Phytoplankton community in the tropical lake of Lagoa Santa (Brazil): Conditions favoring a persistent bloom of Cylindrospermopsis raciborskii

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A B S T R A C T

This study presents data on seasonal changes of the phytoplanktonic community of a small tropical lake, Lagoa Santa, in the Brazilian cerrado. Temporal variation in the community structure was small and we observed a permanent dominance of the cyanobacteria Cylindrospermopsis raciborskii. This dominance could be associated to the stability of several environmental conditions. Especially water temperature, always within the optimal growth range for C. raciborskii, and the constant mixed water column may have been important factors driving to the long term dominance of this species in the lake. Remarkable seasonal variation in rainfall, as well as the occasional and non-seasonal variation in nutrient concentrations, were important to explain changes in environmental and biological variables, but were not related to the dominance of C. raciborskii. Pearson’s correlation and PCA could just in part explain the stable dominance of this cyanobacterium. Meteorological and chemical factors seem to have no clear control on the variability of the phytoplankton dynamics in Lagoa Santa. The weak relationship between C. raciborskii abundance and environmental variables points to additional intrinsic factors associated to this species that may be important in structuring the phytoplankton assemblage.

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Introduction

The competitive exclusion principle suggests that the superior competitor species would dominate a constant environment and lead to a low community richness and diversity. Contradicting this principle, phytoplankton communities generally consist of a wide variety of species in a believed stable environment, which was described as paradoxical (Hutchinson 1961). The Hutchinson’s dilemma named “Paradox of the Plankton” was explained by non equilibrium conditions due the fluctuations of the environment (Hutchinson 1961), related to annual cycles of physical, chemical, and biological factors. Most pelagic systems are extremely sensitive to these environmental changes resulting in unstable conditions and discontinuously advantageous habitat features for different species (Reynolds 1997; Calijuri et al. 2002). Studies about population dynamic and ecological succession have showed that a fluctuating environment results in phytoplankton communities comprising different species at different seasons (Sommer et al. 1986; Talling 1987; Giani 1994; Figueredo and Giani 2001). Meteorological conditions play a major role in the dynamic of aquatic systems. The temporal cyclic patterns of phytoplankton composition are well-known in temperate regions, where temperature, stratification, light, and nutrients availability exhibit recurrent seasonal dynamics (Sommer et al. 1986; Grover and Chrzanowski 2006). In tropical lakes, oscillations of total radiation and water temperature are relatively small, but seasonal patterns of phytoplankton communities are not negligible (Talling 1987). These environments also exhibit seasonal changes in climate (especially related to precipitation) that induce modifications in the physical and chemical characteristics of the water and influence phytoplankton dynamics (Costa and Silva 1995; Figueredo and Giani 2001). Sedimentation, grazing, light, CO2, or nutrient concentrations act as forces distinguishing among phytoplankton species, and selecting those better adapted to a particular environmental condition (Anneville et al. 2004). Based on the Intermediate Disturbance Hypothesis (Connell 1978), Reynolds (1993) states that succession in a phytoplankton community should lead to the organization and maintenance of an energetic steady-state, but the direction of the events is deviated by stochastic environmental variability. The final phytoplankton composition results from the balance between gains and losses within the pool of species adapted to survive in that particular environment (Reynolds 1997).

Considering the previously mentioned studies, the presence of cyclic patterns in the communities and their surrounding environment during a long period of time indicates stable conditions (Zohary 2004), but does not necessarily represent a constantly equilibrated ecosystem. For Sommer et al. (1993) a phytoplankton...
community is considered to be at equilibrium when: (i) 1, 2, or 3 species contribute for more than 80% of the biomass; (ii) their existence or coexistence persists for more than 2 weeks; and (iii) during that period the total biomass does not increase significantly. The common non-equilibrium conditions found in natural environments (Reynolds 1988) strengthened Hutchinson ideas and intensified succession studies. However a paradoxical question in phytoplankton ecology today is the potential existence of equilibrium conditions, in which the competitive exclusion principle could be playing an important role. According to Reynolds (1988), there are a few examples of natural phytoplankton populations living at equilibrium, such as the long periods of Microcystis dominance in some equatorial lakes subject to small seasonal climatic variation. The long periods of cyanobacteria absolute dominance, with short oscillations in successional events, may resemble an equilibrated state of phytoplanktonic communities and are an interesting subject of study.

Cyanobacterial blooms, as regular events in the phytoplankton seasonal succession, are often predictable, although their intensity and extent varies substantially from year to year (Kanoshina et al. 2003). Several factors can influence the dominance of cyanobacteria in phytoplankton communities, but it is difficult to determine which are the most important because synergistic forces are usually involved. Some studies have shown that an equilibrium condition with cyanobacterial dominance could be expected in some stable environments. Scheffer et al. (1997), for example, consider that the dominance of Oscillatoriaeae can be an alternative stable state in the algal community of shallow lakes, because their high density increases turbidity, which favors themselves due to their competitive advantage to tolerate shade conditions. However, the constant dominance of other cyanobacteria populations is not so clearly understood.

Cylindropermopsis raciborskii (Woloszynska) Seenaya and Subba Raju is a toxic tropical cyanobacterium that can dominate the phytoplankton biomass for long periods (Padisák 1997; McGregor and Fabbro 2000), responding weakly to environmental variability. For Reynolds (1988) an important characteristic of a successful species is its physiological flexibility giving resistance to environmental changes or permitting to survive critical phases, during which physiological tolerance limits may be temporarily exceeded. In this sense, C. raciborskii could be considered a highly successful competitor. Several competitive characteristics have been suggested to explain the success of C. raciborskii in aquatic systems: high affinity for phosphorus and high P-storage capacity (Isvánovics et al. 2000); superior shade tolerance (Briand et al. 2002); N₂-fixation; high affinity for ammonium, allowing it to capitalize on the cheapest N source while other heterocytic species must fix N₂; resistance to grazing due to toxicity; buoynancy control; ability to form akinetes, allowing easy dispersal and environmental resistance (Padisák 1997), wide thermal tolerance (Briand et al. 2004) and allelopathic interference (Figueredo et al. 2007).

The physiological attributes of C. raciborskii could permit its invasion on several regions around the world including temperate systems at high latitude (Padisák 1997, Mischke 2003). In some Florida lakes, this species appears to have replaced other bloom-forming cyanobacteria (Chapman and Schelske 1997). In Constance Lake, Canada, a temperature increase of a few degrees was sufficient to shift the dominance to C. raciborskii, independently of ambient nutrient concentrations (Hamilton et al. 2005). Antenucci et al. (2005) showed that destratification did not change the dominance of C. raciborskii, although it was successful in reducing chlorophyll a (Chl a) in downstream areas. After its appearance, blooms of C. raciborskii generally follow a seasonal pattern, although the occurrence of persistent blooms has become more frequent (Padisák 1997; McGregor and Fabbro 2000).

Lagoa Santa is a small shallow Brazilian lake whose phytoplankton community exhibits a dominance of C. raciborskii during at least the last four years. Here we examined seasonal dynamics of the phytoplanktonic community and especially that of C. raciborskii biomass in response to environmental variables. Our main objectives were to identify and to rank the main environmental factors affecting the phytoplankton structure and seasonal dynamic in Lagoa Santa.

Study site

Lagoa Santa is a shallow natural lake situated at 740 m altitude and located at 19°38’S and 43°53’W in the Brazilian savannah (cerrado). It has a surface area of 1.31 km² and a catchment area of 11.34 km² (Parizzi et al. 1998). The region presents a striking seasonality with a dry season lasting from May to September, with less than 7% of annual rains, and a distinct rainy season from October to April. Lagoa Santa has suffered environmental degradation, which is reflected in increasing eutrophication and the loss of fish diversity (Pompeu and Alves 2003). It is characterized by permanently turbid water, maybe due to the low depth of this system, high chlorophyll a concentrations and the stable dominance of C. raciborskii.

Methods

To assess seasonality in the phytoplankton community and the environmental variables, a site located near the central pelagic region of the lake was monthly sampled from May 2005 to August 2006. Maximal depth at this site varied according to the season (dry or rainy), with a mean of 4.5 (±0.5 m) during our study. The starting time of sampling was always around 9:30 a.m.

Water transparency was measured with a Secchi disk and was used as a measurement of light availability. Light availability was also quantified as the ratio between the depth of mixing zone (z_m, considered to be equal to the total depth since the lake is polytomic) and the depth of the euphotic zone (z_e, considered to be equal to the Secchi depth, multiplied by 3). (DKolul and Teubner 2000). In situ profiles of temperature, pH, and dissolved oxygen (DO) were obtained in 0.5 m intervals with a multi-parameter probe (Horiba U-10) prior to water sampling. Depth-integrated samples were stored in polyethylene bottles on ice and transported to the laboratory. In the laboratory, water samples were immediately filtered (filter S&S GFA, pore size 1.2 µm), frozen, and subsequently analyzed for dissolved nutrients (ammonium, nitrite, nitrogen, and soluble reactive phosphorus). Except for nitrate, nutrients were analyzed using standard colorimetric techniques (APHA 1995). Nitrate was electrochemically measured using a low-level calibrated nitrate-sensitive electrode (Hach Platinum Series combination electrode 51920, Hach Company, Loveland, USA) connected to a volt meter (Hach Senslon 2, Hach Company, Loveland, USA). Measurements were performed under controlled temperature conditions (±0.3 °C variation in sample temperature). To avoid interference effects of varying chloride concentrations, the chloro dilutions of the samples were adjusted to the chloride concentrations of the nitrate standards prior to analysis using a chloride-sensitive electrode (Orion Chlorid Ionplus Electrode 9617BN, Thermo Fisher Scientific, Waltham, USA) connected to a volt meter (Hach Senslon 2, Hach Company, Loveland, USA). Unfiltered water samples were frozen for subsequent analyses of total nitrogen and total phosphorus by acidic and buffered persulphate oxidation, respectively. Filters were used to obtain total, organic, and inorganic suspended solids (APHA 1995), and chlorophyll a concentrations in water. Chlorophyll a...
concentration was calculated from spectrophotometric measurements after extraction in 90% hot ethanol (Nusch 1980). Molar total-N:total-P ratios were calculated.

In situ, a fraction of the integrated sample was stored in a 500 mL flask and immediately preserved with Lugol's iodine solution for subsequent phytoplankton counts. Counts were performed on an inverted Olympus microscope following the Utermöhl technique (1958). The number of heterocytes by trichome was registered for each sample. Species biovolumes were calculated from cell numbers and mean cell volumes, which were obtained using geometrical models (Rott 1981).

Climate data (rainfall, air temperature, and wind speed) were kindly provided as monthly means by the meteorological Station of Tancredo Neves Airport (located at ca. 5 km from Lagoa Santa).

Statistical methods

To examine individual relationships between variables, a Pearson correlation matrix was calculated. To extract the main tendencies between environmental variables and phytoplankton data from the data pool, a principal component analysis (PCA) was performed using STATISTICA 5.0 Software (1995, Tulsa, USA). Three PCA's were performed separately for (i) environmental variables only, (ii) environmental variables and phytoplankton biomass (expressed as total chlorophyll a concentrations and total phytoplankton biovolume), and (iii) environmental data and the biomass of each phytoplankton group (expressed as biovolume), including that of the dominant species C. raciborskii. Due to the high autocorrelation observed in the Person's analysis, not all variables were included in the PCA. Nitrogen, for example, was represented in the analysis just by one or two of its different forms that include NH₄⁺, NO₂⁻, NO₃⁻, dissolved inorganic nitrogen (DIN), or others nitrogen sources like total-N or total Kjeldahl nitrogen (TKN). The profiles of water temperature, pH, and DO were represented just by mean values in statistical analyses. Normality tests were performed using the Shapiro–Wilk's test and homocedasticity was evaluated by the Brown–Forsythe test. In order to obtain the normality and homocedasticity required and to evaluate data under a similar scale, all variables were log 10 transformed prior the Pearson correlations and PCA analysis.

Results

Climatic, physical, and chemical characteristics

Climatic conditions were typical for the region, characterized by rainy summers and dry winters (Fig. 1). The annual precipitation (September 2005–August 2006) was 1105 mm and monthly means of air temperature ranged from 17.2 to 24.1°C (September 2005–August 2006) was 1105 mm and monthly means of rainfall oscillated in small amplitude (0.8–1.2 m) during the year. The water column was always isothermic and just once (November/2005) showed small temperature differences from surface to bottom, always allowing the water mass to circulate. The same pattern was observed for pH and DO, and there was no evidence of lack of oxygen in the deep water. The seasonal fluctuation of water temperature followed the air temperature pattern. The minimum and maximum water temperatures were recorded in July 2005 (20.0°C) and February 2006 (28.1°C), respectively. Total suspended solids concentrations exceeded 6.0 mg L⁻¹ and the organic fraction was generally more important than the inorganic (Fig. 3). Water transparency oscillated in small amplitude (0.8–1.2 m) during the sampled period (Fig. 3). Secchi measurements and suspended particles concentrations did not show any seasonal cyclic trend and did not exhibit any expected negative relationship.

Nutrients

Maximum and minimum concentrations of NH₄⁺, NO₃⁻, DIN, and total-N were 7.7–55.2, 9.0–91.0, 19.9–134.6, and 412.2–692.7 μg L⁻¹, respectively. Nitrite concentration constituted an insignificant portion of the dissolved nitrogen pool (<2.0%). No seasonal patterns were observed for these variables. All dissolved nitrogen sources showed similar temporal dynamics and exhibited highly positive auto-correlations. For this reason, these variables were represented by DIN (r = 0.91 for DIN and NH₄⁺, and k = 0.93 for DIN and NO₃⁻, p < 0.01).

Maximum and minimum concentrations of total-P were 15.2 and 30.5, respectively. SRP concentrations varied from non-detectable values up to 7.6 μg L⁻¹. Both total-P and SRP showed decreasing concentrations during the rainfall period as a consequence of dilution. Such dilution effects were reinforced by the significant (p < 0.05) negative correlations between rainfall and SRP (r = −0.56) and between rainfall and P-total (r = −0.62). Total-N:total-P ratio presented no seasonal trend and ranged from 34.8 to 89.5 over the studied period.

Phytoplankton community

Chlorophyll a concentrations ranged from 23.0 to 43.2 μg L⁻¹ over the studied period and were not significantly correlated to phytoplankton biovolume (r = 0.12, p > 0.05). During the sampling period, the algal community of Lagoa Santa was abundant, with a mean biovolume of 4.3 mm³ L⁻¹. A discrete seasonal variation in phytoplankton total biovolume was observed (Fig. 4), ranging from 2.3 mm³ L⁻¹ in March 2006 to 6.7 mm³ L⁻¹ in October 2005. Cyanobacteria dominated the phytoplankton community throughout the year (Fig. 4). The dominant species was always C. raciborskii, accounting for nearly 70% of total phytoplankton biovolume during almost all studied period. Variation of this species generally affected changes in the total phytoplankton biomass, as can be seen in Figs. 4 and 5.

Fig. 5 shows the contribution of the most abundant species that together accounted to 80% of the total phytoplankton biovolume. The relative contribution of C. raciborskii exhibited a significant decrease just for three of the fifteen months studied, especially when the diatoms Cyclotella sp. Kützting and Aulacoseira granulata (Ehrenberg) Simonsen showed an intense growth in June and July 2005 and Peridinium umbonatum F. Stein (Dinophyta) in February 2006. Akinetes were never present and heterocytes were recorded in less than 20% of the trichomes (Fig. 6). Although
Fig. 2. Profiles of temperature, pH, and dissolved oxygen in Lagoa Santa during the studied period.

Fig. 3. Seasonal changes in the Secchi disk depth and in the concentrations of the organic and inorganic fractions of total suspended solids in Lagoa Santa during the studied period.

Fig. 4. Phytoplankton community structure in Lagoa Santa during the studied period. (Others: Chrysophyta, Bacillariophyta, Euglenophyta, Dinophyta and Cryptophyta.)

Fig. 5. Proportional contribution of C. raciborskii and other phytoplanktonic species to the total phytoplanktonic biovolume in Lagoa Santa during the studied period (total biovolume is considered as 1, and specific biovolumes are represented by a proportion of this value).
heterocytes were rare, we could observe a negative correlation between this variable and DIN ($r = -0.59, p < 0.05$).

Interestingly, the biovolume of *C. raciborskii*, total cyanobacteria, and total phytoplankton were not significantly correlated to water temperature, light availability, and concentrations of nitrogen and phosphorus forms. This suggests that climatic variables and nutrients, when analyzed separately, could have a weak influence on the phytoplankton dynamic and structure of Lagoa Santa. Light conditions ($Z_m:Z_{eu}$) were only positively correlated to other less relevant cyanobacteria ($r = 0.52; p < 0.05$), mainly represented by three species of *Planktolyngbya* Anagnostidis and Komárek.

**Principal component analysis**

The results of the PCA on environmental variables pointed out that climate, nutrients, pH, DO, and suspended solids were ‘master variables’ driving variation in water characteristics (Fig. 7). These variables were related to 60% of the total environmental variability in Lagoa Santa. The first factor explained about 33% of the total variability and was correlated to variables that exhibited a seasonal variation (rainfall, water temperature, SRP, and total-P). The second factor explained about 30% of the total variability. It had suspended solids and dissolved nitrogen ($\text{NH}_4^+$ and $\text{NO}_3^-$) as major constituents and reflected the weak connection between these variables and the climate (Fig. 7). A third axis accounted to just 12% of the variance and had light condition as the main explanatory variable.

When including biological variables representing total phytoplankton community (chlorophyll $\alpha$ concentration and total phytoplankton biovolume), the first two factors of the PCA explained 51% of the total variability (Fig. 8). As observed in the PCA performed for environmental factors only, the first factor was correlated to variables with seasonal trends (rainfall, water temperature, total-P, and, in minor scale, SRP) and accounted to 31.9% of the total variability (Fig. 8). Suspended solids and DIN, used as nitrogen data to this analysis, were correlated to the second factor and accounted to 19% of the total variability in the data pool. Light availability and phytoplankton biovolume, with inverse relationship, were correlated to the third factor and accounted to 15% of the total variability.

A second PCA was run for biological variables as taxonomic phytoplankton groups, including the biovolume of the dominant species *C. raciborskii*. The first factor was correlated to climatic data (rainfall and temperature), phosphorus, and the Cryptophyte biovolume (Fig. 9) and accounted to about 30% of the total variability. The second factor accounted to 17% of the total variability and was correlated to DO, light availability, and the biovolume of ‘other cyanobacteria’ group, all of them positively correlated each other. The third axis maintained its explanatory capacity of ca. 15%, having pH and SRP as the main variables.

**Discussion**

**Climatic, physical, and chemical characteristics**

As the air temperature, water temperature also showed a clear seasonal pattern, although varied in small amplitude at high
values. The relative stable temperature conditions may have contributed to the stability of the phytoplankton community in Lagoa Santa, which was dominated by *C. raciborskii* throughout the entire studied period. It is well known that cyanobacteria have high temperature optima (Padisák 1997; Briand et al. 2002; Bormans et al. 2005; Grover and Chrzanowski 2006). The lack of significant correlations between phytoplankton variables and temperature in the present study probably resulted from the small temperature changes in Lagoa Santa, which were very close to cyanobacteria optima values. Despite the temperature stability, tropical regions however can present striking phytoplankton seasonality. In a Brazilian reservoir (Jurumirim reservoir, São Paulo State, Brazil), Nogueira (2000) reported a succession of species characterized by the dominance of *Microcystis aruginosa* in summer, *Anabaena circinalis* and *A. spiroides* during fall/winter, and the diatoms *Aulacoseira granulata* and *A. italica* in spring has been reported. In tropical regions, rainfall promotes physical disturbance in the water column and is sometimes considered to be more important than temperature and solar radiation in regulating seasonal phytoplankton dynamics in tropical aquatic systems (Figueiredo and Giani 2001). Since rainfall showed a remarkable seasonal variation in Lagoa Santa region during the studied period, we could expect to find a correlation with the phytoplankton community. However, the phytoplankton was permanently dominated by the cyanobacteria *C. raciborskii*. Additionally, the water-column in Lagoa Santa did not show any stratification phase during the sampling period, meaning that mixing was affected not only by rainfall. This mixed condition probably result from the shallow depth of the lake associated to the weak, but almost constant, winds (7.4–11.1 km h⁻¹) throughout the year. Although the presence and dominance of cyanobacteria are generally associated to higher stability of the water column (Caljuri et al. 2002; Komárová et al. 2003), this relationship has not been verified for *C. raciborskii*. Some authors consider this species to be well adapted to both stable (Harris and Baxter 1996) and unstable (Dokulil and Teubner 2000; Burford et al. 2006) water column conditions. Antenucci et al. (2005) reported a dominance of *C. raciborskii* in the North Pine Reservoir (Australia) under stable stratified and unstable water column resulting from the installation of an artificial destratification system. Constant vertical mixing in Lagoa Santa could be responsible for the phytoplankton stability. Other variables, such as pH and DO, presented no seasonal patterns and were not significantly correlated to the total phytoplankton or the *C. raciborskii* biovolume.

Underwater light availability regulates phytoplankton growth patterns and consequently phytoplankton community structure. Several authors consider light availability as directly related to cyanobacteria dominance in freshwater systems and mixing events may influence light conditions through the resuspension of sediment particles (Mischke 2003). However, neither the total concentrations of suspended solids nor the concentrations of their organic and inorganic fractions were significantly correlated to light parameters measured in Lagoa Santa. Light availability, based on Secchi depth measurements or calculated by the $z_{m:eu}$ ratio, oscillated along the year with no clear seasonal pattern. The $z_{m:eu}$ ratio gives an idea of the exposure time of phytoplankton to light in the water column. When $z_{m:eu} = 1$, cells are constantly illuminated and photosynthesis is continuous during the daylight period, but if $z_{m}$ becomes greater than $z_{eu}$ ($z_{m:eu} > 1$), phytoplankton remains in the dark during part of their daylight period and subsequently photosynthesis decreases (Dokulil and Teubner 2000; Bormans et al. 2005). In Lagoa Santa, $z_{m:eu}$ ratios have never reached values above 1.9 (mean value $= 1.5$), suggesting that phytoplanktonic cells may have not been limited by long dark periods.

More turbid conditions can be advantageous to those cyanobacteria species which are highly shade tolerant, such as species belonging to the Oscillatoriales group (Reynolds et al. 2002). Interestingly, in our work the group of "other cyanobacteria" was almost exclusively constituted by Oscillatoriales (three Planktolyngbya species contributing to 90% of the biomass of the group) and as expected showed a correlation with the $z_{m:eu}$ ratio. Co-occurrence of abundant populations of *C. raciborskii* and Oscillatoriales species was also observed in other freshwater ecosystems (Burford et al. 2006). Fabbro and Duivenvoorden (2000) reported that assemblages of *Cylindrospermopsis*, *Planktolyngbya*, and *Limnothrix* are common in hypertrophic lakes because they are able to grow under low light intensities. In a review, Dokulil and Teubner (2000) related cyanobacterial dominance of *Microcystis*, *Planktothrix agardhii* or *C. raciborskii* at low light availability ($z_{m:eu} > 2$) in turbulent conditions. However, in Lagoa Santa *C. raciborskii* was not correlated to light, but it was the dominant species at $z_{m:eu}$ ratios never higher than 1.9 (mean value $= 1.5$).

**Nutrients**

In a review on the ecology of *C. raciborskii*, Padisák (1997) pointed out the great affinity for ammonium and phosphate and the ability to fix nitrogen as the physiological advantages that mostly contribute to the success of this cyanobacterium throughout the world. Environments that present total-P concentrations around or above 100 µg L⁻¹ have high probabilities to show cyanobacteria dominance, while the abundance of cyanobacteria decreases at total-P levels below 30 µg L⁻¹ (Downing et al. 2001). Although total-P concentrations were not despicable in Lagoa Santa, they were always lower than 30 µg L⁻¹ and the biovolume of *C. raciborskii* was not significantly correlated to both total-P and SRP concentrations. The relatively low concentration of phosphorus and the absence of correlations between the biomass of the dominant cyanobacteria and the phosphorus availability in the lake would suggest other variables or even synergism between...
variables to be important factors favoring the constant dominance of *C. raciborskii*.

Like phosphorus, nitrogen was not scarce in Lagoa Santa and probably could not justify the constant dominance of an N-fixing cyanobacteria in the lake. Huszar et al. (2000) recorded several *Cylindrospermopsis* populations dominating the phytoplankton community under N sufficient conditions in five reservoirs in Northeastern Brazil. In their study, heterocytes were found in only 10% of the trichomes, and the authors considered this low frequency as a consequence of unneccesary heterocyte production. *C. raciborskii* preferentially uses ammonium and nitrate over atmospheric nitrogen (Spröber et al. 2003; Burford et al. 2006), since heterocytes production and N-fixation have a high energetic demand (Reynolds 1997). As observed in the Brazilian Northeastern reservoirs, heterocyte increments in *C. raciborskii* populations of Lagoa Santa were never high (often < 10% and never reaching 20% heterotriched trichomes). Organic nitrogen was the most abundant nitrogen form in Lagoa Santa and varied little throughout the year. It is possible that organic compounds contribute to the nitrogen requirements of the phytoplankton community, including *C. raciborskii* (Burford et al. 2006). This possibility suggests that N could have been sufficient even during periods of NH4 and NO3 shortage, and would explain the low heterocytes production. However, the clear inverse trend between DIN and the heterocyte:trichome ratios in Lagoa Santa suggest that the heterocyte production, even though low, could have some importance during periods of shortage of dissolved N sources.

Based on Redfield stoichiometry, aquatic ecosystems with a N:P molar ratio around 10 are generally considered to be N-deficient, whereas those with N:P molar ratios above 20 are considered P-limited (Redfield 1958). Thus, Lagoa Santa may be considered to be P-limited. To estimate the temporal nutrient availability for phytoplankton, however, the absolute concentrations of N and P are more important. The explanation for this goes back to the Liebig's Law of the Minimum that states that an organism will become limited by the resource, which is in lowest supply compared to the organism's needs. At this moment, the competitive attributes of each species will contribute to the different species-specific responses to the availability of the limiting nutrient, independently of the abundance of other nutrients (Reynolds 1997). Lagoa Santa presented relatively high total-N:total-P ratios throughout the year, being always higher than the critical value of 29 suggested to favor the dominance of cyanobacteria (Smith 1983) or the value of 16 suggested to favor N2-fixing cyanobacteria (Dokulil and Teubner 2000). The ratios emphasized the absence of N limitation in Lagoa Santa and suggested that other factors should be crucial in explaining the constant dominance of *C. raciborskii* in this system.

**Phytoplankton community and equilibrium state**

The lack of a positive correlation between chlorophyll *a* concentrations and phytoplankton biovolume could be a consequence of the different species composition in the samples.

Interestingly, the phytoplankton community of Lagoa Santa was characterized by a permanent dominance of *C. raciborskii*, not clearly related to temporal changes in environmental factors. The dinophyte *Peridinium umbonatum* and the diatom *Cyclotella* sp. had only a minor, but relatively important contribution to the total phytoplankton biovolume. *Planktolyngbya* species were very abundant, but had a minor contribution to the total phytoplankton biovolume due to their small dimensions. The co-existence of *C. raciborskii* and Oscillatoriales species, both considered R-strategists well adapted to low light conditions (Padisák and Reynolds 1998), has been often reported in tropical and temperate seas (Dokulil and Mayer 1996; Mcgregor and Fabbro 2000; Padisák et al. 2003).

Seasonal changes in the phytoplankton community are often explained by competition for nutrients and light (Arndtisits et al. 2004). Cyanobacteria have several kinds of adaptive strategies that allow them to dominate over other phytoplankton groups and lead to their mass occurrence (Dokulil and Teubner 2000). For instance, some blooms of Oscillatoriales are favored under turbid conditions caused by their own growth and dominance. They are known to become self-sustaining by creating light-limited environments for competitors (Scheffer et al. 1997). In general, however, this fact cannot direct succession to a permanent monoculture, because spatial and temporal heterogeneity of the environment would prevent competitive exclusion (Scheffer et al. 1997), making blue-green blooms temporally “patchy”. Nevertheless, less sharp seasonality in the tropics may favor long-lasting cyanobacteria stages, as observed in the present study. Similarly to our findings, cyanobacteria dominance has been observed during entire annual cycles in some Brazilian reservoirs (Huszar et al. 2000). Cyanobacteria dominance, but with a succession of different cyanobacteria species (Nogueira 2000), has also been recorded in another Brazilian system, Jururimirim reservoir. Roelke and Buyukates (2002) consider toxic cyanobacteria blooms to be a deviation from the “normal” ecological system, especially in lakes where recurrent and near-monospecific blooms have disrupted the pattern of phytoplankton succession. The phytoplankton community in Kinneret Lake (Israel), for example, followed a clear seasonal pattern during decades, but cyanobacteria have increased in both their absolute biomass and relative contribution to total phytoplankton biomass (Zohary 2004). During the last years, the author detected strong expansion of cyanobacteria species considered invaders of Kinneret Lake, such as *Cylindrospermopsis* and *Anabaenizonemon ovalisporum*. It is possible that a similar phenomenon is occurring in Lagoa Santa and other Brazilian lakes and reservoirs, but we lack previous data to support this hypothesis. Lagoa Santa may be vulnerable to phytoplankton invaders because constant mixing of the water column acts as a disturbance factor and high disturbance frequency (Connell 1978) might drive to low succession dynamics and creates a system more sensitive to invasion and dominance by exotic or previously less abundant species (Roelke and Buyukates 2002). Some authors (e.g. Calijuri et al. 2002) suggest that the strength of the mixing forces determines the community structure and the existence of an equilibrium state. Although phytoplankton community of Lagoa Santa is clearly very stable, not all the criteria of a reliable equilibrium phase defined by Sommer et al. (1993) could be tested. For example, these authors recommended comparisons at two weeks intervals, while in our study samples were taken every month not allowing inferences at smaller time scales. However, our data suggest that the phytoplankton community in Lagoa Santa is at equilibrium because three phytoplanktonic species accounted for up to 80% of the total biomass throughout the year, as predicted by the Sommer. This equilibrium showed two phases in Lagoa Santa. Initially, the total phytoplankton biomass was almost exclusively represented by *C. raciborskii*, followed by minor abundances of *Peridinium umbonatum* and *Cyclotella* sp. In the second phase, *Planktolyngbya breviculurias* took place instead of *Cyclotella* sp. High stability associated to *C. raciborskii* dominance is not a rare phenomenon worldwide. Bormans et al (2005) studying different locations in an Australian river showed higher stability in a site dominated by *C. raciborskii* when compared to another site of similar chemical and physical characteristics, but dominated by other cyanobacteria. This observation points to the possible importance of synergistic interactions to determine *C. raciborskii* dominance, since small differences among several
environmental variables may have a cumulative effect over the species.

Synergism between variables can be more important in determining phytoplankton structure and the occurrence of blooms than individual variables alone (Dokulil and Teubner 2000; Roelke and Buyukates 2002; Grover and Chrzanowski 2000; Roelke and Buyukates 2002; Grover and Chrzanowski 2004). Environmental variables, generally expected to be significantly correlated to <i>C. raciborskii</i>, such as temperature, pH, TP, <i>z_{ini}/z_{eau}</i> ratio, and NO3 (Pádisák 1997; Huszar et al. 2000), had no clear effects on the dynamic of this species in Lagoa Santa. Contrary to the expectation, however, PCA results were able to identify the main measured variables characterizing the system, but they could not provide more information about <i>C. raciborskii</i> dominance than that obtained by simple Pearson’s correlation. The total variability in the data was mostly caused by variability in climatic variables, as well as in the phosphorus concentrations. Nitrogen data and suspended solids were also important to characterize the system. Since PCA suggested climate and nutrients as the main variables characterizing Lagoa Santa, we would expect more evident effects on the structure of the phytoplanktonic community and on the abundance patterns of the dominant species <i>C. raciborskii</i>. However, according to the PCA, no direct influence of the investigated environmental variables could be related to phytoplankton species. Since the main explanatory variables were those exhibiting remarkable seasonal variation, they may be not important to direct <i>C. raciborskii</i> dynamic in Lagoa Santa, species that showed stable dominance.

The relative stability of <i>C. raciborskii</i> in a system characterized by changing environmental conditions could be originated by its ability to inhibit other phytoplanktonic species by the introduction, for example, of self-shading conditions. <i>C. raciborskii</i> is a shade-tolerant species (Briand et al. 2002) and, as other cyanobacteria, could be competitively stronger under low light conditions, caused by its own growth. Nevertheless, light seems no limiting to phytoplankton growth in Lagoa Santa. Another explanation for the success of <i>C. raciborskii</i> in Lagoa Santa could be a possible allelopathic ability of this species (Figueroedo et al. 2007). There are few studies on allelopathic interactions in aquatic environments. Studying 39 reservoirs in Northeastern Brazil, Bouvy et al. (2000) found that <i>C. raciborskii</i> dense blooms seem to decrease the local biodiversity by eliminating other phytoplankton species. In Lagoa Santa, because of the oscillating environmental conditions, we should have been able to observe the co-existence of other phytoplankton species, or at least more related cyanobacteria species, but we have not. Thanks to the particular conditions of this environment, it is possible that biological interactions, like allelopathy, are more important than environmental variables to explain the stable dominance of <i>C. raciborskii</i> in this system.

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