by the integrated analysis, CCA axis 1 represented a seasonal gradient separating the phytoplankton functional groups according to the abiotic scenario of summer and winter periods, characterized by low-water and high-water periods, and nutrient availability. Axis 2 showed a spatial gradient along the longitudinal distribution of sampling points, ordering together the center and south units and indicating the northern part of Mangueira Lake as a dissimilar region within the ecosystem.

**Discussion**

Phytoplankton functional groups structure was clearly constrained by the environment during the study period in Mangueira Lake, demonstrating the spatial heterogeneity of that ecosystem. Integrating the abiotic and biological data it was observed that



**Fig. 6.** Ordination diagram of the canonical correspondence analysis (CCA) for the morphological functional groups (FGs) of Mangueira Lake during winter (W – solid symbols) and summer (S – open symbols) in the north (circle), center (triangle) and south (square) of the lake.

the nutrient availability, as a response to the combined interactions of seasonality and spatiality, determined the phytoplankton dissimilar distribution in the three studied sites of the lake.

Large shallow lakes provide suitable conditions for the development of spatial heterogeneity, which might cause an irregular distribution of phytoplankton (Carrick et al., 1993), especially considering hydrodynamic features which might lead to a strong wind influence (Verhagen, 1994; Cardoso and Motta-Marques, 2009; Hennemann and Petrucio, 2011).

Heterogeneity in the distribution of phytoplankton functional groups was clearly demonstrated in the CCA. The grouping of sampling units from the center and south parts of the lake showed the similarity between these two points in the composition and abundance of functional groups. On the other hand, the north part of the lake proved to differ in phytoplankton structure. A similarly heterogeneous distribution of the fish community in Mangueira Lake was reported by Rodrigues et al. (2011), as a consequence of wind action and of the structural complexity of the lake/wetland interface in the north. The great length of Mangueira Lake favors the wind action in the two most likely directions along the largest fetch, northeast in summer and southeast in winter (Fragoso et al., 2008). This may explain the differences in the composition of the phytoplankton functional groups found in the north, together with the greater availability of SRP observed at this sampling point and the influence of the adjacent wetland.

Although wind direction was not shown to be a strong descriptive factor in the ordination analysis for the present study, the influence of wind on the phytoplankton should not be neglected. Wind may be the dominant factor controlling phytoplankton patchiness in lakes (George and Heaney, 1978; George, 1981; Webster, 1990; Cardoso et al., 2012) producing advective downwind movements of surface waters (Marcé et al., 2007). More recently, Cardoso and Motta-Marques (2003), in a nearby subtropical shallow ecosystem (Itapeva Lake, southern Brazil), showed that the interaction between wind on a daily scale (hours) and the ecosystem shape was the determinant factor for the very high rates of change found for the phytoplankton community. According to Vidal et al. (2010), the diurnal cycles of heating and cooling, and the timing and direction of the prevailing winds are expected to change on a seasonal scale, selecting different populations through the year. Hence, the longitudinal distribution of phytoplankton and the time scales for development or destruction of horizontal patchiness should change over seasonal time scales. Modeling studies for Mangueira Lake (Fragoso et al., 2008) have shown that wind-induced currents can be considered an important factor controlling transport of substances and phytoplankton. For instance, a southwest wind, with magnitude approximately greater than  $4 \text{ m s}^{-1}$ , can cause a significant transport of water mass and substances from south to north in Lake Mangueira, producing an almost instantaneous increase of the water level in the northeastern parts, and hence a decrease of water level in the southwestern areas (Fragoso et al., 2008).

Besides the wind, the seasonality found in both environmental variables and functional-group patterns was closely related to the temperature in the summer and winter, and especially to the water-level variations due to the large withdrawal of water for adjacent rice fields. Water-level fluctuations emerged as the decisive element of the hydrology, especially in shallow lakes embedded in wetlands that are particularly sensitive to any rapid change in water level and input (Coops et al., 2003), as is the case for Mangueira Lake. Several studies have demonstrated the influence of water-level variations on the structure of phytoplankton (e.g., Huszar and Reynolds, 1997; García de Emiliani, 1997; Izaguirre et al., 2004; Crossetti et al., 2007; Bovo-Scomparin and Train, 2008; Mihaljević et al., 2010; Wang et al., 2011). In the present study, the high-water

period coincided mostly with winter, and was characterized by high  $\text{CO}_2$  and  $\text{N-NO}_3^-$  availability.

The phytoplankton functional-groups approach has been widely used and has proved to be a useful tool for monitoring purposes (see Crossetti and Bicudo, 2008a; Becker et al., 2009). Moreover, its relationship to the habitat template has been tested and proved since the original work of Reynolds et al. (2002), which gave the habitat description as well as the tolerances and sensitivities for each codon. This synchrony between the functional-group responses to environmental variations has been well demonstrated in the case of Mangueira Lake, revealing the spatial heterogeneity in that ecosystem. The most important phytoplankton assemblages found in Mangueira Lake are related to clear or turbid mixed environments (Reynolds et al., 2002; Padisák et al., 2009). Padisák et al. (2009) stated that the assemblages **MP**, **S1**, and **J** composed by shade-adapted members, occur in turbid mixed environments. In the present study, **F**, **S1**, **K** and **J** occurred under lower concentrations of SRP, in winter, the high-water period, especially in the center and south parts of Mangueira Lake, probably influenced by the high turbulence. Functional group **MP** occurred most at the north sampling station under higher concentrations of SRP, especially in the high-water period. This codon was characterized as occurring in frequently stirred up, inorganically turbid shallow lakes (Padisák et al., 2009), and was firstly described for periphytic diatoms that occasionally occur in lake plankton due to wind suspension (Padisák et al., 2006).

The **M** functional group was basically found in the low-water period at all the sampling stations, when probably water turbulence was not so intense, under high concentrations of  $\text{N-NO}_3^-$ ,  $\text{CO}_2$  and pH. This abiotic scenario also favored **L<sub>0</sub>**, although this assemblage preferred the center and south stations, while **M** preferred the north and center sample areas, especially in the low water period. Both groups are mentioned as dependent on stable conditions to succeed (Reynolds et al., 2002), although their occurrence has already been registered in non-stratified conditions (Crossetti and Bicudo, 2008b).

In summary, the phytoplankton functional groups of Mangueira Lake proved to be driven by environmental variables, being constrained especially by those related to hydrodynamics, regarding the spatial heterogeneity of the lake, proving to be an adequate tool in heterogeneous ecosystems. Monitoring and evaluation of the dynamics of this ecosystem may be well achieved with the descriptive potential of this functional-diversity approach, which appropriately showed the main tendencies observed in this ecosystem.

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