Article

Temporal variability determines phytoplankton structure over spatial organization in a large shallow heterogeneous subtropical lake

Lacina M. Freitas-Teixeira,[1,2] Juliana E. Bohnenberger,[3] Lucia R. Rodrigues,[3] Uwe H. Schulz,[3] David da Motta-Marques,[3] and Luciane O. Crossetti[4]*

[1] *Instituto Federal Sul-Rio-Grandense, Campus Sapucaia do Sul, Piratini, Sapucaia do Sul, RS, Brazil*
[2] *Universidade do Vale do Rio dos Sinos, Cristo Rei, São Leopoldo, RS, Brazil*
[3] *Instituto de Pesquisas Hidráulicas, Universidade Federal do Rio Grande do Sul, Agronomia, Porto Alegre, RS, Brazil*
[4] *Departmento de Ecologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Agronomia, Porto Alegre, RS, Brazil*
Corresponding author: luciane.crossetti@ufrgs.br

Abstract

Spatial heterogeneity is associated with the temporal variability of the habitat and may affect the structural patterns of biological communities. This study evaluated the influence of spatial and temporal heterogeneity on the phytoplankton structure in a large shallow subtropical lake, Lake Mangueira in southern Brazil (Z_{max} = 6 m; length = 90 km; width = 3–10 km). The lake is continuous warm polymictic, oligo-mesotrophic, under the direct influence of an adjacent wetland on the north, and has extensive aquatic macrophyte beds. Samples for abiotic and biological analyses were taken quarterly for 2 years at 19 points at the water subsurface, comprising the pelagic and littoral zones and the southern, central, and northern areas of the lake. The phytoplankton structure was analyzed with measurements of chlorophyll *a*, biomass, richness, diversity, and descriptor species. Of the 117 phytoplankton species identified, Cyanobacteria (e.g., *Chroococcus limneticus*, *Aphanocapsa conferta*, *Aphanothece smithii,* and *Planktolyngbya contorta*) was the major group in all areas and both zones of the lake. Total biomass levels were highest in the northern area, whereas the richness and the descriptor species showed no clear spatial differences. A redundancy analysis (RDA) indicated strong temporal organization of the species according to the abiotic conditions, indicating that the high level of temporal variability due to local hydrodynamics was the main factor structuring the phytoplankton community in Lake Mangueira during the study period.

Key words: horizontal heterogeneity, littoral zone, pelagic zone, spatiality, temporality

Introduction

Biological dynamics, distributions, and community structure can be explained by a variety of biotic and abiotic factors related to spatial and temporal heterogeneity. Diversity patterns in biological communities can also be explained by environmental heterogeneity (Simpson 1949, MacArthur and MacArthur 1961, Bazzaz 1975). More-complex habitats are presumed to host a number of micro-habitats, favoring different modes of resource exploitation and thus increasing species diversity (Bazzaz 1975). For example, sites that differ in the degree of environmental heterogeneity may have similar species richness, but the species composition may be unequal due to differing niche requirements for each species (Vasconcelos et al. 2009).

The heterogeneity of habitats in shallow aquatic ecosystems may be associated with spatial patterns related to changes in environmental conditions and resources, both horizontally (pelagic and littoral zones) and vertically (with depth), and also to temporal patterns when conditions and

resources for biological communities vary over time. Spatial variability in shallow lakes can often be associated with the presence of a littoral zone or adjacent wetlands densely inhabited by aquatic macrophytes (Scheffer 1998). Aquatic plants are key components in the spatial heterogeneity of the landscape, contributing to habitat complexity and influencing diversity on various spatial scales (Thomaz et al. 2008). Aquatic macrophytes may affect many ecosystem processes, including nutrient cycling (Barko et al. 1991, Gumbricht 1993), reducing water turbulence (Madsen et al. 2001), providing refuges for many species (Genkai-Kato 2007), and influencing the structure and dynamics of the phytoplankton community (Crossetti and Bicudo 2008, Fonseca and Bicudo 2010, Villamagna and Murphy 2010).

Temporally, the occurrence of perturbations and seasonal events may further complicate the spatial structure of an ecosystem (Nogueira et al. 1999), especially in tropical and subtropical ecosystems where these temporal changes are highly influenced by precipitation and wind patterns (Berkley et al. 2010). The physical or temporal stability of habitats and the degree of interactions among the species within the community determine the degree of community variability (Bengtsson et al. 1997).

The combination of hydrodynamic processes at different spatial and temporal scales can control the community dynamics for phytoplankton (Borges et al. 2008, Schneck et al. 2011, Moura et al. 2012), especially in heterogeneous environments where dynamic variations may change the composition of algal species, depending on their survival strategies (Reynolds 1994). Studies have indicated the importance of the environmental conditions, the spatial variability of resources, and the high temporal variability of the phytoplankton community organization, both in reservoirs (Becker et al. 2008, Borges et al. 2008, Schneck et al. 2011) and shallow lakes (Cardoso et al. 2012, Crossetti et al. 2013, 2014, Mukhortova et al. 2015).

Assuming that resource variability common in many aquatic ecosystems is due to spatial and temporal heterogeneity, the variation of phytoplankton in time and space is, consequently, expected. The objective of this study was to evaluate the influence of spatial and temporal heterogeneity on the phytoplankton community structure (biomass, richness, diversity, and descriptor species) in a large shallow subtropical lake.

Methods

Area of study

The study was conducted in Lake Mangueira, located in the Taim Hydrological System in Rio Grande do Sul state, southern Brazil (32°20′–33°00′S; 052°20′–052°45′W). Lake Mangueira, situated on a narrow strip of land

between the Atlantic Ocean and Mirim Lake in a subtropical climate (Kottek et al. 2006), is a large shallow lake (Z_{max} = 6 m, Z_{mean} = 2.6 m), 90 km long and 3–10 km wide (Fig. 1), with a surface area of 820 km². The main axis of the lake is northeast–southwest (Fragoso et al. 2008). The system is a continuous warm polymictic lake (Lewis 1983), with daily mixing from strong winds and rare periods of stratification. Water inflow is insignificant except for some small streams on the lake's western boundary (Rodrigues et al. 2015), but the lake is connected with wetlands to the north and extensive macrophyte banks (*Potamogeton illinoensis* Morong, *Cabomba caroliniana* Gray, *Egeria densa* Planch., *Myriophyllum spicatum* L., *Nitella* sp., *Potamogeton pectinatus* L., *Ceratophyllum demersum* L., *Utricularia* sp., *Zizaniopsis bonariensis* Speg., *Schoenoplectus californicus* (Mey.) Soják, and *Myriophyllum aquaticum* (Vell.) Verdc.) on its margins, especially in the south where the macrophytes cover ~27.1% of the littoral area (here defined as the near shore area, within ~1 km). The trophic state ranges from oligotrophic to mesotrophic. Mesotrophic conditions occur in spring and summer when water is withdrawn to irrigate rice fields (~2 L ha⁻¹ s⁻¹ for 100 d), and high nutrient loads enter from the watershed (Fragoso et al. 2008). The water withdrawal determines the hydroperiod, composed of dry periods (usually in spring and summer) and flooding (usually in autumn and winter).
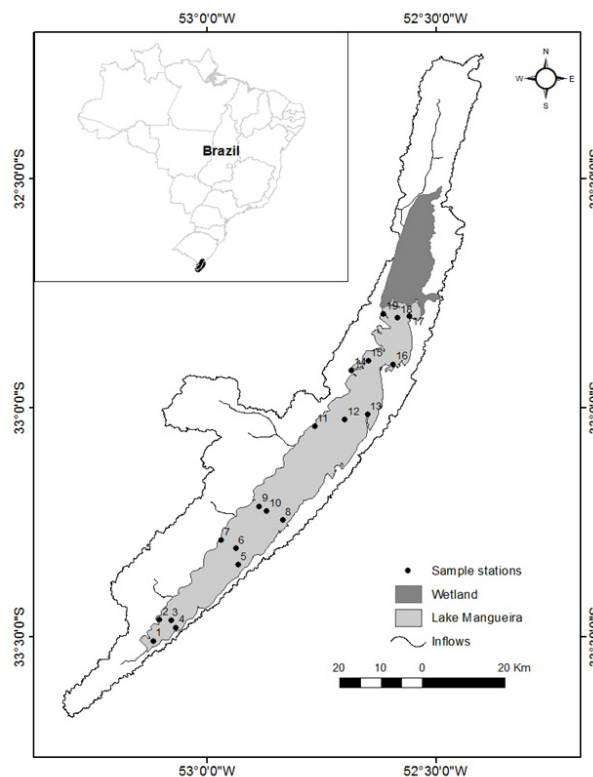

Fig. 1. Lake Mangueira; black dots indicate the sampling points..

Sampling abiotic and biological variables

Water subsurface samples were collected seasonally (4 samples per year) from 2010 to 2011 at 19 points along the length of the lake, including the southern, central, and northern areas. The sampling points included the pelagic (sampling points 1, 3, 6, 10, 12, 15, and 18), left littoral (western sampling points 2, 7, 9, 11, 14, and 19), and right littoral (eastern sampling points 4, 5, 8, 13, 16, and 17) zones (Fig. 1). Littoral samples were taken avoiding macrophyte stands.

Meteorological data (wind direction and velocity, precipitation) were provided by the closest meteorological station (at Santa Vitória do Palmar city, INMET-RS), which measures climate variables at different times of the day. The data were interpolated according to the time spent at each sampling site. The nutrients analyzed were total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN), ammonium (NH_4^+-N), nitrate (NO_3^--N; Mackereth et al. 1989), soluble reactive silica (SRSi), and total suspended solids (TSS; APHA 1992). Water transparency (determined using a Secchi disk), water temperature, pH, electrical conductivity, and dissolved oxygen (determined using a YSI 6920 probe) were also measured. Turbidity was determined using spectrophotometry (APHA 1992), carbon forms were evaluated using TOC V equipment (Shimadzu 5000), and humic acids were evaluated using a spectrum-fluorometer (BBE-Moldaenke).

The biomass of phytoplankton was determined through biovolume measurements (mm^3 L^{-1}). The samples were preserved with 1% acetic Lugol for the quantitative analysis, following Utermöhl (1958) and the settling time of Lund et al. (1958). The diversity index (Shannon and Weaver 1963) and species richness (Simpson 1949) were used to assess the structure of the phytoplankton community. The indicator species were considered those that contributed a minimum of 1% of the total biomass in at least one sampling unit.

Data analysis

Descriptive statistical analysis of the environmental and biological variables was executed to explore their variation amplitudes. Principal components analysis (PCA) was performed to assess the primary spatial and temporal trends of the abiotic variables after transforming the data by log (x + 1).

Detrended correspondence analysis (DCA) was performed to indicate the unimodal or linear ordering method to be used in the integration of the biological and abiotic variables (indicator species). Redundancy analysis (RDA) of the transformed (log x + 1) environmental and biological variables was completed after retrieving the

result of the DCA (gradient length: 2.259, linear method) to observe their ordination, depending on the spatial and temporal variations.

Nonmetric multidimensional scaling (NMDS) ordination was used to evaluate the similarities among sampling sites considering the biomass of the phytoplankton descriptor species, based on the Sørensen (Bray-Curtis) distance matrix. NMDS can be used to assess dimensionality (McCune and Grace 2002) by representing, as closely as possible, the pairwise dissimilarity between objects in a low-dimensional space (Buttigieg and Ramette 2014). The goal is to construct a graph in which dissimilar objects are placed farther apart in the ordering space while like objects are placed closer to each other (Gotelli and Ellison 2011). To avoid the influence of seasonality, the analyses were performed for each season during both years (2010 and 2011). The number of 3 dimensions was chosen to minimize the stress (i.e., to maximize the rank correlation between the calculated similarity distances and the plotted distances). The statistical software PC-ORD 6 was used for these analyses (McCune and Mefford 2011).

Results

The northern area of Lake Mangueira showed the highest concentrations of SRP (56 µg L^{-1}) and NO_3^--N (411 µg L^{-1}) and the highest values of turbidity (80 NTU) and TSS (28 mg L^{-1}; Table 1). A north-to-south spatial gradient of nutrients was apparent; the north showed the highest concentrations of dissolved nutrients and the south higher values of transparency (2.7 m) and dissolved oxygen (11.8 mg L^{-1}). Higher mean concentrations of NH_4^+-N (95 µg L^{-1}) were observed in the pelagic zone. Temporally, the availability of SRP and TP was highest in spring (mean values 32.1 and 50 µg L^{-1}, respectively; Table 1).

PCA summarized 56.4% of the total abiotic data variability on the first 2 axes ($p = 0.001$; Fig. 2). The variables that contributed most to the ordination of axis 1 ($r > 0.6$) were turbidity and alkalinity; conductivity, turbidity, and wind speed were the main contributors to axis 2. The ordination diagram indicated a strong temporal variation, separating the sample units according to seasonality in the years studied. The PCA ordination showed no separation in the pelagic and littoral zones, although the northern part of the lake differed spatially from the central and southern areas because of higher levels of turbidity, TSS, and dissolved nutrients (Fig. 2).

We identified 117 phytoplankton species belonging to 7 major algal groups (Bacillariophyceae, Chlorophyceae, Chrysophyceae, Cyanobacteria, Dinophyceae, Eugleno-

Table 1. Mean, standard deviation, and minimum and maximum values of the environmental variables sampled in the 4 seasons (2010 and 2011) at 19 sampling locations in Lake Mangueira. Legend: S = South ($n = 56$), C = Center ($n = 48$), North = N ($n = 48$), lm = left margin ($n = 48$), pel = pelagic zone ($n = 56$), rm = right margin ($n = 48$), spr = spring ($n = 48$), sum = summer ($n = 38$), aut = autumn ($n = 38$), win = winter ($n = 38$).

Variable	S	C	N	lm	pel	rm	spr	sum	aut	win
Temperature (°C)	10–25 (18 ± 5)	11–25 (18 ± 4.9)	12–25 (19 ± 4.8)	10–25 (18 ± 4.9)	10–25 (18 ± 4.9)	10–25 (18 ± 4.8)	21–26 (23 ± 1.4)	20–28 (23 ± 0.9)	13–18 (17 ± 1.5)	10–13 (12 ± 0.8)
elocity (m s^{-1})	1–9 (2.8 ± 2.5)	0–8 (3.1 ± 2.5)	1–8 (4.2 ± 2.6)	0–9 (3.4 ± 2.6)	0–9 (3.3 ± 2.5)	0–9 (3.4 ± 2.7)	2–8 (4.7 ± 2.2)	0–2 (1.3 ± 0.7)	0–9 (4.5 ± 3.3)	1–8 (2.8 ± 1.8)
Precipitation (mm)	0–2.1 (0.3 ± 0.7)	0–13.7 (1.7 ± 4.6)	0–13.7 (1.7 ± 4.6)	0–13.7 (1.2 ± 3.8)	0–13.7 (1.1 ± 3.6)	0–13.7 (1.2 ± 3.8)	0–0 (0 ± 0.0)	0–0 (0 ± 0.0)	0–13.7 (4.7 ± 0.0)	0–0.1 (0.03 ± 0.04)
Transparency (m)	0.6–2.7 (1.3 ± 0.5)	0.3–2.4 (0.9 ± 0.4)	0.4–1.7 (0.9 ± 0.4)	0.3–2.4 (1 ± 0.4)	0.3–2.7 (1 ± 0.5)	0.3–2.4 (1.1 ± 0.5)	0.5–1.6 (0.9 ± 0.3)	0.7–2.1 (1.1 ± 0.4)	0.6–2.35 (1.1 ± 0.4)	0.3–2.7 (1.1 ± 0.7)
Depth (m)	1.4–5.7 (2.9 ± 1.4)	0.8–7.0 (3.2 ± 1.9)	1.1–3.7 (2.3 ± 0.7)	0.8–2.7 (1.6 ± 0.4)	1.5–7 (3.6 ± 1.6)	1–5.2 (2.9 ± 1.1)	1–7 (3.3 ± 1.6)	0.9–6.3 (2.6 ± 1.3)	0.8–6.3 (2.6 ± 1.5)	1.2–6.8 (3.1 ± 1.6)
pH	7.4–9 (7.9 ± 0.4)	7.4–9.1 (7.9 ± 0.5)	7.4–9.2 (7.9 ± 0.5)	7.4–9 (7.9 ± 0.4)	7.4–9 (7.9 ± 0.4)	7.4–9 (7.9 ± 0.5)	7.4–8.6 (7.9 ± 0.3)	7.4–9.2 (8.4 ± 0.5)	7.4–8.3 (7.9 ± 0.2)	7.4–8.0 (7.6 ± 0.2)
Conductivity (mS cm^{-1})	0.2–0.4 (0.3 ± 0.05)	0.3–0.5 (0.3 ± 0.05)	0.3–0.5 (0.3 ± 0.06)	0.2–0.5 (0.3 ± 0.06)	0.3–0.5 (0.3 ± 0.05)	0.3–0.5 (0.3 ± 0.05)	0.3–0.5 (0.4 ± 0.06)	0.2–0.4 (0.3 ± 0.02)	0.3–0.4 (0.3 ± 0.05)	0.3–0.3 (0.3 ± 0.01)
Dissolved oxygen (mg L^{-1})	7.8–11.8 (9.3 ± 1.0)	8.1–11.7 (9.5 ± 0.9)	8.0–11.9 (9.6 ± 0.8)	7.8–11.8 (9.4 ± 0.9)	7.8–11.9 (9.5 ± 1.0)	7.9–11.8 (9.5 ± 0.9)	7.8–9.0 (8.5 ± 0.4)	8.6–9.9 (9.0 ± 0.4)	8.8–10 (9.6 ± 0.3)	10–11 (10.7 ± 0.7)
Alkalinity (mg L^{-1})	48–84 (69 ± 8.2)	59–84 (70 ± 6.4)	59–101 (71 ± 8.8)	47–101 (68 ± 9)	58–84 (70 ± 7)	57–85 (70 ± 7)	68–101 (74 ± 6.1)	59–84 (72 ± 10.4)	57–70 (64 ± 3.5)	47–74 (68 ± 5.9)
Turbidity (NTU)	3–59 (17.7 ± 14.3)	6–52 (22 ± 14.3)	1–80 (25 ± 17.7)	1–80 (22 ± 16)	3–59 (20 ± 15)	4–55 (21 ± 15)	18–80 (37 ± 15)	5–55 (24 ± 12)	1–17 (8 ± 3.6)	3–41 (15 ± 9.6)
Total suspended solids (mg L^{-1})	4–28 (13 ± 5.9)	5–25 (13.2 ± 5.2)	1.5–27.5 (12.9 ± 6.1)	1.5–28 (13.3 ± 5.7)	3–25 (13.1 ± 5.4)	2–28 (12.7 ± 6.2)	2–27 (13.0 ± 5.2)	7.5–23 (12.9 ± 3.4)	1.5–25 (11.5 ± 6.6)	5–28 (14.8 ± 6.7)
Total phosphorus (µg L^{-1})	11.6–85.2 (30.2 ± 19.8)	15–80.5 (35.9 ± 16.8)	14–75 (42 ± 14.7)	13–82 (34 ± 17)	11.6–82 (35.7 ± 18.8)	15.6–37 (37 ± 17)	14.8–85 (49 ± 23)	17.0–53 (33 ± 9)	11.6–48 (25 ± 8.7)	12.8–80 (34 ± 17.3)
Soluble reactive phosphorus (µg L^{-1})	6.9–56.3 (19.3 ± 13.7)	1.5–52.1 (19.8 ± 11.4)	9.1–55.1 (27.8 ± 12.2)	1.5–56.3 (20.8 ± 13.3)	7.1–44 (20.4 ± 12.4)	7.4–54 (22.6 ± 13.6)	9.5–56 (32.1 ± 17.7)	6.9–38 (16.9 ± 8.4)	1.5–45 (17.9 ± 8.4)	8–37 (17.9 ± 8.5)
Total nitrogen (µg L^{-1})	110–561 (345 ± 131)	105–562 (349 ± 131)	86–905 (380 ± 182)	110–597 (360 ± 144)	105–721 (352 ± 151)	86–905 (361 ± 153)	86–617 (340 ± 162)	161–721 (370 ± 126)	110–543 (325 ± 134)	205–905 (394 ± 166)
Dissolved inorganic nitrogen (µg L^{-1})	98–550 (293 ± 125)	81–561 (297 ± 129)	95–524 (304 ± 135)	98–512 (304 ± 136)	81–550 (291 ± 131)	95–561 (300 ± 122)	81–524 (294 ± 145)	124–561 (311 ± 117)	95–512 (284 ± 117)	139–513 (302 ± 138)
Ammonium (µg L^{-1})	10–2000 (107 ± 268)	2.6–235 (58 ± 53)	8–277 (63 ± 53)	8–264 (62 ± 62)	2.6–2000 (94 ± 266)	10–301 (74 ± 66)	11–348 (109 ± 90)	9–159 (43 ± 31)	10–2000 (83 ± 319)	2–230 (75 ± 55)
Nitrate (µg L^{-1})	10–293 (96 ± 66)	10–325 (107 ± 72)	9–410 (105 ± 78)	10–410 (107 ± 79)	10–293 (96 ± 68)	9–299 (104 ± 68)	35–410 (125 ± 70)	10–325 (127 ± 95)	9–73 (40 ± 21)	14–192 (117 ± 33)
Soluble reactive silica (mg L^{-1})	1.5–4.1 (2.8 ± 0.6)	1.6–4.2 (2.9 ± 0.6)	1.3–4.2 (2.7 ± 0.7)	1.3–4.2 (2.7 ± 0.7)	1.5–4.1 (2.8 ± 0.6)	1.6–4.2 (2.8 ± 0.6)	2.4–4.2 (3.3 ± 0.7)	2.7–3.5 (3.0 ± 0.2)	1.7–3.3 (2.7 ± 0.3)	1.3–2.8 (2.1 ± 0.4)
Dissolved inorganic carbon (mg L^{-1})	9.4–26 (14.8 ± 4.1)	8.0–117 (16.1 ± 15.4)	9.6–24 (15.6 ± 3.8)	9.4–23 (14.5 ± 3.8)	9.4–24 (14.6 ± 3.8)	8.0–117 (16.5 ± 15.4)	8.9–23 (23.3 ± 16.7)	8.8–16 (12.9 ± 1.7)	9.4–15 (13.1 ± 1.3)	8.0–117 (17.1 ± 16.9)
Humic acids–350 nm	0.004–0.05 (0.01 ± 0.01)	0.004–0.03 (0.01 ± 0.01)	0.007–0.04 (0.02 ± 0.01)	0.006–0.05 (0.02 ± 0.01)	0.004–0.04 (0.01 ± 0.01)	0.005–0.05 (0.02 ± 0.01)	0.01–0.04 (0.02 ± 0.01)	0.0–0.03 (0.01 ± 0.01)	0.01–0.05 (0.01 ± 0.01)	0.01–0.05 (0.02 ± 0.01)

phyceae, and Zygnematophyceae). Cyanobacteria had larger relative biomass in the southern (89.8%), central (88.3%), and northern (90.0%) areas, on the left and right margins (91.4 and 88.9%, respectively), and in the pelagic zone (88.0%). By contrast, Euglenophyceae had the lowest values (<0.1%).

Although the largest biomass (23 mm³ L⁻¹) was observed in the center of the lake on the left bank in spring 2010 (Fig. 3a–c), the northern area of Lake Mangueira presented greater total biomass variation amplitudes (Fig. 3a). Similarly, the area on the left margin showed wide variation in biomass levels, followed by the pelagic zone (Fig. 3b). The mean biomass levels in spring and summer (8.8 and 8.0 mg L⁻¹, respectively) were higher than in other periods (Fig. 3d). Spatially, the ordination axes in the NMDS (final solution with 2 dimensions, stress for the 4 seasons' analyses between 0.07 and 0.12) indicated that sampling sites were homogeneous for biomass of phytoplankton species (Fig. 4a–d) in each season separately because no spatial organization was observed. A slight separation of northern sampling sites was apparent only in winter (Fig. 4d).

The richness and diversity of species showed no clear spatial pattern (Fig. 5 and 6). The highest species richness was seen in the central area of Lake Mangueira at the left margin (41 species; Fig. 5a–c), and the highest diversity (2.6 bits mm⁻³) was found in the central pelagic zone (Fig. 6a–c). Temporally, the highest mean values of richness and diversity were observed in the summer for most sampling sites (24 species, 1.8 bits mm⁻³, respectively; Fig. 5d and 6d).

We identified 16 indicator species (Table 2) with no clear spatial or seasonal preference at any sampling site (Fig. 4). Most were Cyanobacteria; *Chroococcus limneticus* and *Aphanocapsa conferta* primarily contributed to the total biomass at each sampling site in each sampling period.

The integrated analysis between the abiotic variables and the biomass of the descriptor species conducted using an RDA indicated a strong correlation between the matrices for axis 1 ($r = 0.837$) and axis 2 ($r = 0.846$). The Monte Carlo test indicated that the ordinations of axes 1 and 2 were statistically significant ($p < 0.01$) and did not occur randomly (Fig. 7).

The most important variables for the ordination of axis 1 were alkalinity ($r = -0.63$), turbidity ($r = -0.59$), and NO_3^--N ($r = -0.54$), whereas precipitation ($r = 0.66$) and TP ($r = -0.46$) were the most important variables for axis 2. The formation of a guild associated with higher NO_3^--N concentrations and high temperature and turbidity was observed in summer, composed of *Aphanothece stagnina*, *Chroococcus dispersus*, *Chroococcus giganteus*, *Chroococcus limneticus*, *Coelomoron* sp., *Gomphosphaeria aponina*, *Planktolyngbya contorta*, Sy*nechocystis aquatilis*, *Oocystis lacustris*, and *Scenedesmus obtusus*. *Aphanocapsa conferta* and *Aphanothece smithii* were associated with higher levels of SRP. *Fragilaria acus*, *Aphanothece* sp., and *Chroococcus planctonicus* were associated with higher precipitation in autumn. *Tetraedron minimum* was influenced by the highest values of dissolved inorganic nitrogen in the sampling units located on the left margin, especially in the northern part of the lake. Generally, the integrated ordination of the abiotic and biological variables showed a strong temporal organization of the phytoplankton.
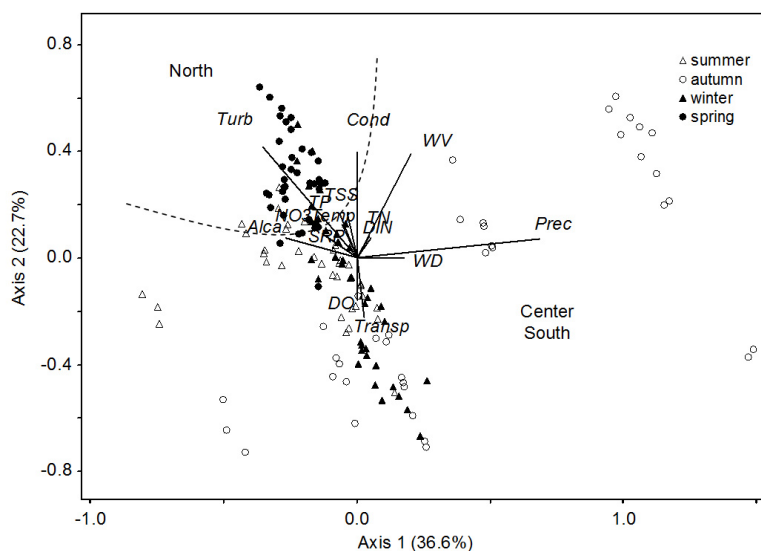

Fig. 2. PCA ordination (axes 1 and 2) of the sample units for the abiotic variables in Lake Mangueira. Legend: Turb = conductivity, Cond = conductivity, TSS = dissolved suspended solids, TP = total phosphorus, Temp = temperature, NO_3 = nitrate-N, TN = total nitrogen, SRP = soluble reactive phosphorus, DIN = dissolved inorganic nitrogen, Alca = alkalinity, Transp = transparency, DO = dissolved oxygen, Prec = precipitation, WD = wind direction, WV = wind speed.
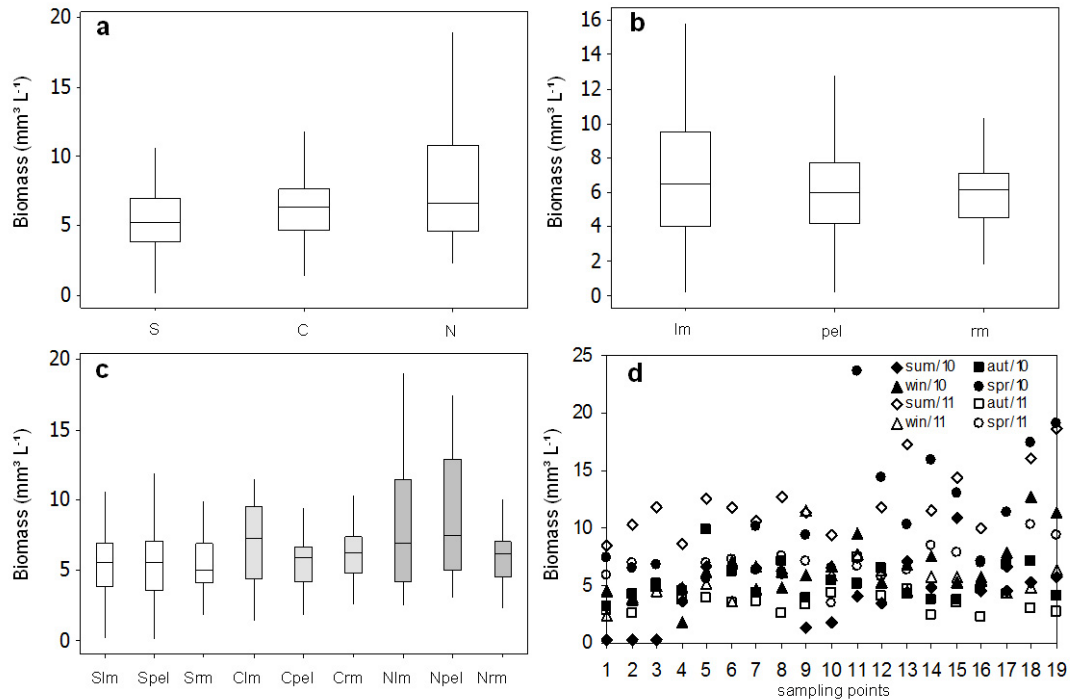
Fig. 3. Biomass (mm³ L⁻¹) along the (a–c) spatial and (d) temporal gradients of Lake Mangueira. Legend: Slm = south left margin ($n = 16$), Spel = south pelagic zone ($n = 24$), Srm = southern right margin ($n = 16$), Clm = center left margin ($n = 16$) Cpel = center pelagic zone ($n = 16$), Crm = center right margin ($n = 16$), Nlm = north left margin ($n = 16$), Npel = north pelagic zone ($n = 16$), Nrm = north right margin ($n = 16$); see Table 1 for other abbreviations.
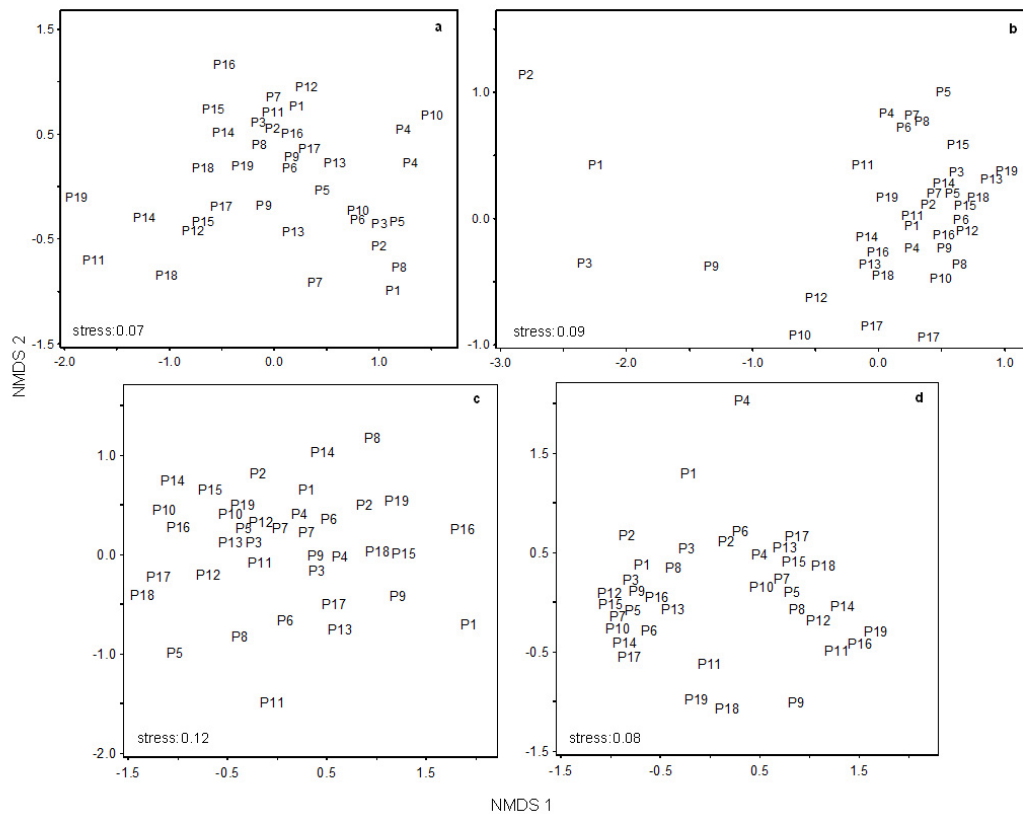

Fig. 4. NMDS ordination biplots of biomass of phytoplankton descriptor species, in (a) spring, (b) summer, (c) autumn, and (d) winter, at 19 sampling sites (P1–P19) along Lake Mangueira in 2010 and 2011.
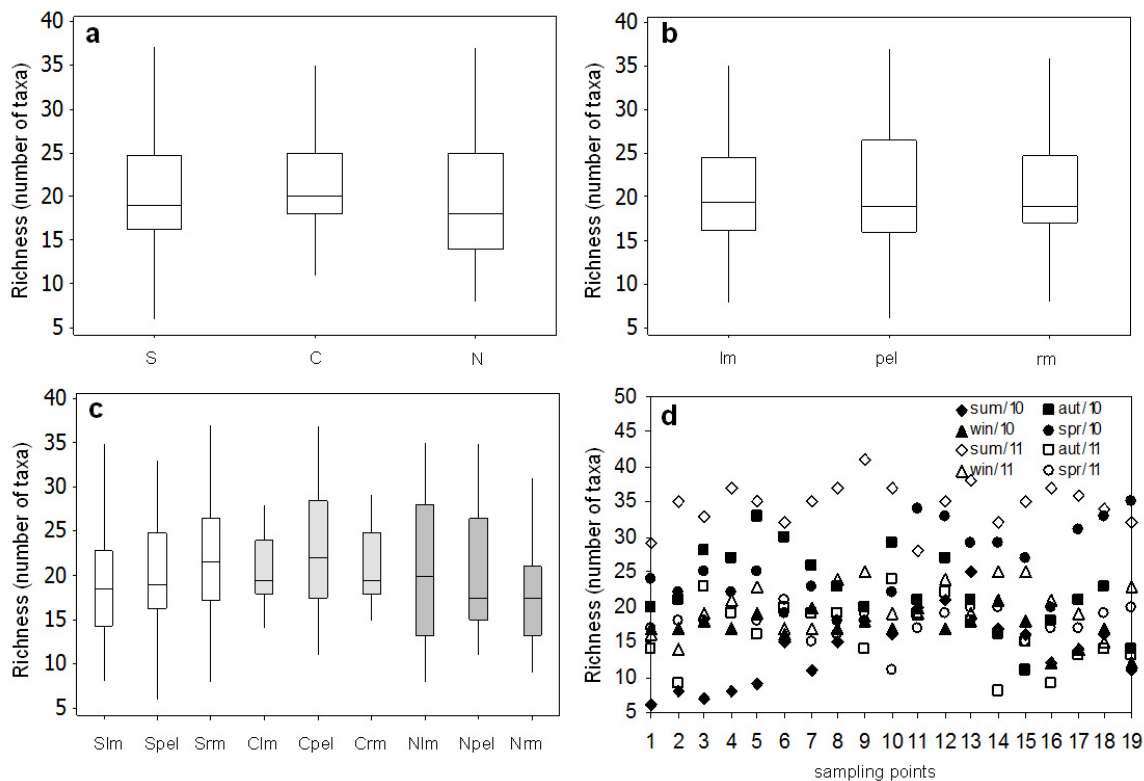
Fig. 5. Richness (number of taxa) along the (a–c) spatial and (d) temporal gradients of Lake Mangueira. Legend: see Fig. 3.
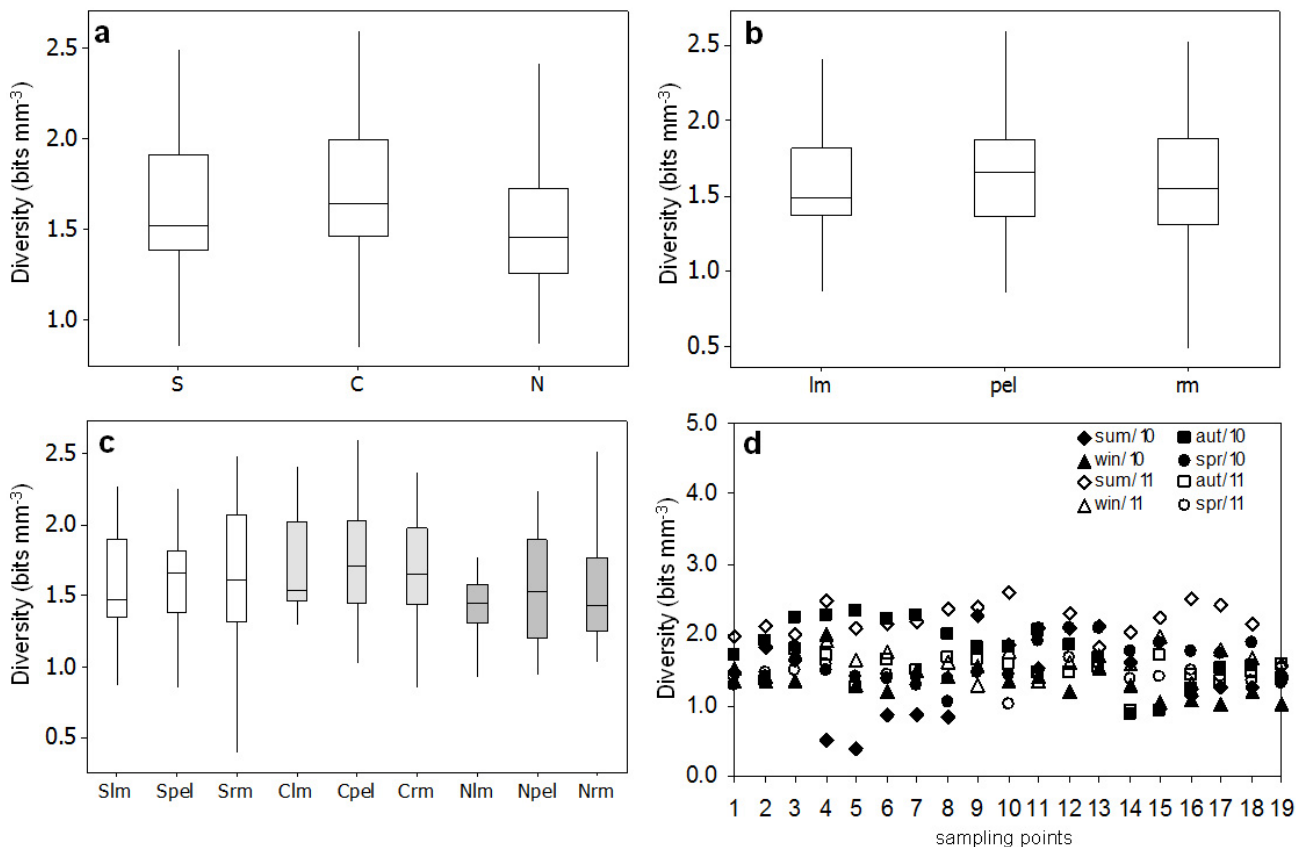

Fig. 6. Diversity (bits mm^{-3}) along the (a–c) spatial and (d) temporal gradients of Lake Mangueira. Legend: see Fig. 3.

Table 2. Relative biomass (%) of the indicator species in Lake Mangueira. Legend: See Table 1.

Abbrev.	Descriptors species	S	C	N	LM	PEL	RM	SPR	SUM	AUT	WIN
Acon	*Aphanocapsa conferta* (W.West & G.S.West) Komárková-Legnerová & Cronberg	28.4	30.9	36.3	38.4	28.9	28.8	35.4	40.0	14.5	30.1
Asmi	*Aphanothece smithii* Komárková-Legnerová & G.Cronberg	7.0	6.9	8.2	7.5	7.5	7.3	8.3	6.2	6.1	8.9
Apsp	*Aphanothece* sp.	0.5	0.3	0.4	0.3	0.3	0.6	0.0	0.1	2.4	0.0
Asta	*Aphanothece stagnina* (Sprengel) A.Braun	0.5	0.6	0.5	0.5	0.5	0.5	0.1	1.2	0.7	0.1
Cdis	*Chroococcus dispersus* (Keissler) Lemmermann	1.3	2.4	1.6	2.1	1.5	1.8	1.7	2.8	1.1	1.0
Cgig	*Chroococcus giganteus* West	0.6	0.6	1.0	0.6	0.8	0.8	0.8	1.4	0.2	0.1
Clim	*Chroococcus limneticus* Lemmermann	41.1	35.7	34.4	33.3	38.8	38.7	38.5	21.4	51.4	44.4
Cpla	*Chroococcus planctonicus* Bethge	1.6	1.4	0.2	0.9	1.1	1.1	0.7	0.2	3.1	1.2
Cosp	*Coelomeron* sp	0.5	0.5	0.4	0.3	0.5	0.6	0.0	1.2	0.2	0.2
Gapo	*Gomphosphaeria aponina* Kützing	0.6	0.9	1.7	0.9	1.0	1.3	0.6	2.9	0.2	0.1
Olac	*Oocystis lacustris* Chodat	0.7	2.2	2.6	1.7	2.1	1.7	1.8	4.2	0.1	0.1
Pcon	*Planktolyngbya contorta* (Lemmermann) Anagnostidis & Komárek	1.3	1.6	0.9	1.0	1.4	1.3	1.3	1.5	0.9	0.9
Sobt	*Scenedesmus obtusus* Meyen	1.2	2.0	0.9	0.6	2.1	1.3	0.9	3.4	0.3	0.2
Saqu	Synechocystis aquatilis Sauvageau	3.5	3.5	3.3	3.3	3.5	3.6	2.2	3.0	5.1	4.6
Facu	*Fragilaria acus* (Kützing) Lange-Bertalot	1.0	0.3	0.5	0.5	0.7	0.5	0.3	0.1	2.4	0.2
Tmin	*Tetraedron minimum* (A.Braun) Hansgirg	2.9	2.6	2.5	2.5	2.6	2.9	1.9	1.7	4.1	4.0
	Total contribution (%)	92.6	92.5	95.4	94.4	93.5	92.7	94.4	91.1	92.8	96.2

Fig. 7. RDA ordination (axes 1 and 2) of the descriptor species according to abiotic variables in Lake Mangueira. Legends: see Fig. 3 and Table 2.

Discussion

Our results demonstrated that the structure of the phytoplankton community in Lake Mangueira was explained more by the seasonal variations than the sampled spatial amplitude. Both the habitat heterogeneity and the presence of disturbances can profoundly influence ecological systems through the many ecological and biological levels of organization (Brown 2007). Aquatic ecosystems are subject to spatial and temporal variability that result in a high degree of uncertainty in relation to phytoplankton assemblies (Calijuri et al. 2002). Because the degree of temporal variability tends to determine the physical and chemical characteristics of the habitat (Bengtsson et al. 1997), highly dynamic and heterogeneous ecosystems, such as shallow lakes, can offer different conditions and resources in time and space for different phytoplankton species.

Many processes can explain the higher environmental dissimilarity of the communities over time as a result of extinction and colonization events or the different responses of populations to environmental fluctuations (Schneck et al. 2011). By contrast, many studies have found repeated seasonal patterns of phytoplankton, especially conditioned by temperature and variations of abiotic parameters (e.g., Komárková and Tavera 2003, Becker et al. 2009). The abiotic scenario, however, is
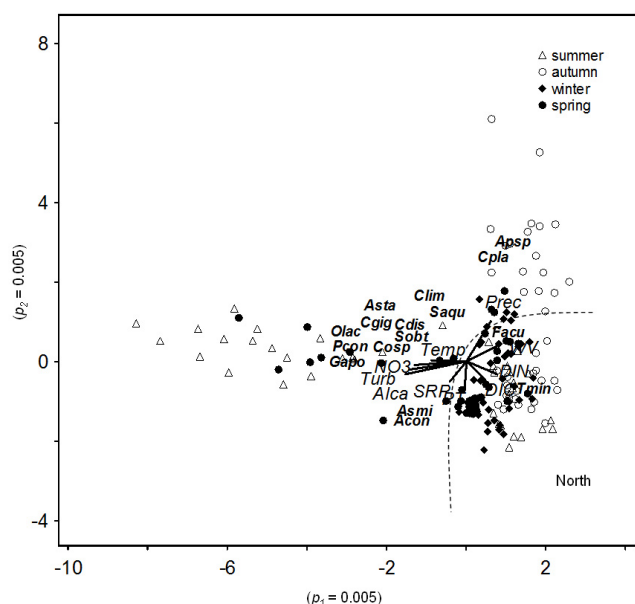
especially susceptible to constant change through recruitment of species from the local pool in shallow coastal aquatic systems strongly influenced by wind, as in the case of Lake Mangueira. This susceptibility would explain the observed strong temporality in the phytoplankton organization patterns. The importance of wind in the dynamics of shallow aquatic ecosystems (Carrick et al. 1993) is well documented, highlighting its importance for plankton communities in such environments. According to Reynolds (1994), the level of turbulence is less important in the organization of different algal compositions in intensively mixed kinetic systems than the spatial extent or temporal permanence.

Shallow lakes are typically known for their numerous interfaces, especially in littoral zones configured into more physically and chemically variable areas (Howard-Williams and Lenton 1975), not only because they are generally inhabited by aquatic macrophytes that modify the environment (Lampert and Sommer 1997, They Hg et al. 2013), but because these areas have the most contact with neighboring systems and can also be influenced by external factors (Crossetti et al. 2013). Shading or competition for nutrients by macrophytes may inhibit phytoplankton growth (Crossetti and Bicudo 2008, Fonseca and Bicudo 2010), which in shallow lakes tends to establish a clear pattern of heterogeneous horizontal distribution of phytoplankton (Reynolds 1984). The present study found no spatial differences in the structural attributes of the phytoplankton in the pelagic and littoral zones. The hydrodynamics of Lake Mangueira may explain many of the similarities in the pelagic and littoral zones and the north–south gradients.

In Lake Mangueira, wind-driven hydrodynamics create zones with particular water dynamics (Fragoso et al. 2008). The velocity and direction of currents and water levels change quickly. Because of its length (~90 km) and width (~12 km), Lake Mangueira is particularly prone to wind-caused seiches, which function as a conveyor belt for vertical mixing and some horizontal transport (Cardoso et al. 2012). This process might influence the spatial tendency to higher biomass levels in the northern area of the ecosystem observed here, associated with the higher values of dissolved nutrients. Light limitation necessary for phytoplankton productivity has also been found in the north; however, the largest concentrations of NO_3-N and turbidity, as shown by the statistical analysis, were primarily associated with the indicator species capable of strategically overcoming the reduced availability of light and utilizing the larger concentration of dissolved nutrients, as observed for *Tetraedron minimum* and *Fragilaria acus*.

Cardoso et al. (2012) demonstrated that wind-induced currents are the dominant factor controlling the transport of substances and phytoplankton in Lake Mangueira, producing advective movement of surface water masses. Using ecological modeling, they demonstrated the significant transport of phytoplankton and nutrients from the littoral to the pelagic zones through hydrodynamic processes from shallow to deeper areas (Cardoso et al. 2012). This finding may explain the similarities between the littoral and pelagic zones observed here, evidenced by the lack of differences in species richness, diversity, and composition. Other studies have attributed the lack of significant differences in chemical parameters and phytoplankton biovolume to the uniform conditions throughout the basin, caused by large horizontal water movements (Leoni et al. 2014).

Historically, since the biogeographical approach of ecosystems dynamics, size is said to matter for biological community structure (McArthur and Wilson 1967). The horizontal distribution of communities in lakes might be closely related to the ecosystem size because it directly or indirectly influences limnological processes (Scheffer and Van Ness 2007). This relationship has been demonstrated by some studies (e.g., Guildford et al. 1994, Post et al. 2000, Borics et al. 2011), suggesting that size may also matter for phytoplankton horizontal distribution. Recently, Borics et al. (2016) demonstrated that functional properties of phytoplankton are shaped by the lake size, showing that taxa with no active locomotion ability and high sinking rates were more likely to occur in large waterbodies associated with the suitable habitat provided by well-mixed water columns. The larger the lake, the greater the fetch and the likelihood of a more-homogeneous distribution of phytoplankton. Homogeneous horizontal distribution of phytoplankton was also found by Padisák and Dokulil (1994) in the open-water area of a large shallow lake (Neusiedlersee, Austria/Hungary).

In short, the spatial heterogeneity analyzed from the various sampling points along the length of Lake Mangueira, including the pelagic and littoral zones, did not affect the biomass, richness, diversity, or biomass of the descriptor species. These phytoplankton attributes were all higher in the northern area, however, related especially to the greater availability of dissolved nutrients, a result explained by the strong contribution from the adjacent wetland (Fragoso et al. 2008). The high degree of temporal variability resulting from the local hydrodynamics is reflected in the seasonal patterns, where their effects on abiotic water patterns were the main drivers of the phytoplankton community in Lake Mangueira.

Acknowledgements

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