

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE BIOCÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

**SPATIAL AND TEMPORAL VARIABILITY OF ZOOPLANKTON-
PHYTOPLANKTON INTERACTIONS IN A LARGE SUBTROPICAL
SHALLOW LAKE DOMINATED BY NON-TOXIC CYANOBACTERIA**

LUANA MORAIS DA ROSA

PORTO ALEGRE

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NON-TOXIC CYANOBACTERIA**

Dissertação apresentada ao Programa de Pós-Graduação em Botânica do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Botânica.

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PORTO ALEGRE

2015

AGRADECIMENTOS

Gostaria de fazer um agradecimento especial à minha orientadora Luciana de Souza Cardoso, pelo imensurável apoio e aprendizagem, além da preciosa parceria e amizade durante este tempo todo que compartilhamos; não só pelo aprendizado profissional que me possibilitou grande crescimento, mas pelo imenso carinho e desenvolvimento pessoal que esta relação acrescentou em minha vida.

À minha família, por sempre apoiar minhas decisões e entender todas as dificuldades. Por tornar essa jornada muito mais fácil e agradável. Sem vocês seria muito mais difícil chegar até aqui.

Ao meu namorado Rafael por todo apoio técnico, emocional e companheirismo.

Aos grandes amigos e colegas de jornada que desde muito tempo fazem parte da minha trajetória de crescimento, sempre compartilhando os momentos de satisfatória descontração e alegria, além das grandes lições de vida que aprendo com eles.

Ao Programa de Pós-Graduação em Botânica, por todo auxílio e pelo imenso aprendizado que carrego comigo.

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pelo auxílio financeiro.

À equipe do Instituto de Pesquisas Hidráulicas pelo apoio técnico e pela oportunidade de desenvolver este trabalho.

INTRODUÇÃO GERAL

Há muitas razões para valorizar e preservar a diversidade dos sistemas de água doce, variando desde questões éticas a econômicas (Moss, 2000). Num panorama global, as pesquisas em ecossistemas lacustres tradicionalmente estiveram direcionadas a lagos profundos, mas estudos recentes têm considerado a importância das inúmeras funções, valores e contribuições ecológicas de lagos rasos e áreas úmidas para as espécies aquáticas e semi-aquáticas (Cardoso et al., 2012; Crossetti et al., 2013). Lagos rasos variam consideravelmente em riqueza de espécies, e a nível regional, podem contribuir mais para a diversidade biológica do que outros ecossistemas de água doce, como rios e lagoas temporárias (Williams et al., 2003).

Devido a sua pouca profundidade, os lagos rasos tendem a ser amplamente colonizados por macrófitas aquáticas, que desempenham um papel fundamental na sua estruturação. As macrófitas aquáticas podem reduzir as forças hidrodinâmicas, conseqüentemente diminuindo a ressuspensão de partículas e nutrientes; podem oferecer microhabitats espacialmente complexos, servindo de refúgio a diversas comunidades; e reduzir a concentração de nutrientes disponíveis na massa de água (Scheffer et al., 1993; Rodrigues, 2009; Kruk et al., 2009). A ressuspensão de sedimentos e sua interação na coluna d'água, juntamente com o papel da vegetação aquática nesses procedimentos fazem o funcionamento de lagos rasos ser muito diferente dos lagos profundos (Scheffer, 2005).

Grandes lagos rasos apresentam desafios particulares tanto para gestores que visam proteger e manter seus recursos, quanto para cientistas limnólogos que buscam compreender sua dinâmica (James et al., 2009). Esses desafios decorrem em grande parte da dinâmica imprevisível das propriedades do ecossistema impulsionado por eventos estocásticos como vendavais, que causam ressuspensão dos sedimentos, e inundações e secas, que alteram substancialmente o volume de água do lago (Havens et al., 2007). A variabilidade física e química de lagos rasos costeiros é amplamente dependente da hidrodinâmica e dos impactos antrópicos, tal como são suas comunidades (Scheffer, 2005). Esses ecossistemas proporcionam condições adequadas para o desenvolvimento da heterogeneidade espacial, podendo causar distribuição irregular de suas comunidades biológicas, especialmente considerando as características hidrodinâmicas que podem ter uma forte influência do regime de ventos (Carrick et al., 1993; Cardoso & Motta Marques, 2009).

A planície costeira do extremo sul do Brasil é formada por um grande número de lagoas rasas que se originaram no quaternário, como conseqüência de regressões e transgressões marinhas. Há uma grande variedade no tamanho e extensão de macrófitas aquáticas nessas lagoas costeiras, mas todas têm em comum a forte ação dos ventos atuantes na região. As numerosas lagoas juntas

correspondem a 63 % da área total da planície costeira, e normalmente apresentam sistemas de banhados associados (Schwarzbold & Schäfer, 1984; Haig-They et al., 2014).

O sistema hidrológico do Taim é um ecossistema de áreas úmidas interligadas por lagoas de grande extensão no sul do Brasil, circundado por uma grande variedade de habitats como praias, dunas, florestas, campos, lagos e banhados. Ecossistemas de banhados são considerados ambientes de alta produtividade biológica. Além de fornecer áreas disponíveis para a colonização e crescimento de macrófitas, as taxas de produção primária estão entre as mais elevadas já registradas para qualquer ecossistema (Bertilsson & Jones, 2003). Excepcional diversidade biológica motivou as autoridades federais brasileiras a considerar parte deste sistema hidrológico como a Estação Ecológica do Taim (ESEC-Taim) a partir de 1978 (Motta Marques et al., 2002). Tal status de conservação tem sido crucial para proteger o ecossistema dos impactos antrópicos que têm aumentado no seu entorno, como o desvio de água para irrigação de arroz e atividades de pesca (Garcia et al., 2006).

O cultivo de arroz é a mais importante atividade econômica da região. A manutenção da alta produtividade já verificada exige uma lâmina permanente de água sobre o plantio por um período de aproximadamente 90 dias. Esse método de irrigação por inundação contínua tem uma demanda elevada de água, a qual é fornecida por levantes hidráulicos que bombeiam água das Lagoas Mangueira, Caiubá, Flores e Mirim, para um sistema de canais de distribuição (Motta Marques et al., 2002). Após o período de irrigação, parte da água é devolvida para as lagoas enriquecida com nutrientes e matéria orgânica (Motta Marques et al., 1997), gerando um potencial aumento de trofia do sistema, capaz de promover alterações nas comunidades aquáticas em curto prazo (Lima, 2011). Diante de tais circunstâncias, é extremamente importante desenvolver dados de base envolvendo os atributos das comunidades aquáticas para uma eficaz conservação e gestão nesta unidade de conservação.

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A dissertação é apresentada na forma de manuscrito a ser submetido para a revista científica *Journal of Plankton Research*. A formatação segue as normas da revista, disponibilizadas ao final deste trabalho.

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Spatial and temporal variability of zooplankton-phytoplankton interactions in a large subtropical shallow lake dominated by non-toxic cyanobacteria

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To evaluate the size-specific and composition relationships between zooplankton and phytoplankton in a large, subtropical lake, as well as the influence of environmental variability on temporal and spatial scales, we conducted seasonal sampling for two years, covering three areas (south, center and north) and the pelagic and littoral zones in Mangueira Lake (southern Brazil). The zooplankton to phytoplankton biomass ratio was usually very low, indicating a weak control on phytoplankton. However, the strength of this interaction varied with the zooplankton composition and temporal/spatial variability of the environmental factors. Environmental, bottom-up and probably top-down forces involved the structure of zooplankton, while phytoplankton was mainly controlled by nutrients. The phytoplankton predominant biomass consisted of colonial forms of non-toxic cyanobacteria. Rotifers (90-150 μm) were more able to benefit from phytoplankton production, while large-bodied zooplankton, when present in higher biomass, were not related to phytoplankton. High contribution of small ciliates and significant positive correlations between zooplankton and total phosphorus presuppose that microbial food webs primarily sustain the macro-zooplankton production in this system. The environmental variability induced by wind action and/or diversification of niches also played a substantial role in the structure of the plankton community, and the strength of zooplankton-phytoplankton interactions.

KEYWORDS: MLD maximum linear dimension; BZ:BP ratio; micro-zooplankton; top-down; inter-annual variation

INTRODUCTION

Zooplankton and phytoplankton are the first linkage in aquatic food webs. Selective grazing by zooplankton is an important factor affecting the structure of phytoplankton communities, whereas phytoplankton structure can also influence the taxonomic composition and dominance of the zooplankton (Goldyn and Madura, 2008). The effect of grazing by zooplankton on phytoplankton is related to their body size as well as their taxonomic composition (Cyr and Curtis, 1999). The maximum size of edible particles is generally considered to depend on the grazer body size (Burns, 1968), but many factors other than algal size affect food selectivity by zooplankton, such as shape, taste, motility, nutrient content, surface characteristics and toxicity (Butler et al., 1989; DeMott, 1990). Furthermore, the algae size range of zooplankton grazing is still controversial. Brooks and Dodson (1965) proposed that all planktonic herbivores utilize small organic particles (1-15 μm), while Cyr and Curtis (1999) suggested that the size of grazed algae is not constant, (ranging between 16-78 μm in different communities) and varies with the size distribution and taxonomic composition of the zooplankton community.

Intense effectiveness in control and reduction of phytoplankton biomass is widely associated with the presence of large-bodied zooplankton (Brooks and Dodson, 1965). In temperate lakes, the key role of large zooplankton such as *Daphnia* as consumers of phytoplankton is well-established (Crisman and Beaver, 1990), whereas in subtropical lakes the probability of successful control of phytoplankton by zooplankton is predicted to be very low (Havens et al., 2011). However, generally only cladocerans and copepods are considered in zooplankton grazing estimations, while the impact of rotifers and protozoans is usually neglected (Agasild et al., 2007). Grazing has also been much less studied in subtropical communities, and most studies focused on the effects of fish predation (Meerhoff et al., 2007; Lacerot et al., 2013).

The plankton community is a dynamic system, whose understanding requires a combination of biotic and abiotic descriptive factors in order to reach more realistic and consistent predictions about its ecology (Pinel-Alloul et al., 1999). The environmental processes controlling the plankton community structure in freshwater ecosystems are more complex than a duality between bottom-up and top-down forces (Masson et al., 2004). For example, seasonality is one of the important basic factors structuring the dynamics of plankton communities in lakes (Sommer et al., 1986), as well as their spatial heterogeneity as consequence of both physical and behavioral processes (Pinel-Alloul et al., 1988).

The “multiple driving forces hypothesis” (Pinel-Alloul, 1995) predicts that on large spatial scales, physical processes (wind, wind-induced currents, water temperature) are thought to have

strong control over the spatial distribution of the organisms, but on smaller scales the strength of biological drivers, such as predation, competition, size of organisms and food resources increases. Such complexities are particularly strong in shallow lakes. These ecosystems provide suitable conditions for the development of spatial heterogeneity, promoting irregular distribution of planktonic organisms, especially considering the hydrodynamic characteristics that may be driven by wind (Carrick et al., 1993). Recent studies have considered other factors, more than fish predation, to explain spatial and seasonal patterns influencing grazing effects of zooplankton (Blukacz et al., 2009, 2010; Chang et al., 2014). This approach considers the role of physical and chemical factors, food availability, size, and distribution of organisms to understand the temporal and/or spatial variations driving predator-prey interactions.

Taking into account that many natural zooplankton communities graze on a broader range of algal sizes than has been assumed (Cyr and Curtis, 1999), this study was undertaken in the belief that zooplankton-phytoplankton relationships are size-specific (Brooks and Dodson, 1965), and influenced by several environmental mechanisms promoting variability in space and time. Thus, the main objectives of the present study were: i) to evaluate the size-specific and composition interactions between zooplankton and phytoplankton in a large subtropical lake and ii) understand the influence of environmental variability involving shallow lakes and the strength of physical and chemical factors in structuring their planktonic communities on temporal and spatial scales.

METHOD

Study Area

Mangueira Lake (32°20' and 33°00'S and 52°20' and 52° 45'W) is a large shallow coastal lake 90 km long and 3-10 km wide, located in the Taim Hydrological System (THS, 2254 km²) in southern Brazil (Crossetti et al., 2013). The system area contains the Taim Ecological Station (ESEC-Taim), created to protect the exceptional biological diversity contained in a variety of habitats including dunes, forests, grasslands, and two wetlands (Motta-Marques et al., 2002; Cardoso et al., 2012). The region is associated with a subtropical climate (Kottek et al., 2006) and is subject to strong winds. The lake covers an area of 820 km² with a mean depth of 2.6 m and a maximum depth of 6 m (Cardoso et al., 2012). The main axis is oriented northeast-southwest, aligned with the prevailing winds. The trophic state ranges from oligo- to mesotrophic. The mesotrophic conditions occur during the spring and summer when there is a remarkable withdrawal of water, as well as a high load input of nutrients from the watershed due to the irrigation of rice

fields (Fragoso Jr et al., 2008). The lake is influenced by a wetland at the north end, and by a dense macrophyte bank at the south end (Crossetti et al., 2014). Along the coastline of the lake, there are large tracts of emerging and submerged communities of aquatic plants, including approximately 128 species of macrophytes (Motta Marques et al., 2002).

Sampling, Abiotic and Biological Variables

Samples of sub-surface water were collected for two years on a seasonal scale: summer (March), autumn (May), winter (August) and spring (November) of 2010 and 2011. Nine points were selected covering the three areas (south, center and north) and two zones (pelagic and littoral zones) in each season during the study period (Fig. 1). Meteorological data (wind direction and velocity, precipitation, nebulosity, insolation and evaporation) were collected three times per day (12am, 12pm and 6pm) and provided by the Santa Vitória do Palmar Meteorological Station (INMET-RS), located approximately 23 km from the lake. The data were interpolated according to time spent in each sampling point. Samples were analyzed for limnological variables (dissolved oxygen - DO, water temperature, conductivity and pH) with a multi-parameter probe (Yellow Spring YSI model 6920), total suspended solids - TSS (APHA, 1999), turbidity (turbidimeter), and Secchi transparency (Preisendorfer, 1986). Nutrients such as soluble reactive phosphorus (PO_4), total phosphorus (TP), nitrate (NO_3), and total nitrogen (TN) were analyzed according to Mackeret et al. (1989). Chlorophyll *a* (Chl-*a*) was extracted from GF/F filters into 90% ethanol (Jespersen and Christoffersen, 1987) and measured in a spectrophotometer (CETESB, 1990).

Zooplankton samples were taken with a suction pump, where 100 L were filtered through a 25 μm mesh nylon net, concentrated to 250 mL and fixed with 4% formaldehyde solution (Wetzel and Likens, 2000). Quantitative analysis was performed using a Sedgewick-Rafter chamber (APHA, 1999) with a minimum 80% efficiency (Papas and Stoermer, 1996). Zooplankton biomass was estimated from biovolume using geometric formulas for the specific forms or length-weight regression (Dumont et al., 1975; Bottrell et al., 1976; Ruttner-Kolisko, 1977; Malley et al., 1989). The structure of the community was defined in terms of biomass of taxonomic groups and size classes. All taxa were grouped according to the maximum body length and divided in five size categories: class I (<60 μm), class II (60-90 μm), class III (90-150 μm), class IV (150-300 μm) and class V (>300 μm). The smallest ciliates and tecamoebae composed class I, while the biggest ciliates and tecamoebae together with small rotifers composed class II. Class III was formed only by rotifers of the predominant size range, and class IV grouped larger rotifers with cladocerans and

nauplii. Class V consisted of only copepodits, the largest body length and scarcer organisms in the lake.

Phytoplankton samples were collected with a Van Dorn bottle and quantitatively estimated according to Utermöhl (1958); sedimentation time followed Lund et al. (1958). Biomass (mg.L^{-1}) was estimated through biovolume in accordance with Hillebrand et al. (1999). The structure of the community was analyzed through the approach of functional attributes related to size structure and life forms. Size was classified using the maximum axial linear dimension values (MLD) in four defined categories: MLD I ($<10 \mu\text{m}$), MLD II ($11\text{-}20 \mu\text{m}$), MLD III ($21\text{-}50 \mu\text{m}$) and MLD IV ($>50 \mu\text{m}$). Life forms were divided in unicellular flagellates (UF), colonial flagellates (CF), unicellular non-flagellated (UNF), colonial non-flagellated (including coenobia; CNF), and filaments (Fi).

Data Analysis

Descriptive analysis and variance analysis (ANOVA Two-way) of data was performed using the Statistica® software version 7, searching for significant variations between the space (three areas or two zones) and time (seasonality). Principal Components Analysis (PCA) was run using the analysis of variance and covariance. ANOVA and PCA analysis were processed with the transformed abiotic data matrix $[\log (x + 1)]$. Correlation analysis was conducted between zooplankton and phytoplankton categories searching for possible grazing interactions, and between plankton community and environmental variables in order to identify and select the descriptors of temporal and/or spatial patterns. The analysis was performed with the data matrix covering the entire year's variables (annual correlation), and then separately with the data matrix covering the variables of each season (seasonal correlations). Redundancy Analysis (RDA) was used to identify the abiotic variables that drove the spatial and/or seasonal pattern of the plankton community in Mangureira Lake in each year. The multivariate analyses were performed using the software PCORD version 6.08 (McCune and Mefford, 2011).

RESULTS

Environmental Data

The meteorological data were analyzed for the week preceding the sampling date in every season using three daily measurements (Fig. 2). Wind direction (WD) changed constantly in the two years studied, especially in summer and spring 2011. The predominant WDs were SE, S and SW.

Wind velocity (WV) had the highest means and values in autumn 2010 and winter 2011, reaching maximum values between 9 and 10 m.s⁻¹, followed by both summers. However, on the sampling days, high WV was recorded in the autumn 2010 (9 m.s⁻¹) and spring 2011 (8 m.s⁻¹; Supplementary data, Table I). Nebulosity was more homogeneous in 2011 than 2010. Regarding precipitation, 2011 was a rainy year, although on sampling days, precipitation was only recorded in autumn 2010 and less so in winter 2011, but both summers were rainy. Insolation and evaporation were always higher in spring and summer, following the typical seasonal cycle.

Mangueira Lake is deeper in the central pelagic zone. In both years studied, conductivity, water temperature, redox potential (ORP), pH and DO varied seasonally. Temperature and ORP were higher in the warm seasons, while DO and Secchi transparency increased in the cold seasons. TSS, turbidity and nutrients had highest mean values in 2011, but in both years these variables and Chl-*a* characterized the north area, where the lake is physically associated with Taim Wetland. Secchi transparency, forms of nitrogen and turbidity showed both spatial and seasonal variation. Spatially, greater transparency characterized the south, contrasting with higher turbidity in the north. Conditions of higher turbulence coinciding with high WV were observed in winter and spring 2011. This last season showed the highest values of nutrients that caused a decrease in transparency (Supplementary data, Table I and II).

The environmental spatial heterogeneity was noted in both years. The Principal Components Analysis (PCA) explained 70.7 % of the 11 environmental data variability on axes 1 and 2 in 2010 ($p < 0.001$), affecting the ordination of samples in space and time (Fig. 3). The first axis revealed strong seasonality, where insolation ($r = -0.9$) and evaporation ($r = -0.61$) were the variables more strongly correlated to summer, while WV ($r = 0.97$), nebulosity ($r = 0.86$), precipitation ($r = 0.83$) and conductivity ($r = 0.64$) were to autumn. The second axis clearly demonstrated the expected spatial heterogeneity, where TP ($r = 0.70$), turbidity ($r = 0.62$), TSS ($r = 0.63$) and Chl-*a* ($r = 0.60$) exhibited a decreasing gradient N→S, while the Secchi transparency ($r = -0.55$) drove a gradient in the opposite direction, showing the typical spatial particularities in the lake. The center was a transition area between the two extremes of the lake.

In 2011, the PCA selected 12 abiotic variables as responsible for ordinate the sampling units, with 72.7% of explicability on axis 1 and 2 ($p < 0.04$; Fig. 3). The variables most strongly correlated with axis 1 were WD ($r = 0.9$) and WV ($r = 0.68$), while pH ($r = -0.85$), DO ($r = -0.64$), and Secchi transparency ($r = -0.63$) were responsible for separating the summer and autumn sampling points on axis 2, except the center point which worked as an outlier. Probably it was related to windlessness registered during the sampling day at these center points (summer and autumn). On the other hand, conductivity ($r = -0.78$), insolation ($r = 0.75$), ORP ($r = 0.73$), TP ($r =$

0.63), TN ($r = 0.6$), PO₄ ($r = 0.53$), and TSS ($r = 0.47$) were correlated to spring and winter on axis 2. Winter and spring were grouped in the same quadrant due to an increase in WV, creating a condition of incremental increase of nutrients and TSS, and low Secchi transparency in these seasons, opposite to the autumn and summer. Although each sampling area was plotted together into the same season, the seasonality was the main driver of the sampling units in 2011.

Plankton Community

The zooplankton community was similar between the two years, represented by 52 taxa (22 protists, 25 rotifers, 3 cladocerans and 2 stages of copepods) in 2010, and 59 taxa (27 protists, 28 rotifers, 2 cladocerans and the same 2 stages of copepods) in 2011. When we refer to copepods, we mean mainly the larval stage nauplii and rarely copepodits, because adult copepods were not found in quantitative or qualitative analyses. Rotifers were the most significant group in 2010, contributing with 66.45% for the total biomass of zooplankton (BZ) this year, corresponding basically to class III (Fig. 4); however, in 2011, the BZ was represented similarly by rotifers, copepods and protists (36.3%, 23.17%, and 22.28% of total biomass, respectively). Unlike the previous year, in 2011, class IV was the most significant and represented more than 60% of the BZ, due to a greater contribution of Cladocera in this year (Fig. 4).

Otherwise, the phytoplankton community was much more similar and homogeneous in both years than zooplankton, and represented mainly by Chlorophyceae (42 species), non-toxic Cyanobacteria (38 species), and Bacillariophyceae (15 species). Cyanobacteria contributed on average with 90% of the total biomass of phytoplankton (BP), followed by green algae (8.4%) and diatoms (1.2%). The structure and composition of the community was dominated by cyanobacteria of MLD III and life forms CNF in both years (Fig. 4). The other size classes and forms did not contribute significantly for BP in this study.

Total BZ was very low in both years: 0.76 mg.L⁻¹ in the first and 0.67 mg.L⁻¹ in the second year, but showed the large inter-annual variability to which the system was exposed. In 2010, more than 50% of the BZ was recorded in the summer (0.396 mg.L⁻¹), followed by winter (0.18 mg.L⁻¹; Fig. 5a), while in 2011, more than 80% BZ (0.54 mg.L⁻¹) was registered in spring (Fig. 6a). Spatially, the greatest BZ occurred in the south in 2010 (Fig. 5a), and in the next year, the highest values were found in the north (Fig. 6a). Those responsible for the biomass peaks were not the same in both years. In 2010, the highest biomass values were always associated with the presence of class III rotifers, while in 2011 there was a greater evenness in the contribution of groups to increase the total biomass, and a greater contribution of class IV.

The variance analysis (ANOVA Two-way) showed that the zooplankton community presented significant seasonal variation for all taxonomic groups and size classes ($p < 0.05$) in both years, independent of the spatial factors tested (areas/zones), except for class V and cladocerans in 2010 (Table III). Spatial heterogeneity was also confirmed by the analysis, but was much more evident in 2010, indicating a spatial gradient for the BZ, rotifers and zooplankton of classes II and III ($p < 0.05$), independent of the temporal or spatial factors tested. In 2011, the spatiality factor did not change significantly for the BZ ($p > 0.05$), although it was significant for cladocerans and zooplankton of class III ($p < 0.05$). Class II was the only one to present significant spatial variation among zones in this study ($p < 0.05$; Table III).

The BP showed an opposite seasonal pattern of BZ in the two years studied (Fig. 5b; 6b), and an opposite spatial pattern in 2010, suggesting top-down control. BP was higher in spring 2010 (84 mg.L^{-1}) and summer 2011 (100.5 mg.L^{-1}), coinciding with the lowest values of BZ recorded in the study. The increase in spring 2010 BP (Fig. 5b) was negatively related to decline in spring 2010 BZ ($r\text{-Pearson} = -0.68$). The lowest BP values also coincided with the largest BZ peaks in the two years, especially in summer 2010 when the zooplankton community was mainly composed by rotifers. Spatially, only in 2010 did BP present an inverse pattern to BZ, showing higher biomass values in the north area of the lake (Fig. 5b).

The ANOVA Two-way confirmed higher BP values for the north in this year, presenting significance for BP, MLD I, MLD II, MLD III, and for the dominant life forms CNF and UNF ($p < 0.05$). Furthermore, significant seasonal variation for BP, MLD III, MLD IV, and the life forms Fi and CNF ($p < 0.05$) was also demonstrated by the analysis (Table III). In 2011, significant spatial variation was only detected for MLD I and Fi forms ($p < 0.05$), but the seasonally varied significantly for BP, all size classes and life forms (except for UF and CF), demonstrating that seasonality was more important for the whole plankton community in this year. The biomass ratio of zooplankton to phytoplankton (BZ:BP) was very low in Mangueira Lake. The BZ:BP ratio increased on two different occasions: summer 2010 and spring 2011 (Fig. 5c; 6c, respectively). In these seasons, there was a greater contribution of larger body length zooplankton (class III and IV), indicating a possible enhanced grazing on phytoplankton. Seasonal variation was significant for BZ:BP in the two years ($p < 0.05$), while spatial heterogeneity was observed only in 2010 ($p < 0.05$; Table III). In this year, the BZ:BP ratio was higher in south (Fig. 5c).

Analyzing the relationship between zooplankton and phytoplankton through composition and size categories, it is noticeable that possible grazing relations were more evident in 2010 than in 2011, based on the fact that inverse correlations ($r\text{-Pearson}$, $p < 0.05$) were found not only between BZ and BP, but also among the zooplankton groups and classes with the size categories and life

forms of phytoplankton (Table IV). There was evidence of grazing action of zooplankton on all phytoplankton size spectra and preferably in life forms CNF and UNF in 2010. In summer, the increased BZ and the predominant community reflected more effective control in MLD I, with strong inverse correlation between this phytoplankton size fraction and rotifers ($r = -0.72$), cladocerans ($r = -0.71$) and class III ($r = -0.72$). The highest BZ in the south suppressed BP in this area.

In 2011, there was no significant correlation between the BZ and BP, but some inverse relationships between zooplankton and phytoplankton categories were significant (Table IV). Despite the higher contributions of class IV for BZ, the interactions between zooplankton and phytoplankton occurred mainly between the smaller size categories, influenced by the proto-zooplankton action (ciliates and class I). In spring, when more interactions between producers and consumers due to increased BZ and dominance of class IV were expected, only class II of zooplankton was negatively correlated with BP ($r = -0.83$). The rotifers' contribution to total BZ was lower in this season, but when their biomass was higher (southeast margin – Se), a decrease in BP was registered. Zooplankton of Class V and phytoflagellate forms didn't exhibit relevant correlations in this study, probably due to their insignificant biomass values and very low frequency.

Plankton and Abiotic Parameters

The correlation analysis (r -Pearson, $p < 0.05$) showed large inter-annual variation on the environmental factors that influenced the plankton community. In 2011, phytoplankton and zooplankton were mainly driven by seasonal factors, while in 2010 the spatiality also played an important role.

In 2011, the zooplankton community structure was much more related to the environment than in 2010, and the environmental factors that influenced the community were the opposite of the previous year (Table V). Throughout the study, zooplankton had negative correlation with nebulosity and positive with insolation. The correlation analysis between the BZ and the abiotic data of 2010 showed a positive correlation with variables that were higher in summer (pH, $r = 0.58$; insolation, $r = 0.49$; Chl-*a*, $r = 0.34$), and negative with nutrients (PO_4 , $r = -0.41$; NO_3 , $r = -0.39$), which were higher in the north. The correlation analysis with seasonal data evidenced BZ inversely correlated with nutrients and WV in the warm seasons (r -Pearson: TN = -0.68 , TP = -0.76 , WV = -0.72). Class III rotifers, prevalent in the community, had similar correlations. Despite the high variability of the data over a year, the annual correlation analysis in 2011 showed a strong

correlation between the BZ and the variables that characterized the spring (r -Pearson: WV = 0.75, TP = 0.74, conductivity = 0.72, PO₄ = 0.70, insolation = 0.66, evaporation = 0.54, water temperature = 0.55, ORP = 0.49), and negative with those had the lowest values in this season (DO, r = -0.61; pH, r = -0.59), indicating an opposite response to that observed in 2010. This scenario was repeated for all zooplankton taxonomic groups and size classes (except for class V), demonstrating a greater evenness in community composition. Class I was correlated with TP and PO₄ throughout the entire study (Table V). Seasonally, BZ was highly correlated with PO₄ (r = 0.81) and TP (r = 0.74) in autumn, where a notable event with a high contribution of ciliates and class I for the BZ was recorded.

The interactions between the phytoplankton and the environmental variables showed strong influence of increased NO₃ on BP, recorded in spring 2010 and summer 2011. Contrary to zooplankton patterns, phytoplankton was positively influenced by nutrients, WV and nebulosity in 2010, and negatively related to pH. In this year, phytoplankton community and abiotic correlations demonstrated strong spatiality, presenting positive correlation with variables that characterized the north (NO₃, PO₄ and turbidity) and inverse with the Secchi transparency that characterized the south (Table V). When BP reached the highest values in spring, the described patterns became more evident and its correlations with abiotic data were stronger: r -Pearson Chl-*a* = 0.95, TSS = 0.93, Turb = 0.93, TP = 0.87, WV = 0.79, Secchi transparency = -0.88. The variables correlated with BP in 2011 showed seasonal character: NO₃ (r = 0.65), evaporation (r = 0.52), water temperature (r = 0.45) and insolation (r = 0.41, Table V).

Thirteen abiotic variables mainly related to plankton community were selected to perform the RDA in both years. In 2010, five variables were responsible for explaining 36.4% of the variance of data in the first two axes (Fig. 7). The first axis revealed seasonal distribution (27.7%, $p < 0.001$), with nutrient PO₄ grouping with spring (r = 0.59), pH and Chl-*a* separating in summer (r = -0.55 and r = -0.51, respectively). Axis 1 was more strongly related to phytoplankton size categories and life forms, due to their correlation with PO₄. Zooplankton of classes III (r = -0.79) and IV (r = -0.70) were also related to first axis by their positive correlations with pH and Chl-*a*, and negative with WV. The second axis explained the north spatiality (8.7%), forming a decreasing TP gradient from the north to the south. Class I zooplankton were more related to axis 2 (r = -0.73), probably through its strong correlation with TP.

In 2011, nine variables were selected to explain the variability of data on axes 1 and 2 (52.4%, $p < 0.001$; Fig. 7). The first axis differentiated the summer based on the increase in NO₃ (r = 0.68) and was highly correlated with phytoplankton in almost all categories: MLD I (r = 0.82), MLD II (r = 0.86), MLD III (r = 0.66), MLD IV (r = 0.87), UNF (r = 0.82), Fi (r = 0.86) and CNF

($r = 0.68$), demonstrating the importance of this nutrient for the phytoplankton community. Seasonal heterogeneity was further evidenced on axis 2, where pH ($r = 0.76$), DO ($r = 0.75$) and Secchi transparency ($r = 0.50$) grouped the autumn and winter, while PO₄ ($r = -0.7$), TP ($r = -0.66$) and WV ($r = -0.48$) separated spring. Insolation ($r = -0.86$) and water temperature ($r = -0.74$) approached the warmer seasons. Most zooplankton classes were strongly related to axis 2 and were plotted with spring because of strong correlations with WV and forms of phosphorus: class II ($r = -0.64$), class III ($r = -0.78$), class IV ($r = -0.73$) and class V ($r = -0.42$). Class I was plotted along with TP and PO₄ showing their strong relationship observed throughout the study period. The RDA showed that in 2011 the seasonal abiotic variables were much more important to the structure of plankton communities.

DISCUSSION

Dynamics of Zooplankton and Phytoplankton Interactions

Our results suggest that subtropical lakes contain very low BZ and biomass of macrozooplankton grazers, making the zooplankton control on BP very weak. These finds are in accordance with previous studies in subtropical lakes (Crisman and Beaver, 1990; Havens, 2002; Lacerot et al., 2013). Despite the great temporal variability in the size structure and composition of zooplankton during the two years, the constant homogeneity in the structural composition of phytoplankton and the very low values of the BZ:BP ratio showed that zooplankton did not exert strong control on phytoplankton. However, our finds showed that in a large shallow lake, which is often characterized by significant spatial and temporal heterogeneity in the distributions of populations (Crossetti et al., 2013), the strength of zooplankton control on BP can also vary on such scales. An irregular horizontal distribution was previously related for phytoplankton, periphyton and fish communities in Mangueira Lake (Crossetti et al., 2013, 2014; Faria et al., 2015; Rodrigues et al., 2015).

The BZ:BP ratio is used as an indicator of zooplankton grazing pressure on phytoplankton (Muylaert et al., 2003), and high ratios represent stronger top-down control on BP (Ye et al., 2013). The values of BZ:BP ratio found in Mangueira Lake were similar to the lowest values reported in the literature for shallow lakes (Jeppesen et al., 2007; Havens et al., 2009). Variations in the BZ:BP ratio were driven mainly by variations in BZ and were little affected by variations in BP, as observed in other subtropical shallow lakes (Havens and Beaver, 2013). Summer 2010 was the only

occasion when the increase in BZ:BP ratio was also correlated with the decrease in BP, indicating a possible zooplankton grazing.

Rotifers, which dominated the zooplankton community in 2010, nauplii, and to a lesser extent cladocerans, seem to have been responsible for higher grazing pressure on phytoplankton. We assigned a greater grazing pressure to rotifers, when cladocerans had very low biomass and nauplii did not affect BP in other seasons. In aquatic environments where cladocerans are typically small or correspond to very low biomass, the ecological role of rotifers may be more important than previously thought (Paggi et al., 2012). In a shallow eutrophic lake, the microzooplankton (ciliates and rotifers) dominated zooplankton filtering and grazing activity over a major part of the seasonal cycle, being the primary consumer of phytoplankton (Agasild et al., 2007).

Although rotifers (90-150 μm) and cladocerans had exerted control over most size classes of phytoplankton and life forms CNF and UNF, a stronger pressure in MLD I spectra ($<10\mu\text{m}$) and UNF forms was evidenced in the seasonal correlations analysis, demonstrating that zooplankton trophic interactions are size-specific (Blukacz et al., 2010). Negative influence of rotifers on nanoplanktonic algae was also observed in a temperate shallow lake (Goldyn and Madura, 2008). The small particles present in open waters (1-15 μm) are the most important food element for all planktonic herbivores, including rotifers and cladocerans (Brooks and Dodson, 1965). Preference of zooplankton for non-flagellated forms (unicellular $>$ colonial) may reflect the greater capacity of flagellate algae to escape the grazing pressure of zooplankton (Goldyn and Madura, 2008).

Even if it is well recognized that cyanobacteria are a poor food source for zooplankton due to their filamentous or colonial structure, low digestibility and toxin production (Gragani et al., 1999; DeMott et al., 2001), the phytoplankton community in Mangueira Lake was mainly composed of small non-toxic species of cyanobacteria. The filamentous form corresponded only to 2.1% BP, and even the colonial forms rarely exceed 50 μm . Grazers' ability to deal with colonial algae apparently depends more on the dimensions of the colony as a whole, than the individual cells (Cyr and Curtis, 1999). On the other hand, poor nutritional quality of cyanobacteria could induce limitations to the growth and reproduction of zooplanktonic organisms (DeMott et al., 2001). This could partly explain why the presence of larger species of cladocerans and *Daphnia* in Mangueira Lake was never recorded, as well the extremely low species richness of this group in the system. Higher species richness and larger body size cladocerans (*Daphnia* species included) had already been recorded in other subtropical lakes in southern Brazil with similar characteristics (Cardoso and Motta-Marques, 2004a; Gazulha et al., 2011), probably due to a greater availability of good quality food for zooplankton (such as diatoms; Cardoso and Motta-Marques, 2004b), assuming that they must be exposed to similar predation pressure in those systems. An extensive zooplankton

consumption of bacteria and cyanobacteria (filamentous and colonial) was found in subtropical lakes where chlorophytes and diatoms were not abundant (Gragnani et al., 1999; Work and Havens, 2003). The zooplankton may be unable to avoid consuming cyanobacteria (and bacteria) in lakes where their populations dominate, and may need to supplement their diet with less favorable food when there is a scarcity of 'edible' food sources. Furthermore, populations of zooplankton that coexist with cyanobacteria dominated populations may be better able to digest this type of food than unexposed zooplankton (Work and Havens, 2003).

When phytoplankton is not efficiently grazed by zooplankton (crustaceans and rotifers) in a classical linear food chain, they enter to the less efficient microbial loop mediated by bacteria and protists (Agasild et al., 2013). In Mangureira Lake, the contribution of ciliates (<60 μm) for BZ increased after the summer 2010 peak, and became particularly high in autumn 2011, when this group was very representative. Added to this, the weakening of the relationship between phytoplankton and zooplankton strongly evidences that the detrital food chain is the main pathway of energy transfer in Mangureira Lake, and prevails most of the time. Data about the regulators of bacterioplankton in Mangureira Lake during 2010 (Kist et al., 2011) showed that periods with highlighted bacterivory coincided with the highest BZ periods (summer and winter). The grazing activity was detected mainly on the coccus morphotype, the lowest and least complex form preferred by zooplankton, which better reflects the top-down control (Jürgens et al., 1999; Corno and Jürgens, 2006). Bacteria might serve as an important source of carbon in the planktonic food web and they also may take up carbon that is unavailable to phytoplankton (Kisand and Nöges, 1998). This carbon source constituted half of the total carbon flow to protozoans and microzooplankton in a subtropical shallow lake (Work et al., 2005), while ciliates grazed nearly 100% of the biomass production of suspended bacteria in a shallow eutrophic lake (Zingel et al., 2007).

In spring 2011, the second occasion with higher BZ:BP ratio, the change in zooplankton community for large body size organisms (predominance of class IV) and greater contribution of cladocerans could strengthen the control on phytoplankton. It is well known that communities of large-bodied zooplankton can graze more intensively on phytoplankton than communities composed of smaller species (Peters and Downing, 1984; Cyr and Curtis, 1999). However, a weak and negative effect on BP was only observed by the action of proto-zooplankton of the smaller size classes (class I and class II), while the large-bodied zooplankton were not correlated to phytoplankton. Larger size structure of zooplankton was not always associated with higher grazing pressure and there is little control of phytoplankton by macro-zooplankton in subtropical systems (Crisman and Beaver, 1990; Wang et al., 2007a). Our results corroborate these theories, once

rotifers of intermediate size were more able to benefit from the phytoplankton production. Moreover, cladocerans are adversely affected by high concentrations of cyanobacteria, whereas some rotifers benefit from them or remain unaffected. The feeding apparatus of some rotifers permits the efficient collection of a wide variety of particles, even feeding on the filamentous cyanobacteria, maintaining their growth and reproduction rates (Gilbert and Starkweather, 1977; Weithoff and Walz, 1995). The direct link between cyanobacteria and rotifers can be quantitatively important in aquatic ecosystems, indicating that the food requirements of rotifers may be substantially different from those of other zooplankton or that the food quality of cyanobacteria for rotifers could be better than previously thought (Burian et al., 2014).

In addition to the role of previously discussed food quality in structuring the zooplankton community, there is certainly the top-down control on zooplankton to consider. Despite the copepod nauplii being abundant and frequent in Mangueira Lake, copepodites were rare and adults were not found in quantitative analyses, nor were large cladocerans. Although it was not analyzed in this work, the planktivorous predation pressure on subtropical zooplankton it is well documented by several studies (Havens et al., 2009; Lacerot et al., 2013). In Mangueira Lake, planktivorous fish presented low captured biomass in both north and south areas (Rodrigues et al., 2015), but small omnivorous organisms, such as *Astyanax* species, have continuous reproductive events during the year and could control the large-bodied zooplankton biomass. On the other hand, the shrimp *Palaemonetes argentinus* was already found related to zooplankton in the system (Rodrigues et al., 2014), suggesting that both predation by young fish and the macroinvertebrates may help to explain the low biomass of crustacean zooplankton in the lake. *P. argentinus* was very numerous in Uruguayan subtropical regions and, in almost all of the studied lakes in both temperate and subtropical regions, they were found optimizing the predation pressure exerted by fish (Meerhoff et al., 2007).

The Role of Environmental Variables

The plankton community and zooplankton-phytoplankton interactions were clearly constrained by the environment during the study period in Mangueira Lake. Seasonality of environmental variables seems to play a key role in the structure of planktonic organisms in this system. Both zooplankton and phytoplankton responded to conditions of increased temperature and light intensity, characteristic of the warm seasons. Temperature and climate are thought to be the adjacent factors favoring the zooplankton increase in large lakes during spring and summer (Pinel-Alloul et al., 1999). The BZ peak, as well as the dominance of the size classes and taxonomic

groups, varied between the years. This inter-annual variability of seasonal peaks might be associated with the inter-annual variation of physicochemical environment and/or food availability (Chang et al., 2014). For phytoplankton, the influence of the high concentration of nutrients in this warmer period was even stronger. Higher BP (spring 2010 – summer 2011) coincided with the period when Mangueira Lake can change to a mesotrophic condition, and suffered a notable water withdrawal for irrigation of rice crops, as well as a high load input of nutrients from the watershed (Fragoso Jr. et al., 2008).

In this study, BP was primarily controlled by resource availability, rather than zooplankton grazing, in accordance with previous studies in subtropical lakes, demonstrating that BP is regulated by bottom-up, rather than top-down, forces (Havens, 2002; Wang et al., 2007b). The nutrient availability, in accordance with a set of environmental variables related to water level fluctuations and wind action, in response of the combined interactions of seasonality and spatiality, best explained variations in phytoplankton functional groups and their dissimilar distribution in Mangueira Lake (Crossetti et al., 2013; 2014). Top-down control of zooplankton did not at all affect the phytoplankton distribution patterns in our study, but it was notable in particular conditions of zooplankton taxonomic dominance and size categories that varied in space and time.

In 2010, the abiotic scenario reinforced the previously mentioned stronger zooplankton grazing on phytoplankton in summer. The correlation analysis demonstrated that zooplankton must have been favored by a condition of increased productivity of the system, due to their positive correlations with insolation, Chl-*a*, and pH. Changes in abiotic parameters such as pH, temperature and light intensity govern phytoplankton primary production and autotroph–herbivore interactions (Hessen et al., 2005). While BP was positively correlated with nutrients, BZ showed inverse correlations with BP and nutrients, demonstrating a possible link between BP and BZ.

Such interactions also varied spatially: one time BZ:BP ratio was significantly higher in the south area, as mentioned above. The lake is marked by spatial differences between the north and south areas: the south end is characterized by high water transparency whereas the north end is more turbid due to its connection with Taim wetland (Cardoso et al., 2012). The south area presents large biomass of submerged macrophytes, which can greatly reduce turbidity by a suite of different mechanisms avoiding wave resuspension of sediments (Scheffer et al., 1993). Calmer waters and the reduction of the effects generated by wind action have been already described as favorable to rotifer development (Cardoso and Motta-Marques, 2004a). As there is no evidence that rotifers can move or swim horizontally as far as several meters (Paggi et al., 2012), the reduced current velocity in this microhabitat, could also explain the greatest success of rotifers in controlling the BP in the south area during their summer peaks. In spite of the evidences that aquatic plants are more

dangerous as a potential refuge for zooplankton, due to high risk of planktivorous predation (Meerhoff et al., 2006), rotifers seem to be less affected by fish predation (Schabetsberger et al., 2009).

On the other hand, BP was significantly lower in the south area, enabling a more effective control by zooplankton. Submerged plants are involved in antagonistic relationships with phytoplankton, including strong competition for nutrients and discharge of allelopathic substances that are toxic to algae (Scheffer et al., 1993). Furthermore, a spatial gradient decreasing from the north to the south area was already described for BP in Mangueira Lake, as consequence of greater availability of nutrients due to the influence of the adjacent wetland (Crossetti et al., 2013). Our study did not demonstrate significant differences between pelagic and littoral zones, except for class II zooplankton. This class was largely composed of tecamoebae, and this group varied significantly in the interaction between zone and seasonal factors. Tecamoebae have been already found dominating the plankton in littoral zone of lentic and lotic environments (Velho et al., 1999). The authors attributed these patterns to their thecae structure, which could be heavier because of the presence of exogenous material, limiting their mobility in the pelagic zone.

In 2011, all zooplankton taxonomic groups and size classes (except class V) were highly correlated with TP and PO_4 , but not related to BP. These results are fully consistent with previous studies in Florida lakes, which showed no relationship between BZ and BP, and a significant positive relationship between BZ and TP, supporting the premise that bacteria and a microbial-based food web primarily sustain the macro-zooplankton production in subtropical lakes (Havens, 2002; Work et al., 2005; Havens et al., 2011). This also explains the high correlation of zooplankton class I and ciliates with forms of phosphorus during the entire study period (seasonal and annual correlations). In addition to their role in energy transfer to higher trophic levels, ciliates act in the bio-geochemical cycling of phosphorus and nitrogen and can increase the availability of nutrients for phytoplankton growth (Beaver and Crisman, 1990).

In Mangueira Lake, high availability of phosphorus can be a consequence of high wind velocity recorded in spring sampling day, when all zooplankton taxonomic groups and size classes were strongly correlated with WV. In large shallow lakes, wind-induced mechanisms such as resuspension of solids and availability of nutrients and light generally drive factors leading to both spatial and temporal heterogeneity of phytoplankton (Carrick et al., 1993) and zooplankton (Cardoso and Motta-Marques, 2009). Water turbulence induced by wind is apparently the most important mechanism resuspending phosphorus from sediment to the water column in Mangueira Lake, and wind action has already been recognized as one of the main important features promoting low transparency (Crossetti et al., 2013).

A number of complexities involved the structure of zooplankton as environmental, bottom-up and probably top-down forces, while phytoplankton was mainly controlled by nutrients. The variability of the environmental factors induced by wind action and/or diversification of niches can also direct, or indirectly influence, the distribution patterns and structure of the plankton community, as well as the strength of zooplankton-phytoplankton interactions. Zooplankton had minor importance in controlling BP in this system, probably due to a scarcity of large-bodied potential grazers. However, the micro-zooplankton action (such as rotifers) needs to be considered regarding grazing analysis in subtropical lakes, including their role in the microbial food chain, which seems to be the main pathway of carbon transfer in these systems. Both taxonomic composition and size structure of zooplankton are very relevant features to establish grazing relationships on phytoplankton. In subtropical lakes, the smallest size classes of zooplankton are a key factor to understand the functioning of food webs, in which the main descriptors can vary on spatial and temporal scales.

ACKNOWLEDGEMENTS

We are grateful to IPH (Hydraulic Research Institute, at UFRGS) technicians for sampling support and laboratory analysis.

FUNDING

This work was supported by the research development agencies CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) and CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico).

SUPPLEMENTARY DATA

Supplementary data will be found online at the Journal's homepage.

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TABLE AND FIGURE LEGENDS

Table I: Minimum-maximum and mean \pm standard-deviation values of environmental variables sampled seasonally (2010 and 2011) at nine sampling stations in Mangueira Lake, southern Brazil.

Table II: Minimum-maximum and mean \pm standard-deviation values of environmental variables along a spatial gradient (south, center and north areas) sampled seasonally (2010 and 2011) at nine sampling stations in Mangueira Lake, southern Brazil.

Table III: Variance Analysis (ANOVA-Two Way) of the size structure and composition of plankton community in 2010 and 2011 (NS = non-significant, BZ = total zooplankton biomass, BP

= total phytoplankton biomass, BZ:BP = zooplankton to phytoplankton biomass ratio; see legend on Fig. 4).

Table IV: Correlation analysis (r -Pearson, $p < 0.05$) between zooplankton (total biomass-BZ, size classes and taxonomic groups) and phytoplankton biomass (total biomass-BP, size classes and life forms) in 2010 and 2011 (see legend on Fig. 4).

Table V: Correlation analysis (r -Pearson, $p < 0.05$) between biological community and environmental variables in 2010 and 2010.

Fig. 1: Location of Mangueira Lake in southern Brazil and sampling points (S = south, C = center, N = north, LW = littoral west, LE = littoral east).

Fig. 2: Variation of meteorological data in the previous week of sampling for each season in 2010 and 2011 (Sum = summer, Aut = autumn, Win = winter, Spr = spring).

Fig. 3: Principal Components Analysis (PCA) of the environmental data from 2010 and 2011 in Mangueira Lake at spatial (S = South, C = Center, N = North) and seasonal (Summer, Autumn, Winter, Spring) sampling (Turb = turbidity, Nebul = nebulosity, WV = wind velocity, WD = wind direction, TP = total phosphorus, PO₄ = orthophosphate, TN = total nitrogen, TSS = total suspended solids, ORP = redox potential, DO = dissolved oxygen, Cond = conductivity, Precip = precipitation, Insol = insolation, Evap = evaporation).

Fig. 4: Inter-annual variation in the composition and size structure of zooplankton (Class I - Class V = size classes), and size structure and life forms of phytoplankton communities (MLD = maximum linear dimension, categories I - IV; UF = unicellular flagellates, CF = colonial flagellates, UNF = unicellular non-flagellated, CNF = colonial non-flagellated, including coenobia, and Fi = filaments).

Fig. 5: Spatial and seasonal distribution of total biomass of a) zooplankton (BZ), b) phytoplankton (BP) and c) the biomass ratio between zooplankton and phytoplankton (BZ:BP) in Mangueira Lake during 2010.

Fig. 6: Spatial and seasonal distribution of total biomass of a) zooplankton (BZ), b) phytoplankton (BP) and c) the biomass ratio between zooplankton and phytoplankton (BZ:BP) in Mangueira Lake during 2011.

Fig. 7: Ordination diagrams of Redundancy Analysis showing spatial and seasonal variation of the planktonic community in relation to environmental variability in 2010 and 2010. (Class I - Class V: zooplankton indicators; MLD I - MLD IV, UNF, CNF, Fi, CF and UF life forms: phytoplankton indicators, see legend on Fig. 4).

Table I

Environmental Variables	Year	Summer	Autumn	Winter	Spring
Total Suspended Solids	2010	9.0-23.0 (13.6±5.1)	2.5-21.5 (12.8±6.2)	5.5-16.5 (9.3±3.1)	4.0-27.5 (10.9±7.1)
(mg.L ⁻¹)	2011	8.0-17.5 (10.9±2.75)	1.5-22.0 (9.6±7.63)	11.0-28.0 (18.6±5.74)	13.0-18.0 (15.6±1.65)
Total Phosphorus	2010	0.73-1.77 (1.22±0.3)	0.37-1.01 (0.69±0.23)	0.41-1.53 (0.75±0.36)	0.47-1.58 (0.94±0.34)
(µM.L ⁻¹)	2011	0.55-1.5 (0.92±0.3)	0.48-1.55 (0.96±0.33)	0.96-2.03 (1.44±0.39)	2.03-2.74 (2.28±0.25)
Total Nitrogen	2010	20.7-48.3 (32.7±8.73)	23.3-38.7 (29.1±5.17)	14.9-21.4 (17.9±2.44)	6.16-42.7 (19.9±12.5)
(µM.L ⁻¹)	2011	11.5-27.4 (18.6±4.65)	8.21-25.6 (14.9±5.7)	22.7-44.4 (35.7±6.15)	20.1-44.07 (31.5±8.0)
NO3	2010	0.14-1.82 (0.85±0.66)	0.71-1.18 (0.88±0.15)	1.38-2.41 (1.77±0.38)	0.82-6.62 (2.98±1.85)
(µM.L ⁻¹)	2011	1.85-4.83 (3.17±0.87)	0.16-0.45 (0.3±0.11)	1.53-3.09 (2.18±0.56)	0.78-2.79 (1.74±0.58)
PO4	2010	0.07-0.12 (0.09±0.01)	0.09-0.19 (0.12±0.03)	0.08-0.17 (0.12±0.02)	0.12-0.28 (0.16±0.04)
(µM.L ⁻¹)	2011	0.14-0.4 (0.24±0.08)	0.01-0.47 (0.22±0.13)	0.18-0.39 (0.27±0.06)	0.43-0.55 (0.51±0.05)
Chlorophyll <i>a</i>	2010	3.55-9.14 (6.49±2.20)	0.8-5.2 (3.2±1.6)	2.0-8.1 (4.4±1.8)	1.5-5.7 (3.0±1.3)
(µg.L ⁻¹)	2011	1.85-6.13 (3.2±1.25)	1.85-5.33 (3.18±1.27)	2.11-6.31 (3.84±1.23)	2.20-6.48 (3.42±1.25)
Water Level	2010	1.4-6.3 (3.0±1.7)	1.4-6.2 (2.9±1.6)	1.8-6.8 (3.5±1.6)	1.7-7.0 (3.5±1.7)
(m)	2011	1.0-3.8 (2.5±1.12)	1.1-6.3 (2.85±1.72)	1.7-5.8 (3.16±2.28)	N/D
Transparency	2010	0.9-2.1 (1.3±0.4)	0.7-1.4 (1.0±0.2)	0.7-2.7 (1.8±0.8)	0.6-1.6 (1.1±0.3)
(m)	2011	0.75-1.5 (1.0±0.24)	1.0-2.35 (1.42±0.39)	0.4-1.1 (0.72±0.25)	0.53-0.82 (0.7±0.1)
Temperature	2010	19.8-23.6 (22.3±1.3)	17.6-18.5 (17.9±0.3)	11.0-12.4 (11.6±0.5)	21.3-22.8 (22.1±0.6)
(°C)	2011	21.1-22.7 (21.9±0.58)	13.5-16.1 (15.1±1.0)	10.1-13.1 (11.4±1.1)	24.1-25.7 (24.6±0.54)
Conductivity	2010	0.31-0.35 (0.33±0.01)	0.36-0.38 (0.37±0.01)	0.26-0.31 (0.30±0.02)	0.33-0.35 (0.34±0.01)
(mS/cm)	2011	0.35-0.37 (0.36±0.005)	0.266-0.278 (0.237±0.004)	0.29-0.33 (0.3±0.015)	0.44-0.48 (0.45±0.014)
pH	2010	8.4-8.6 (8.5±0.1)	8.0-8.2 (8.1±0.1)	7.9-8.1 (8.1±0.1)	7.9-8.1 (8.0±0.1)
	2011	8.2-8.4 (8.28±0.09)	8.71-8.79 (8.75±0.03)	8.12-8.45 (8.24±0.13)	7.80-7.94 (7.89±0.05)
Redox Potential	2010	148.1-194.0 (169.8±13.9)	118.9-172.3 (138.3±18.4)	83.3-110.2 (94.5±11.0)	156-178.6 (165.1±7.4)
(mV)	2011	156.6-192.4 (177.3±11.9)	121.3-191.3 (142.7±22.3)	142-191 (178.3±17.3)	200.6-210.9 (204.6±3.83)
Turbidity	2010	2.3-8.2 (4.4±1.9)	2.2-8.9 (5.5±2.5)	2.2-10.2 (5.4±2.9)	1.2-14.9 (4.4±4.2)
(NTU)	2011	1.5-4.2 (3.0±0.97)	2.8-9.1 (5.15±2.16)	6.3-20.1 (11.8±4.9)	4.2-12.9 (6.71±2.57)
Dissolved Oxygen	2010	8.6-9.8 (9.0±0.3)	9.1-9.6 (9.3±0.1)	10.7-11.9 (11.5±0.4)	8.3-8.8 (8.6±0.2)
(mg.L ⁻¹)	2011	8.78-9.47 (9.01±0.27)	9.8-10.0 (9.91±0.07)	10.0-10.0 (10.0±0.0)	7.78-9.0 (8.15±0.37)
Wind Direction	2010	18.0-18.0 (18.0±0.0)	5.0-29.5 (16.4±11.1)	7.0-18.0 (14.6±5.2)	14.0-14.0 (14.0±0.0)
	2011	0.0-32.0 (15.3±13.9)	0.0-18.0 (10.6±8.18)	5.0-14.0 (11.0±4.5)	5.0-9.0 (6.33±2.0)
Wind Velocity	2010	1.0-2.0 (1.7±0.5)	7.0-9.0 (7.9±0.9)	1.5-4.5 (2.2±1.3)	2.0-4.0 (3.0±0.9)
(m.s ⁻¹)	2011	0.0-2.0 (1.0±0.86)	0.0-2.0 (1.33±1.0)	2.0-6.0 (3.11±1.76)	3.0-8.0 (6.0±2.29)
Nebulosity	2010	0.0-3.0 (1.3±1.3)	8.0-10.0 (9.4±0.9)	0.0-8.5 (2.9±4.1)	0.0-9.0 (5.7±4.3)
(dec)	2011	0.0-8.0 (4.33±3.5)	4.0-10.0 (6.0±3.0)	2.0-6.0 (4.5±1.43)	0.0-6.0 (3.0±2.59)
Precipitation	2010	0.0-0.0 (0.0±0.0)	2.1-13.7 (8.5±6.1)	0.0-0.0 (0.0±0.0)	0.0-0.0 (0.0±0.0)
(mm)	2011	0.0-0.0 (0.0±0.0)	0.0-0.0 (0.0±0.0)	0.0-0.1 (0.033±0.05)	0.0-0.0 (0.0±0.0)
Insolation	2010	10.8-10.8 (10.8±0.0)	0.0-0.9 (0.5±0.5)	4.2-7.0 (5.6±1.2)	5.6-5.6 (5.6±0.0)
(h)	2011	8.4-8.4 (8.4±0.0)	5.8-5.8 (5.8±0.0)	6.5-7.0 (6.66±0.25)	10.2-10.2 (10.2±0.0)
Evaporation	2010	4.2-4.2 (4.2±0.0)	0.9-3.8 (2.2±1.5)	2.2-2.8 (2.5±0.3)	3.5-3.5 (3.5±0.0)
(mm)	2011	4.6-4.6 (4.6±0.0)	1.6-1.6 (1.6±0.0)	1.6-2.3 (2.06±0.35)	5.5-5.5 (5.5±0.0)

Table II

Environmental Variables	Year	South	Center	North
Total Suspended Solids	2010	4.0-12.5 (8.3±2.6)	7.5-23.0 (12.4±5.4)	2.5-27.5 (14.4±6.6)
(mg.L ⁻¹)	2011	8.5-28.0 (16.9±6.1)	5.0-23.0 (12.6±5.4)	1.5-18.0 (11.6±5.7)
Total Phosphorus	2010	0.37-1.44 (0.66±0.31)	0.54-1.34 (0.85±0.23)	0.52-1.77 (1.2±0.33)
(μM.L ⁻¹)	2011	0.55-2.74 (1.31±0.79)	0.48-2.15 (1.25±0.6)	1.0-2.32 (1.63±0.46)
Total Nitrogen	2010	15.8-34.6 (24.7±6.3)	9.31-39.3 (22.4±8.35)	6.16-48.2 (27.7±13.9)
(μM.L ⁻¹)	2011	10.2-38.6 (22.1±10.9)	8.21-38.8 (26.08±10.1)	12.1-44.4 (27.3±10.9)
NO ₃	2010	0.14-4.49 (1.6±1.35)	0.14-3.72 (1.33±0.94)	0.82-6.62 (1.94±1.57)
(μM.L ⁻¹)	2011	0.4-3.02 (1.43±0.83)	0.16-3.72 (1.98±1.25)	0.16-4.83 (2.12±1.39)
PO ₄	2010	0.07-0.17 (0.11±0.02)	0.08-0.15 (0.12±0.02)	0.07-0.29 (0.14±0.05)
(μM.L ⁻¹)	2011	0.14-0.55 (0.29±0.15)	0.01-0.54 (0.26±0.15)	0.26-0.55 (0.38±0.1)
Chlorophyll <i>a</i>	2010	1.5-7.6 (2.9±1.7)	2.42-8.48 (4.9±2.08)	0.8-9.1 (5.08±2.16)
(μg.L ⁻¹)	2011	1.85-6.48 (2.96±1.35)	1.98-4.31 (3.17±0.72)	2.72-6.31 (4.1±1.28)
Water Level	2010	1.6-5.2 (3.0±1.5)	1.4-7.0 (4.0±2.2)	1.4-3.7 (2.8±0.7)
(m)	2011	1.4-4.5 (2.41±1.21)	1.0-6.3 (3.6±2.0)	1.1-3.3 (2.25±0.85)
Transparency	2010	1.1-2.7 (1.6±0.6)	0.7-2.4 (1.3±0.5)	0.6-1.4 (0.9±0.3)
(m)	2011	0.63-2.35 (1.15±0.45)	0.42-1.5 (0.92±0.23)	0.4-1.7 (0.82±0.37)
Temperature	2010	11.0-22.4 (18.0±4.4)	11.4-23.1 (18.6±4.6)	11.8-23.6 (18.9±4.7)
(°C)	2011	10.1-24.5 (17.45±5.87)	11.04-24.4 (18.37±5.52)	12.4-25.7 (18.9±5.16)
Conductivity	2010	0.26-0.36 (0.33±0.03)	0.31-0.38 (0.34±0.02)	0.28-0.38 (0.34±0.03)
(mS/cm)	2011	0.27-0.45 (0.34±0.07)	0.27-0.45 (0.34±0.07)	0.28-0.48 (0.36±0.07)
pH	2010	8.0-8.5 (8.2±0.2)	7.9-8.5 (8.2±0.2)	7.9-8.6 (8.2±0.3)
	2011	7.90-8.75 (8.28±0.31)	7.92-8.79 (8.27±0.32)	7.80-8.76 (8.33±0.34)
Redox Potential	2010	83.3-194.0 (145.6±39.2)	85.7-179.4 (142.3±34.7)	96.3-167.3 (138.0±25.8)
(mV)	2011	127.8-203.6 (179.6±23.2)	131.0-202.3 (178.1±25.6)	121.3-210.9 (169.5±31.8)
Turbidity	2010	1.2-4.1 (2.7±0.8)	2.7-8.9 (5.0±1.9)	2.2-14.9 (7.1±3.5)
(NTU)	2011	1.5-12.9 (5.24±3.48)	3.0-12.4 (6.54±3.09)	2.8-20.1 (8.27±5.89)
Dissolved Oxygen	2010	8.3-11.8 (9.5±1.3)	8.5-11.8 (9.6±1.2)	8.5-11.9 (9.7±1.1)
(mg.L ⁻¹)	2011	7.78-10.0 (9.13±0.92)	8.14-10.0 (9.28±0.78)	8.0-10.0 (9.39±0.71)
Wind Direction	2010	5.0-18.0 (13.8±5.5)	5.0-29.5 (17.8±6.6)	7.0-23.0 (15.7±5.9)
	2011	9.0-14.0 (12.75±2.26)	0.0-14.0 (4.75±5.97)	5.0-32.0 (15.0±11.6)
Wind Velocity	2010	1.0-9.0 (3.3±3.2)	1.5-9.0 (3.5±2.6)	2.0-8.0 (4.3±2.3)
(m.s ⁻¹)	2011	2.0-3.0 (2.25±0.45)	0.0-7.0 (2.25±2.98)	1.0-8.0 (4.08±2.93)
Nebulosity	2010	0.0-10.0 (2.5±4.5)	0.5-10.0 (5.1±4.6)	3.0-9.0 (6.9±2.4)
(dec)	2011	0.0-10.0 (4.0±4.43)	3.0-8.0 (4.62±2.06)	2.0-6.0 (4.75±1.13)
Precipitation	2010	0.0-2.1 (0.5±0.9)	0.0-13.7 (2.5±5.3)	0.0-13.7 (3.4±6.2)
(mm)	2011	0.0-0.0 (0.0±0.0)	0.0-0.0 (0.0±0.0)	0.0-0.1 (0.025±0.045)
Insolation	2010	0.0-10.8 (5.9±4.0)	0.0-10.8 (5.7±3.8)	0.9-10.8 (5.4±3.7)
(h)	2011	5.8-10.2 (7.72±1.79)	5.8-10.2 (7.72±1.79)	5.8-10.2 (7.85±1.71)
Evaporation	2010	2.8-4.2 (3.6±0.5)	0.9-4.2 (3.0±1.2)	0.9-4.2 (2.7±1.3)
(mm)	2011	1.6-5.5 (3.5±1.67)	1.6-5.5 (3.5±1.67)	1.6-5.5 (3.32±1.83)

Table III

	Spatial		Temporal	Interaction		
	Areas (A)	Zones (Z)	Seasonal (S)	AS	AZ	ZS
Total BZ 2010	p 0.036	NS	p 0.0004	NS	NS	NS
Total BP 2010	p 0.00009	NS	p 0.0008	NS	NS	NS
BZ:BP 2010	p 0.024	NS	p 0.007	p 0.01	NS	NS
Ciliate 2010	NS	NS	p 0.022	NS	NS	NS
Tecamoebae 2010	NS	NS	p 0.014	NS	NS	p 0.007
Rotifera 2010	p 0.012	NS	p 0.0001	NS	NS	NS
Cladocera 2010	NS	NS	NS	p 0.004	NS	NS
Copepoda 2010	NS	NS	p 0.001	NS	NS	NS
Class I 2010	NS	NS	p 0.011	NS	NS	NS
Class II 2010	p 0.0008	NS	p 0.018	p 0.0003	NS	p 0.002
Class III 2010	p 0.013	NS	p 0.0003	p 0.037	NS	NS
Class IV 2010	NS	NS	p 0.0009	NS	NS	NS
Class V 2010	NS	NS	NS	NS	NS	NS
MLD I 2010	p 0.004	NS	NS	p 0.0004	NS	NS
MLD II 2010	p 0.012	NS	NS	p 0.047	NS	NS
MLD III 2010	p 0.0003	NS	p 0.001	NS	NS	NS
MLD IV 2010	NS	NS	p 0.00001	p 0.004	NS	NS
UNF 2010	p 0.0004	NS	NS	p 0.0003	NS	NS
FI 2010	NS	NS	p 0.001	p 0.001	NS	NS
CNF 2010	p 0.0002	NS	p 0.0009	NS	NS	NS
UF 2010	NS	NS	NS	NS	NS	NS
CF 2010	NS	NS	NS	NS	NS	NS
Total BZ 2011	NS	NS	p 4.4E ⁻⁰⁸	NS	NS	NS
Total BP 2011	NS	NS	p 0.000004	NS	NS	NS
BZ:BP 2011	NS	NS	p 0.000004	NS	NS	NS
Ciliate 2011	NS	NS	p 1.07E ⁻⁰⁷	p 0.03	NS	NS
Tecamoebae 2011	NS	NS	p 0.0007	p 0.025	NS	NS
Rotifera 2011	NS	NS	p 0.0004	NS	NS	NS
Cladocera 2011	p 0.007	NS	p 2.93E ⁻⁰⁷	p 0.0009	NS	NS
Copepoda 2011	NS	NS	p 0.0007	p 0.039	NS	NS
Class I 2011	NS	NS	p 0.00001	p 0.017	NS	NS
Class II 2011	NS	p 0.019	p 4.9E ⁻¹⁰	NS	NS	p 0.007
Class III 2011	p 0.006	NS	p 2.43E ⁻⁰⁷	p 0.045	NS	NS
Class IV 2011	NS	NS	p 0.000003	NS	NS	NS
Class V 2011	NS	NS	NS	NS	NS	NS
MLD I 2011	p 0.011	NS	p 0.000007	NS	NS	NS
MLD II 2011	NS	NS	p 0.00007	NS	NS	NS
MLD III 2011	NS	NS	p 0.00004	NS	NS	NS
MLD IV 2011	NS	NS	p 5.72E ⁻⁰⁸	NS	NS	NS
UNF 2011	NS	NS	p 0.0005	NS	NS	NS
FI 2011	p 0.0002	NS	p 3.44E ⁻¹¹	p 0.001	NS	NS
CNF 2011	NS	NS	p 0.00002	NS	NS	NS
UF 2011	NS	NS	NS	NS	NS	NS
CF 2011	NS	NS	NS	NS	NS	NS

Table IV

	Total BP	BZ:BP	MLD I	MLD II	MLD III	MLD IV	UNF	FI	CNF	UF
Total BZ 2010	-0.47	0.59	-0.33		-0.45	-0.40	-0.38	-0.34	-0.46	
BZ:BP 2010	-0.40		-0.48	-0.33	-0.37		-0.50		-0.38	
Ciliate 2010						-0.36				
Tecamoebae 2010										0.41
Rotifera 2010	-0.48	0.61	-0.34	-0.33	-0.46	-0.37	-0.45		-0.46	
Cladocera 2010	-0.41	0.89	-0.58	-0.42	-0.38		-0.61		-0.38	
Copepoda 2010	-0.37	0.55			-0.35	-0.33			-0.36	
Class I 2010						-0.34				
Class II 2010										
Class III 2010	-0.44	0.64	-0.34	-0.36	-0.41	-0.41	-0.48	-0.35	-0.42	
Class IV 2010	-0.41	0.53	-0.33		-0.39	-0.34			-0.40	
Total BZ 2011		0.93		-0.35		-0.36	-0.34	-0.33		
BZ:BP 2011			-0.38	-0.42		-0.41	-0.45	-0.40		
Ciliate 2011		0.84	-0.42	-0.38			-0.42	-0.34		
Tecamoebae 2011		0.70								
Rotifera 2011		0.85				-0.39		-0.34		
Cladocera 2011		0.74								
Copepoda 2011		0.67								
Class I 2011		0.71	-0.40	-0.36			-0.36	-0.34		
Class II 2011		0.84		-0.33			-0.41			
Class III 2011		0.84								
Class IV 2011		0.86				-0.34				

Table V

	TSS	TP	PO ₄	TN	NO ₂	Chl <i>a</i>	Secchi	Temp	Cond	pH	ORP	Turb	DO	WV	Nebul	Precip	Insol	Evap
Total BZ 2010			-0.41		-0.39	0.34				0.58					-0.41		0.49	
Total BP 2010		0.38	0.72		0.60		-0.39			-0.40		0.52			0.36			
BZ:BP 2010										0.34							0.36	
Ciliate 2010							0.51					0.35			-0.38			
Tecamoebae 2010		0.46				0.50		0.34		0.49							0.38	
Rotifera 2010			-0.42		-0.41					0.52					-0.40		0.43	
Cladocera 2010													-0.34				0.44	0.35
Copepoda 2010		0.36				0.47				0.60							0.48	
Class I 2010	0.33	0.57				0.59		0.34		0.53	0.40						0.50	0.35
Class III 2010			-0.39		-0.39					0.49					-0.42		0.46	
Class IV 2010		0.34				0.45				0.61					-0.38		0.53	0.37
Class V 2010																0.48		-0.39
MLD II 2010	0.45	0.34	0.39									0.45						
MLD III 2010		0.38	0.71		0.62		-0.38			-0.40		0.52			0.34			
MLD IV 2010			0.38			-0.35			0.45	-0.46		-0.33	0.49	0.52			-0.48	
UNF 2010			0.44		0.42							0.41						
FI 2010			0.34	-0.44														
CNF 2010		0.38	0.72		0.60		-0.39			-0.41		0.52			0.36			
UF 2010				0.45						0.39							0.34	
CF 2010		-0.37																
Total BZ 2011		0.74	0.70					0.55	0.72	-0.59	0.49		-0.61	0.75			0.66	0.54
Total BP 2011					0.65			0.45	0.36								0.41	0.52
BZ:BP 2011		0.71	0.65					0.47	0.61	-0.48	0.39		-0.57	0.65			0.56	0.45
Ciliate 2011		0.76	0.76					0.53	0.62	-0.47	0.33		-0.67	0.49	-0.38		0.59	0.50
Tecamoebae 2011		0.60	0.55					0.48	0.64	-0.54	0.46		-0.61	0.54			0.57	0.49
Rotifera 2011		0.69	0.60					0.38	0.53	-0.41	0.37		-0.46	0.56			0.48	0.36
Cladocera 2011		0.63	0.61				-0.34	0.58	0.75	-0.63	0.55		-0.64	0.74			0.67	0.58
Copepoda 2011		0.43	0.43					0.40	0.54	-0.46	0.39		-0.35	0.68			0.48	0.40
Class I 2011		0.65	0.70					0.42	0.46				-0.52	0.35	-0.34		0.41	0.34
Class II 2011		0.76	0.72					0.60	0.75	-0.62	0.53		-0.76	0.61	-0.34		0.73	0.63
Class III 2011		0.77	0.70	0.38			-0.38	0.50	0.70	-0.58	0.48		-0.58	0.68			0.62	0.49
Class IV 2011		0.62	0.58					0.49	0.65	-0.54	0.47		-0.51	0.75			0.59	0.48
Class V 2011														0.34				
MLD I 2011			-0.44		0.70													
MLD II 2011			-0.41		0.61													
MLD III 2011					0.60		-0.33	0.45	0.38	-0.33								
MLD IV 2011		-0.41			0.60							-0.40		-0.46				0.33
UNF 2011			-0.43		0.62													
FI 2011		-0.38			0.62									-0.42				0.36
CNF 2011					0.61			0.45	0.37								0.42	0.52
UF 2011						0.45												

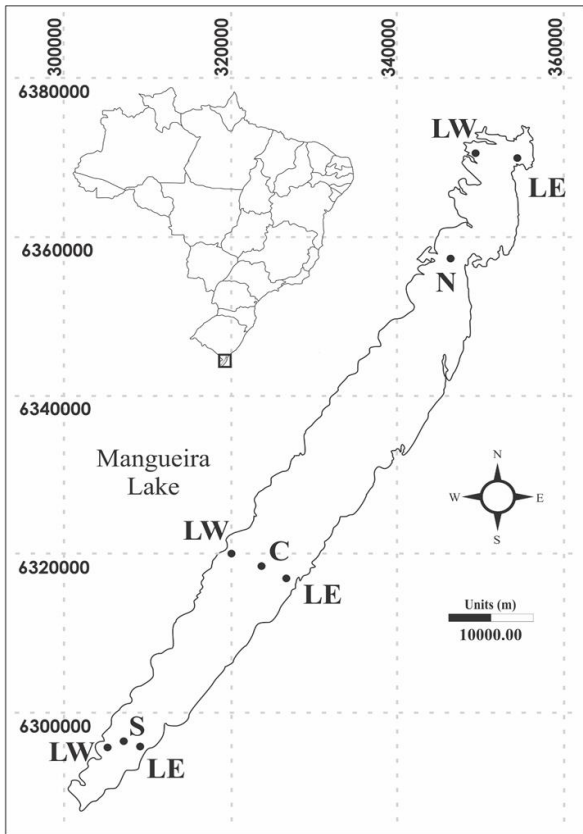


Fig. 1

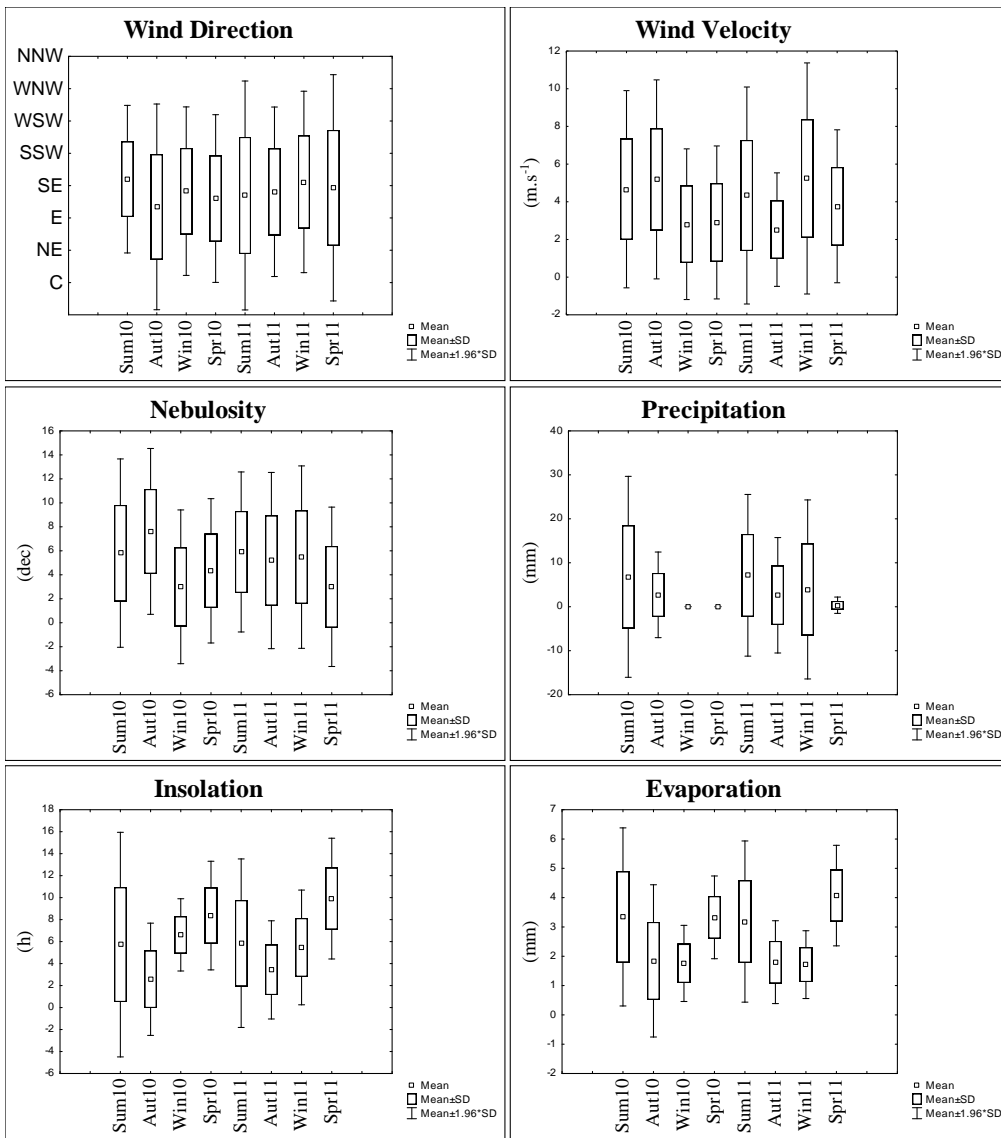


Fig. 2

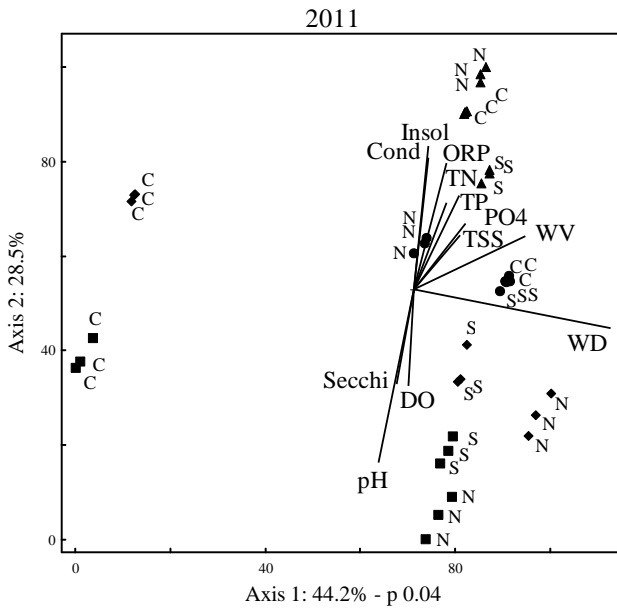
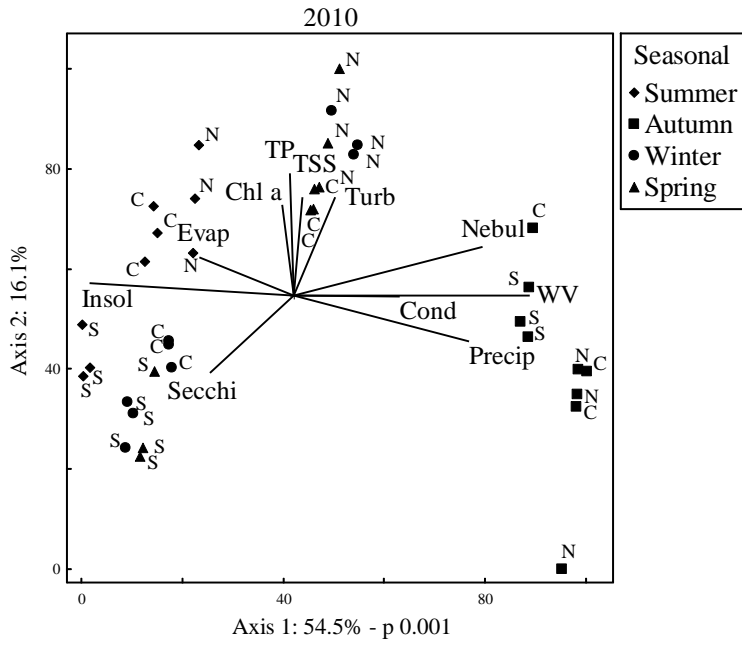


Fig. 3

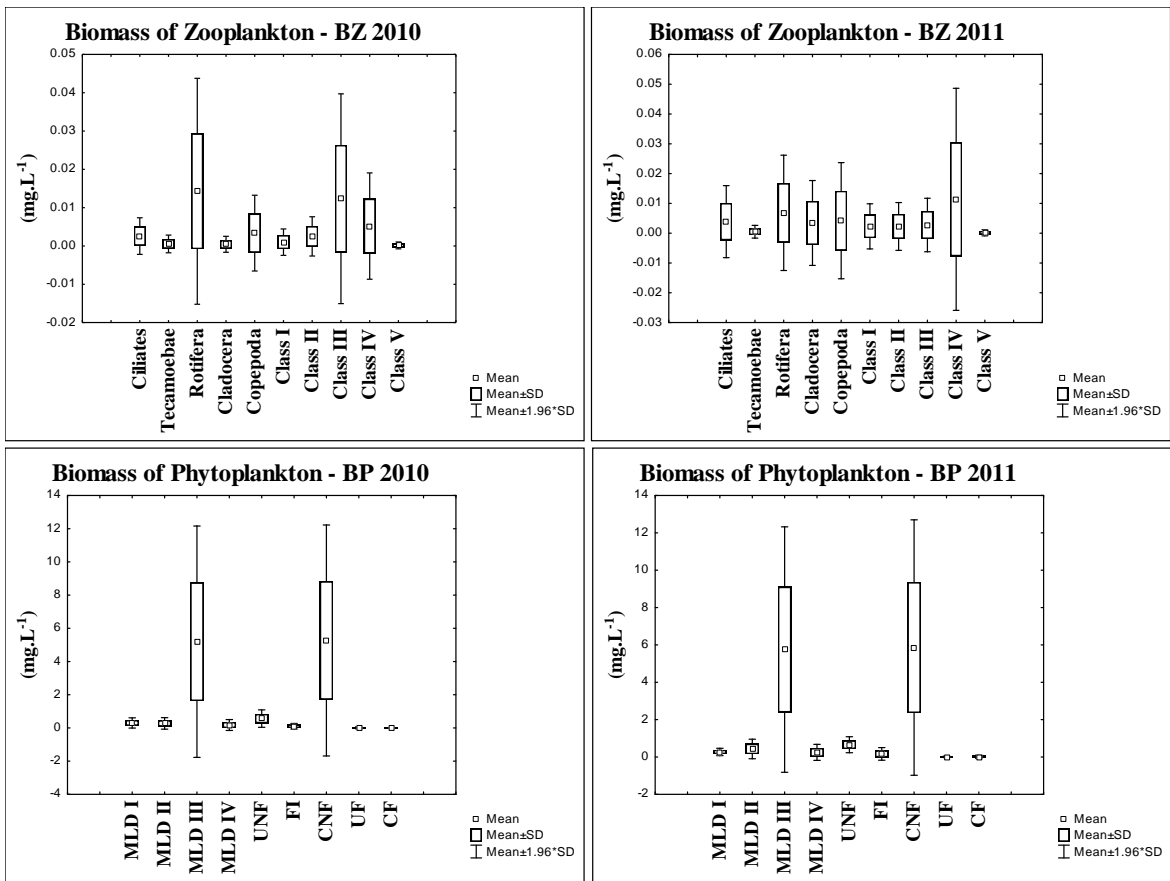


Fig. 4

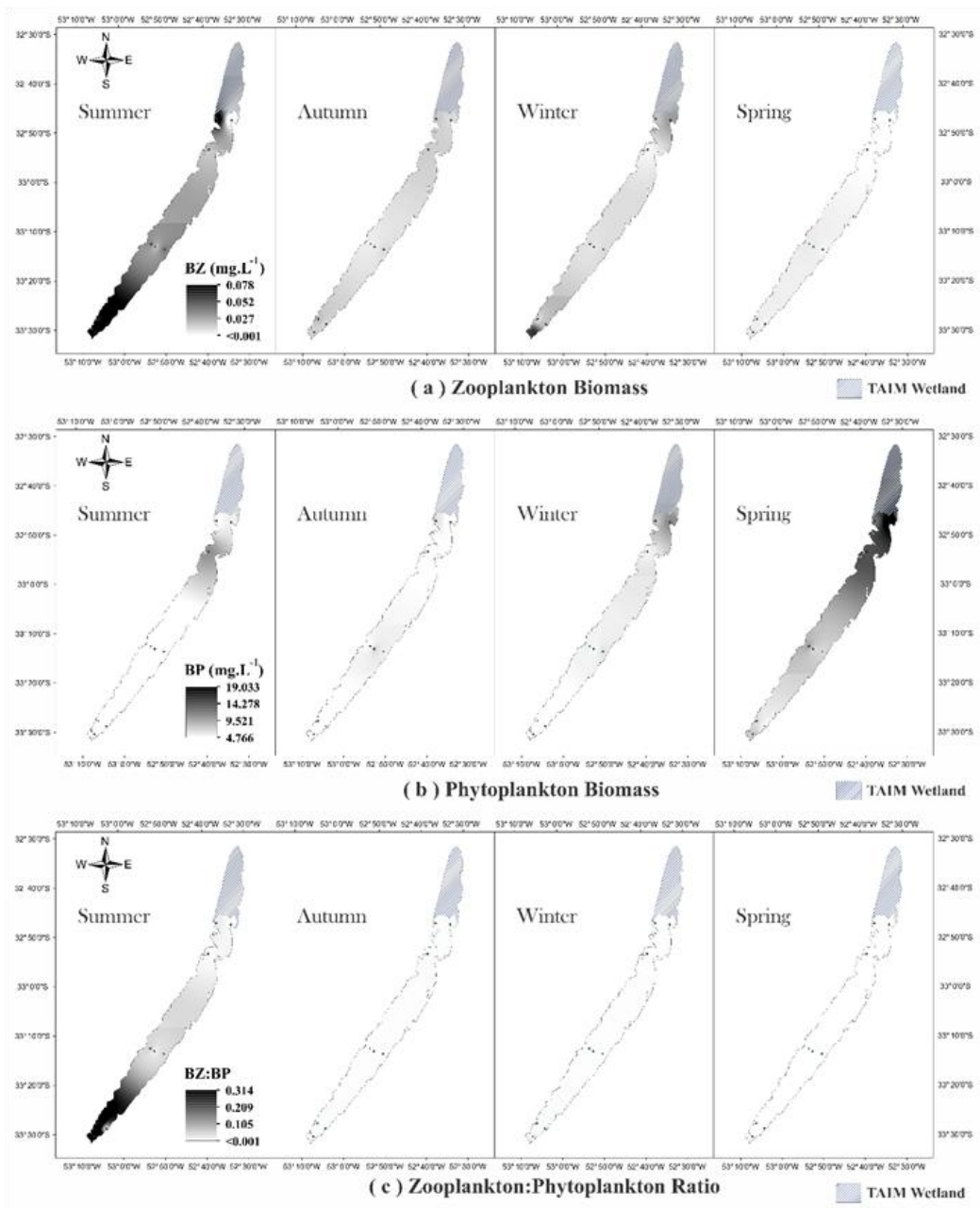


Fig. 5

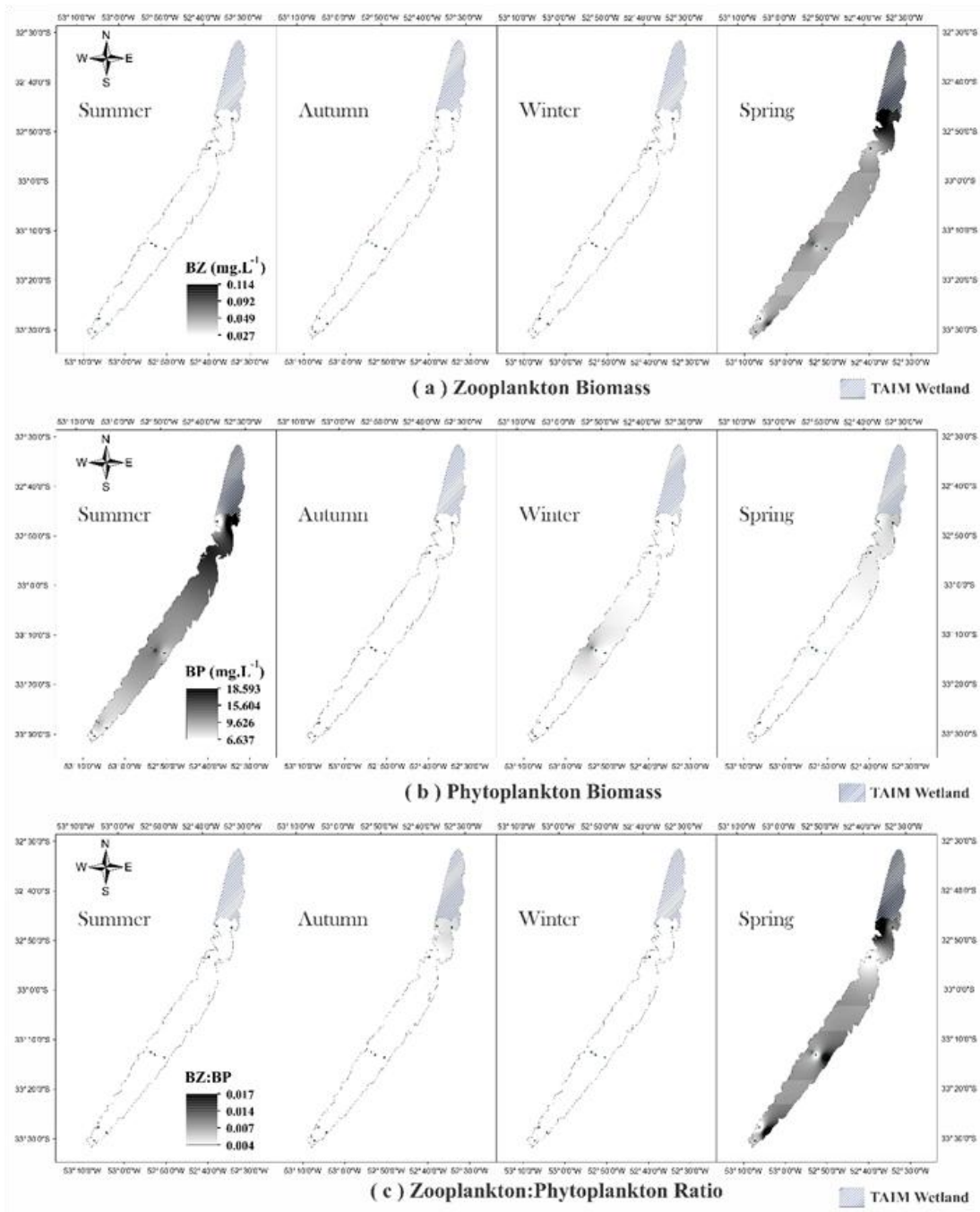


Fig. 6

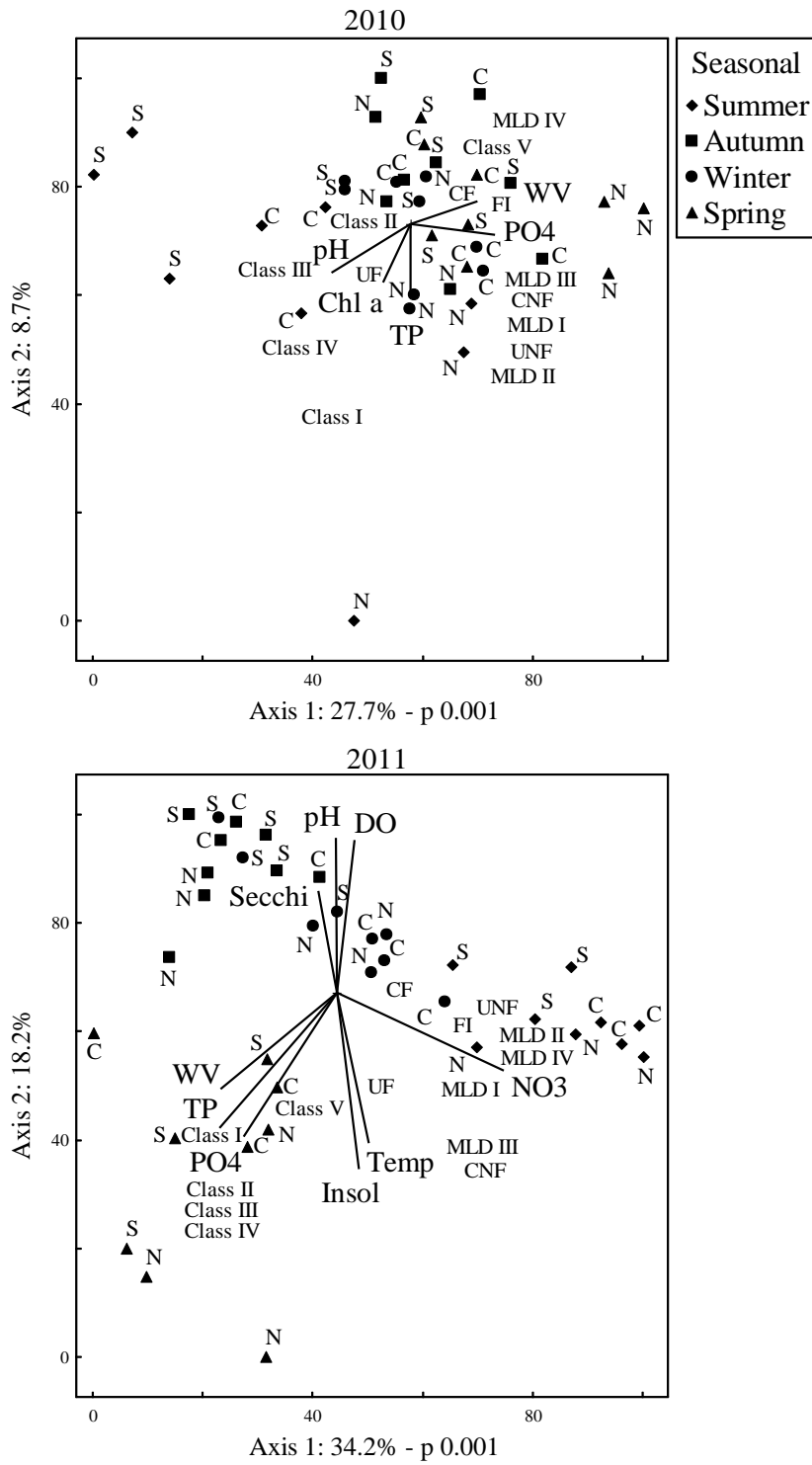


Fig. 7

CONSIDERAÇÕES FINAIS

Este trabalho é um acréscimo ao banco de dados e às informações sobre lagos rasos em sistemas subtropicais, os quais ainda não foram amplamente estudados como em regiões temperadas. Em tais sistemas, o conhecimento avançado da estrutura da cadeia trófica aquática alcançou um patamar onde se tornou possível o desenvolvimento de estratégias de biomanipulação, enquanto nos ecossistemas aquáticos subtropicais ainda há muitas lacunas no conhecimento dos reguladores de tais interações tróficas.

As relações entre algas planctônicas e o zooplâncton tendem a ser muito fracas em ambientes subtropicais, como foi demonstrado neste trabalho. Porém, devido à grande variabilidade ambiental a qual lagos rasos estão permanentemente expostos, a força dessa interação e a capacidade do zooplâncton em controlar a biomassa do fitoplâncton podem variar tanto numa escala de tempo (durante um ano ou entre anos), quanto ao longo de um gradiente espacial formado por diferentes características físicas, químicas e biológicas dentro de um mesmo lago. A partir disso, percebemos a necessidade de compreender melhor a interação dos diversos fatores envolvidos na estruturação das comunidades aquáticas, bem como a importância de incorporar os demais níveis tróficos envolvidos na transferência de energia nesses ecossistemas, como bactérias peixes.

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- always use the latest version of the software program available. Files from older versions often lose integrity when opened in newer versions.

Line Figures

Line figures should be the size intended for publication (maximum dimensions 220 x 164 mm including legends), with uniform lettering style which is in proportion with the overall dimensions of the drawing. All lines, letters and symbols should be black: grey does not reproduce on printing. No additional artwork, re-drawing or typesetting will be done. Scale bars, where appropriate, should be included within the figure, not in the legend.

Photographs

Photographs must be submitted for printing in the desired final size so that reduction can be avoided. Photographs, including their legends, must not exceed 220 x 164 mm. Photographs should be of sufficiently high quality with respect to detail, contrast and fineness of grain to withstand the inevitable loss of contrast and detail inherent in the printing process. Please indicate the magnification by a rule on the photograph. Do not state the magnification in the legend: it may be necessary to change photographs slightly to improve the layout of the paper.

Colour Figures

Colour illustrations are accepted, but will incur a charge of **£350** per figure. Illustrations for which colour is not essential can be reproduced in black and white in the print Journal and, additionally, in colour as online Supplementary Data. This option is not subject to colour charges. Authors should indicate clearly that they would like to take up this option in their original submission.

Colour Figures as Supplementary Data

Illustrations for which colour is not essential can be made available online as Supplementary data, linked to the online manuscript. The availability of additional colour images as Supplementary Data should be mentioned where relevant in the main text of the manuscript.

Process. Authors should indicate clearly that they would like to take up this option in their original submission. Colour figures for online-only reproduction must be submitted at the same time as the main manuscript. They cannot be altered or replaced after the paper has been accepted for publication. The figures must be identical to those reproduced in the print journal, but for the addition of colour.

Conventions

In general, the Journal follows the conventions of the CBE Style Manual (Council of Biology Editors, Bethesda, MD, 1983, 5th edn). Follow Chemical Abstracts and its indexes for chemical names. For guidance in the use of biochemical terminology follow the recommendations issued by the IUPAC-IUB Commission on Biochemical Nomenclature, as given in *Biochemical Nomenclature and Related Documents*, published by the Biochemical Society, UK. For enzymes use the recommended name assigned by the IUPAC-IUB Commission on the Biochemical Nomenclature, 1978, as given in *Enzyme Nomenclature*, published by Academic Press, New York, 1980. Where possible, use the recommended SI (Système International) units. Genotypes should be italicized (underline in typed copy): phenotypes should not be italicized. For bacterial genetics nomenclature follow Demerec *et al.* (1966) *Genetics*, **54**, 61-76.

Abbreviations

Try to restrict the use of abbreviations to SI symbols and those recommended by the IUPAC-IUB. Abbreviations should be defined in brackets after their first mention in the text. Standard units of measurements and chemical symbols of elements may be used without definition in the body of the paper.

Chemical formulae and mathematical equations

Wherever possible, write mathematical equations and chemical formulae on a single line. Submit complicated chemical structures as artwork.