Low disturbances favor steady state: case of cyanobacterial monodominance in a Brazilian coastal lagoon

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Abstract

Steady state occurs mainly under less pronounced abiotic variation, leading to low diversity and nonsuccessional change, opposite from the nonequilibrium concept. Permanent circulation of a waterbody creates a low disturbance status but does not represent a disturbance because it does not change the diversity and dominance of species. Phytoplankton composition was analyzed in a shallow Brazilian coastal lagoon, Peri (Santa Catarina State, Brazil), in the cold-dry and hot-rainy periods during 2009–2010. Uninterrupted steady state conditions occurred along with the monodominance of the cyanobacteria Cylindrospermopsis raciborskii, which dominated under a nonstratification regime and low availability of dissolved nutrients. Primary production measured as resource-use efficiency indicated a capacity for this species to convert phosphorus into biomass as well as its ability to effective exploit resources. Differences in temperature and nitrogen availability seemed to be the driving parameters for interseasonal changes in the phytoplankton community in Peri Lagoon. Models of competition that predict greater diversity, which lead to greater levels of primary productivity and more complete utilization of limiting resources, were not confirmed in this study. The presence of the dinoflagellate Peridinium umbonatum and C. raciborskii together is suggested to represent shallow, mixed, turbid, and nutrient-deficient ecosystems. Although competitive exclusion would be the primary mechanism that selects for species equilibrium, higher adaptability by a few species under selective conditions seems to be the most important factor in the occurrence of steady states.

Key words: cyanobacteria, disturbance, ecological succession, phytoplankton diversity, steady state

Introduction

Equilibrium/steady state and nonequilibrium hypotheses have often been used to explain community succession and have emerged in phytoplankton studies when discussing the diversity–disturbance relationship. Nonequilibrium concepts are linked to the paradox of phytoplankton, which argues that equilibrium states are unlikely to form in planktonic systems (Hutchinson 1961). The equilibrium/steady state concept describes a situation with low variability in species dominance and total biomass across time (Naselli-Flores et al. 2003), represented by a maximum of 3 species dominating the assemblage for at least 3 weeks with little change in total biomass (Sommer et al. 1993). The constant mixing of the water column would be a convenient biotope for the emergence of steady state conditions (Rott 2002) and may support the dominance of certain phytoplankton species (Komárková and Tavera 2003). Biodiversity should be added to species composition, disturbance, nutrient supply, and climate as a major controller of population dynamics and ecosystem structure. Competition models predict that greater diversity leads to greater primary productivity, leading to a more complete utilization of limited resources (Tilman 1999). Diversity is directly related to a community’s responses to environmental disturbances. The Intermediate Disturbance Hypothesis (IDH) states that undisturbed or highly disturbed communities may develop low diversity, and that disturbances of intermediate frequency and intensity are necessary to maintain high levels of diversity (Connell 1978). Disturbances are mainly...
stochastic abiotic events that result in distinct, abrupt changes in the community taxonomic composition, directing its internal organization and ecological equilibrium.

Disturbance events that affect phytoplankton include temperature changes, influx of nutrients, salinity, wind-inducing mixing, and chemical fluctuations (Padišák 1997), as well as the timescale and frequency of algal generation times (Reynolds 1993). The disturbance impact can be evaluated by the responses obtained from biological variables (Sommer 1993). The onset and breakdown of thermal stratification are key disturbances affecting phytoplankton composition (Morabito et al. 2003). Irregularly occurring mixing events are the predominant disturbance to phytoplankton succession in shallow lakes (Mischke and Nixdorf 2003). The application of IDH may elucidate structural regulation in phytoplankton communities, particularly in tropical regions where phytoplankton complexity is not well understood (Lopes et al. 2009).

The occurrence of toxic cyanobacteria in Brazil has degraded water quality, mainly in warm, shallow, and frequently mixed water bodies (Huszar et al. 2000, Tucci and Sant’anna 2003). *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya and Subba Raju is a bloom-forming cyanobacteria (order Nostocales) with potentially high toxicity and negative consequences for human health (Chorus and Bartram 1999, Backer 2002). *C. raciborskii* has become one of the most notorious blue-green algal species because of its potential toxicity and the tendency to form dense blooms in different types of water use and regions. Its ecological success is attributable to many factors, including buoyancy regulation, tolerance of low light, high affinity for phosphorus and ammonia, nitrogen fixing ability, and resistance to grazing by zooplankton (Padišák 1997). Its presence may modify the general structure of other species or cause a substantial decrease in plankton diversity (Borics et al. 2000, Bouvy et al. 2001, Dobberfuhl 2003, Mischke and Nixdorf 2003).

Less harsh seasonality linked to higher temperatures in the tropics may lead to a higher probability for the existence of long-lasting blue-green algal stages (Huszar et al. 2000) that are highly resilient (Dokulil and Mayer 1996). High temperatures in tropical ecosystems promote the development of *C. raciborskii*, which is also capable of adapting to temperature fluctuations (Padišák 1997).

We investigated the factors driving the dominance of *C. raciborskii* in Peri Lagoon, Brazil, and examined mixing events as a predominant disturbance (Connell 1978) controlling the diversity of phytoplankton and its functional groups (Reynolds 2002). Functional groups consist of species with similar morphology and environmental requirements, but they do not necessarily belong to the same phylogenetic group. Reynolds et al. (2002) advocated for the separation of phytoplankton into functional groups based on their traits, differentiating groups of algae according to habitat type and tolerances to key environmental variables. In contrast to long species lists or usage of dominant taxonomic groups, functional groups facilitate examination and comparison of seasonal changes in various lake types and evaluation of biotic responses to environmental conditions and changes (Weithoff et al. 2001, Kruk et al. 2002).

### Study site

The samples were collected from the tropical riverine Peri coastal lagoon (27°44′S; 48°32′W), a shallow lake in the southwest of the island of Santa Catarina State (area = 5.07 km²; maximum depth = 11 m; mean depth = 4.18 m; volume = 21.2 × 10⁶ m³; catchment area = 20.1 km²) in Brazil (Fig. 1). The climate is characteristically subtropical with rainfall concentrated during the spring and summer (Oct–Mar). The marine-influenced climate of Santa Catarina Island has a mean temperature of 15–17 °C in winter and 24–26 °C in summer (Nimer 1989). The hottest months are January and February (maximum temperature ~36 °C), and the coldest is July (minimum = 3 °C). The average annual relative humidity is high at 82%. Precipitation is relatively well distributed throughout the year but is most abundant during the summer. The average rainfall is ~500 mm annually (Freyslebem 1979). Northerly winds are frequent during the hot-rainy season, while southern winds are colder and more intense, reaching up to 80 km h⁻¹.

A coastal lagoon is defined as an inland water body, usually oriented parallel to the coast, separated from the ocean by a barrier, connected to the ocean by one or more restricted inlets, and having depths that seldom exceed a couple of meters. A lagoon may or may not be subject to tidal mixing, and the salinity can vary from completely freshwater (in the case of Peri) to hypersaline, depending on the hydrologic balance (Kjerfve 1994). Coastal lagoons in Brazil are generally shallow without thermal stratification because of the strong influence from winds (Esteves et al. 1984). A low diversity associated with monospecific blooms is common in coastal lagoons and is considered characteristic of immature communities (Margalef 1977). Some studies on phytoplankton diversity in Brazilian coastal lagoons have been carried out in the southeastern region of the country, but southern data are still scarce (Huszar and Silva 1992).

The Peri coastal lagoon is separated from the sea by a sand barrier and has an elevation of 3 m a.s.l. It is located in a preservation area (Municipal Park of Peri), surrounded by the Atlantic Forest with a restricted human occupation.
The freshwater of the lagoon is a result of 2 inflowing rivers, Ribeirão Grande and Cachoeira Grande, and rainfall. The cyanobacteria *C. raciborskii* is the dominant phytoplankton in Peri Lagoon throughout the year (Laudares Silva 1999, Monardo et al. 2006). Despite dominance by this species, the toxin saxitoxin is only present at low concentrations (0.2 µg L^{-1}; Grellmann 2006). In addition to tourism, research, and recreational use, Peri Lagoon supplies drinking water to the local community in the eastern and southern parts of Santa Catarina Island.

**Methods**

Sampling was conducted twice weekly from 2 June to 3 July (cold-dry period) 2009 and from 2 March to 3 April (hot-rainy period) 2010 (10 samples per period). Water temperature, dissolved oxygen, conductivity, and pH were measured in situ with probes (Multi 350i from WTW, Weilheim, Germany) in 1 m intervals at the deepest point of the lake. Phytoplankton, chlorophyll *a* (Chl-*a*), and nutrient samples were collected every 0.5 m until 8 m depth and analyzed as a mixed sample. Nitrite (N-NO₂; Goltermann et al. 1978), nitrate (N-NO₃; Mackereth et al. 1978), ammonium (N-NH₄; Koroleff 1976), soluble reactive phosphorus (SRP; Strickland and Parsons 1968), total phosphorus and total nitrogen (TP and TN; Valderrama 1981), alkalinity (CaCO₃; Laurenti 1997), and silica (SiO₂; Strickland and Parsons 1968) were determined. The photic zone was measured using a Secchi disk. The Chl-*a* concentration was obtained according to Nusch (1980) using equations described by Lorenzen (1967). Aliquots for phytoplankton analyses were fixed with Lugol’s solution.

A standard number of 400 individuals per sample were identified and investigated according to Utermöhl (1958). Biovolume was calculated by measuring the corresponding dimensions using the geometric formulas given by Rott (1981) and Willén (1976). Diversity measurements included richness (number of species) using the Shannon-Wiener index *H'* (equation 1), estimated as:

\[ H' = -\sum_{i=1}^{S} p_i \log p_i, \tag{1} \]

where *P*ᵢ is the biovolume of the *i*th of S species/total biovolume, evenness of Shannon Wiener index (*H'*-*H*ₘₐₓ); and complement of Simpson index (equation 2), estimated as:

\[ 1 - C = \sum_{i=1}^{S} p_i^2, \tag{2} \]

where *P*ᵢ is abundance of the *i*th of S species/total abundance. We also calculated resource use efficiency (RUE) as an estimation of productivity by converting unit of (µg) Chl-*a* per unit of (µg) TP (Ptacnik et al. 2008, Nixdorf et al. 2009). Seasonal differences in measured...
parameters were tested using Wilcoxon Mann-Whitney tests (significant at p < 0.05). Phytoplankton total biovolume data were used in a detrended correspondence analysis (DCA). Vectors representing environmental parameters were fitted to the ordination. Criteria to identify an equilibrium phase were used according to Sommer et al. (1993), where a maximum of 3 species dominate for at least 3 weeks, and the functional groups proposed by Reynolds et al. (2002) were applied.

**Results**

**Abiotic variables**

Significant interseasonal differences (p < 0.05) were observed for most parameters (Table 1). The Secchi depth (median = 1.3 m), water temperature (27 °C), concentration of dissolved oxygen (8.1 mg L\(^{-1}\)), Chl-a (24.3 µg L\(^{-1}\)), alkalinity (8.5 mg L\(^{-1}\) CaCO\(_3\)), and TP (19.2 µg L\(^{-1}\)) were higher during the hot-rainy period.

The variation and concentration of NO\(_3\)-N (from 3.2 to 10.9 µg L\(^{-1}\)) and dissolved inorganic P (DIP; from 4.0 to 13 µg L\(^{-1}\)) were low in both periods. Higher availability of TN (median = 749 µg L\(^{-1}\)), dissolved inorganic nitrogen (DIN):TP (2.5), and TN:TP (47) was observed during the cold-dry period when compared to the hot-rainy period (median = 524 µg L\(^{-1}\), 1.5, and 26.2, respectively). NH\(_4\)-N was also more available during the cold-dry period (maximum = 53.2 µg L\(^{-1}\)) than during the hot-rainy period (maximum = 32.5 µg L\(^{-1}\)), but there were no significant differences between the seasons for this parameter. The silica concentration was similar during both periods (median ~2.2 mg L\(^{-1}\)) and was at a minimum in the hot-rainy period (1.5 mg L\(^{-1}\)). The variation of oxygen availability at the surface and bottom was 2 µg L\(^{-1}\) (mean of saturation 97% at 1 m and 74% at 8 m). The median water temperature was 18.4 °C during the cold-dry period and 27 °C during the hot-rainy period. The depth–time isopleths showed a relative homogeneity of the water column during both periods (Fig. 2). Generally, the temperature difference between the bottom and the surface was 0.5 °C. The tendency of homogeneity and no oxygen deficiency between the depths was also recorded for previous studies in Peri Lagoon (Laudares Silva 1999, Simonassi 2001).

The DCA plot (Fig. 3) shows a clear separation between samples from the hot-rainy and the cold-dry period along the first axis. Distribution along the other axes (2 to 4) does not reflect seasonal differences (data not shown). Changes can be attributed to differences in temperature, NO\(_3\)-N, and TN, as well as TN:TP and DIN:TP. Temperature had a stronger positive correlation to phytoplankton data in the hot-rainy period, while TN, NO\(_3\)-N, DIN:TP, and TN:TP were more positively associated with the cold-dry period.

**Phytoplankton composition and morphology of *C. raciborskii***

Significant differences (p < 0.05) between the 2 periods for the 3 most dominant species were observed (Table 2). *C. raciborskii* (functional group S\(_N\); Table 3) was dominant in both seasons, with higher biovolume during the hot-rainy period (median = 22.7 mm\(^3\) L\(^{-1}\)) than during the cold-dry period (18.6 mm\(^3\) L\(^{-1}\)). The biovolume of Oscillatoriales, represented by *Pseudanabaena galeata* (S1), occupied the second place of dominance and was greater during the cold-dry period (2.1 mm\(^3\) L\(^{-1}\)) compared to the hot-rainy period (0.8 mm\(^3\) L\(^{-1}\)). The Dinophyceae species *Peridinium umbonatum* (L\(_O\)) occupied the third place of dominance (0.9 mm\(^3\) L\(^{-1}\) during the hot-rainy period and 0.2 mm\(^3\) L\(^{-1}\) during the cold-dry period).

*Aulacoseira granulata* (P) was the most important taxon among the Bacillariophyceae and was more abundant in the cold-dry period (0.7 mm\(^3\) L\(^{-1}\)) than in the hot-rainy period (0.3 mm\(^3\) L\(^{-1}\)). The genus *Oscillatoria* (R) and the
species *Planktolyngbya limnetica* (S) were more successful during the cold-dry period but with low biovolumes (0.2 and 0.1 mm$^3$ L$^{-1}$, respectively). *Monoraphidium irregular* (group X1) represented the Chlorophyceae group in terms of abundance (~4500 cells L$^{-1}$) but was not substantial in terms of biovolume (0.05 mm$^3$ L$^{-1}$). Other species of phytoplankton were not abundant (Table 3).

Morphologically, the filaments of *C. raciborskii* had lengths between 9 and 150 µm (mean = 70 µm) and a width of 2.9 µm. Shorter and more abundant trichomes were observed during the hot-rainy period. Terminal heterocysts (8% of all filaments) were positioned at the end of longer filaments. Coiled forms were more evident during the cold-dry period (9% of biovolume) than during the hot-rainy period (<1%). Akinetic forms were not found in Peri Lagoon (Fig. 4).

### Diversity at steady state

Generally, phytoplankton diversity was low in both periods and all the diversity indices were higher in the cold-dry period (Table 2). Significant differences between seasons ($p < 0.05$) were observed for the Shannon-Wiener index (mean = 0.9 in the cold-dry period and 0.7 in the hot-rainy period), evenness (0.2 and 0.16), and Simpson Index (26% and 18%, respectively). No significant differences were observed for the number of species, and the range of richness in both periods was the same (17–23 species). Overall, 39 different species were found in Peri Lagoon, represented by 13 Chlorophyceae (greatest richness but low biovolume), 10 Cyanophyceae, 5 Dinophyceae, 3 Bacillariophyceae, 4 Zygnematales, 2 Chrysophyceae, and 2 Euglenophyceae.

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Table 1. Abiotic parameters, median (min–max), during the studied periods (n = 10 per season). Significant interseasonal differences are indicated (*, $p < 0.05$, Wilcoxon Mann-Whitney test).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Cold–dry</th>
<th>Hot–rainy</th>
</tr>
</thead>
<tbody>
<tr>
<td>Secchi depth (m)</td>
<td>0.9 (0.9–1.0)</td>
<td>1.3 (1.0–1.3)*</td>
</tr>
<tr>
<td>Water temperature (°C)</td>
<td>18.4 (17.0–21.0)</td>
<td>27.0 (25.0–28.0)*</td>
</tr>
<tr>
<td>Conductivity (µS cm$^{-1}$)</td>
<td>73.8 (68.0–76.0)</td>
<td>75.0 (73.3–75.0)</td>
</tr>
<tr>
<td>pH</td>
<td>7.3 (6.6–7.8)</td>
<td>7.8 (6.9–8.1)</td>
</tr>
<tr>
<td>Alkalinity (mg CaCO$_3$ L$^{-1}$)</td>
<td>7.7 (7.2–8.3)</td>
<td>8.5 (7.6–9.1)*</td>
</tr>
<tr>
<td>Silica (mg L$^{-1}$)</td>
<td>2.5 (2.2–2.9)</td>
<td>2.1 (1.5–2.5)*</td>
</tr>
<tr>
<td>Dissolved oxygen (mg L$^{-1}$)</td>
<td>7.8 (7.2–8.4)</td>
<td>8.1 (7.4–8.8)*</td>
</tr>
<tr>
<td>NH$_4$-N (µg L$^{-1}$)</td>
<td>30.9 (21.3–53.2)</td>
<td>26.2 (21.0–32.5)</td>
</tr>
<tr>
<td>NO$_3$-N (µg L$^{-1}$)</td>
<td>9.1 (7.7–10.9)</td>
<td>4.9 (3.2–5.9)*</td>
</tr>
<tr>
<td>TN (µg L$^{-1}$)</td>
<td>749 (622–883)</td>
<td>524 (412–613)*</td>
</tr>
<tr>
<td>DIP (µg L$^{-1}$)</td>
<td>5.0 (4.0–12.0)</td>
<td>6.0 (4.0–13.0)</td>
</tr>
<tr>
<td>TP (µg L$^{-1}$)</td>
<td>15.6 (12.0–18.6)</td>
<td>19.2 (14.0–24.8)*</td>
</tr>
<tr>
<td>DIN:TP mass ratio</td>
<td>2.5 (1.9–4.8)</td>
<td>1.5 (1.3–2.3)*</td>
</tr>
<tr>
<td>TN:TP mass ratio</td>
<td>47.0 (40.1–62.4)</td>
<td>26.2 (16.6–37.8)*</td>
</tr>
<tr>
<td>Chlorophyll a (µg L$^{-1}$)</td>
<td>18.8 (16–21.3)</td>
<td>24.3 (22.6–25.7)*</td>
</tr>
<tr>
<td>Resource use efficiency</td>
<td>1.16 (0.92–1.67)</td>
<td>1.26 (0.97–1.84)</td>
</tr>
</tbody>
</table>

Fig. 3. Plot ordination of phytoplankton total biovolume data from the hot-rainy and cold-dry periods in Peri Lagoon, Brazil. Significantly correlated environmental vectors were overlaid.
Table 2. Median (min–max) of the diversity measures, total biovolume, and abundance of the 3 most dominant species. Significant differences are indicated (*, p < 0.05, Wilcoxon Mann-Whitney test).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Cold-dry</th>
<th>Hot-rainy</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of species</td>
<td>22.0 (17–23)</td>
<td>21.5 (17–23)</td>
</tr>
<tr>
<td>Shannon index</td>
<td>0.87 (0.78–1.00)</td>
<td>0.72 (0.65–0.76)*</td>
</tr>
<tr>
<td>Evenness</td>
<td>0.195 (0.17–0.22)</td>
<td>0.16 (0.15–0.17)*</td>
</tr>
<tr>
<td>Simpson Index</td>
<td>0.26 (0.23–0.3)</td>
<td>0.18 (0.16–0.19)*</td>
</tr>
<tr>
<td>Total biovolume</td>
<td>22.5 (21.7–23.0)</td>
<td>25.2 (25.0–25.6)*</td>
</tr>
<tr>
<td>Biovolume of 3 dominant species</td>
<td>21.1 (20.8–21.8)</td>
<td>24.4 (24.2–24.7)*</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Cold-dry</th>
<th>Hot-rainy</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biovolume (mm$^3$ L$^{-1}$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. raciborskii</td>
<td>18.6 (18.4–19.4)</td>
<td>22.7 (22.6–23.2)*</td>
</tr>
<tr>
<td>P. galeata</td>
<td>2.1 (1.87–2.18)</td>
<td>0.8 (0.66–0.90)*</td>
</tr>
<tr>
<td>P. umbonatum</td>
<td>0.23 (0.15–0.31)</td>
<td>0.86 (0.59–0.91)*</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Relative biovolume</th>
<th>Cold-dry</th>
<th>Hot-rainy</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. raciborskii</td>
<td>0.85 (0.83–0.87)</td>
<td>0.81 (0.66–0.88)*</td>
</tr>
<tr>
<td>P. galeata</td>
<td>0.09 (0.09–0.10)</td>
<td>0.03 (0.03–0.04)*</td>
</tr>
<tr>
<td>P. umbonatum</td>
<td>0.01 (0.01–0.01)</td>
<td>0.03 (0.02–0.03)*</td>
</tr>
</tbody>
</table>

Table 3. Main species with their functional group (based on Reynolds et al. 2002), median of biovolume (mm$^3$ L$^{-1}$), and median of abundance (cells L$^{-1}$) during the cold-dry (CD) and hot-rainy (HR) periods. “—” indicates no data available.

<table>
<thead>
<tr>
<th>Species</th>
<th>Functional group</th>
<th>Biovolume in mm$^3$ L$^{-1}$ (Abundance in cells L$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cylindrospermopsis raciborskii</td>
<td>SN</td>
<td>CD 18.6 (396 140) HR 22.7 (482 709)</td>
</tr>
<tr>
<td>Pseudanabaena galeata</td>
<td>S1</td>
<td>CD 2.1 (94 817) HR 0.8 (46 756)</td>
</tr>
<tr>
<td>Peridinium umbonatum</td>
<td>Lo</td>
<td>CD 0.2 (246) HR 0.9 (610)</td>
</tr>
<tr>
<td>Aulacoseira granulata</td>
<td>P</td>
<td>CD 0.7 (592) HR 0.3 (214)</td>
</tr>
<tr>
<td>Oscillatoria (Phormidium) sp.</td>
<td>R</td>
<td>CD 0.2 (90 185) HR 0.02 (8938)</td>
</tr>
<tr>
<td>Planktostrongyli limnetica</td>
<td>S</td>
<td>CD 0.1 (50 262) HR 0.05 (25 131)</td>
</tr>
<tr>
<td>Gymnodiunum lantzschii</td>
<td>Lo</td>
<td>CD — (—) HR 0.1 (79)</td>
</tr>
<tr>
<td>Gymnodiunum uberrimum</td>
<td>Lo</td>
<td>CD 0.05 (8) HR — (—)</td>
</tr>
<tr>
<td>Monoraphidium irregularre</td>
<td>X1</td>
<td>CD 0.05 (4330) HR 0.05 (4782)</td>
</tr>
<tr>
<td>Gymnodiunum sp.</td>
<td>Lo</td>
<td>CD 0.09 (94) HR 0.01 (16)</td>
</tr>
<tr>
<td>Chrysochromulina parva</td>
<td>X2</td>
<td>CD 0.007 (89) HR 0.06 (1885)</td>
</tr>
<tr>
<td>Stauroastrum tetracerum</td>
<td>P</td>
<td>CD 0.008 (24) HR 0.05 (164)</td>
</tr>
<tr>
<td>Tetraedron minimum</td>
<td>J</td>
<td>CD 0.02 (111) HR 0.08 (621)</td>
</tr>
<tr>
<td>Chlamydomonas sp.</td>
<td>X2</td>
<td>CD 0.008 (79) HR 0.03 (257)</td>
</tr>
<tr>
<td>Phacus sp.</td>
<td>W1</td>
<td>CD 0.02 (5) HR 0.03 (6)</td>
</tr>
<tr>
<td>Peridinium gatunense</td>
<td>Lo</td>
<td>CD 0.02 (6) HR — (—)</td>
</tr>
<tr>
<td>Others</td>
<td>—</td>
<td>CD 0.06 (1747) HR 0.15 (2179)</td>
</tr>
<tr>
<td>Total abundance</td>
<td>—</td>
<td>CD 638 735 HR 574 347</td>
</tr>
<tr>
<td>Total biovolume</td>
<td>—</td>
<td>CD 22.5 HR 25.2</td>
</tr>
</tbody>
</table>
The dominance by a maximum of 3 species (C. raciborskii, P. galeata, and P. umbonatum) supported the equilibrium conditions according to Sommer et al. (1993) during both periods. The portion of biovolume occupied by C. raciborskii (S₅ group) clearly shows its monodominance because this species alone represented >90% of total biovolume (Fig. 5). The decrease of biovolume of this alga during the cold-dry period was offset by the increase of P. galeata, which contributed to maintaining the steady state (9% of total biovolume). This S1 species with more affinity to lower temperature increased 5.5% during the cold-dry period. P. umbonatum was more abundant during the hot-rainy period (3.3% of total biovolume) and decreased to 1.1% biovolume during the cold-dry period.

Fig. 4. Morphology of Cylindrospermopsis raciborskii showing different filament lengths and coiled forms (right) and heterocysts on a terminal cell (left; shown with a black arrow).

Fig. 5. Portion of biovolume (%) of the 3 most dominant phytoplankton species in Peri Lagoon, Brazil.
Discussion

Abiotic parameters

The pH oscillation of Peri Lagoon from mildly acidic to slightly basic was recorded by previous studies (Laudares Silva 1999, Simonassi 2001). Branco and Senna (1991) described high annual pH variation (6.0–10.0) in a Brazilian lake (Paranoá) during abundance of *C. raciborskii*, which seems to tolerate a large pH range. According to Padišák (1997), the most favorable pH for the occurrence of *C. raciborskii* is from 8.0 to 8.7, and its dominance in acidic water seems to be rare. Although the maximum pH value (8.1) occurred in the hot-rainy period, no significant interseasonal differences were found for this parameter. The results showed that *C. raciborskii* in Peri Lagoon dominated at a range of pH beyond the reported ideal pH environment.

Temperature seems to be the most influential factor underlying the abundance of *C. raciborskii*; consequently, perennial populations can persist year-round in Brazilian areas (Bouvy et al. 1999, Komárková et al. 1999). Briand et al. (2004) found a positive net growth in a wide range of temperatures (20–35 °C), with maximum growth rates at ~30 °C, similar to values found in the hot-rainy period. The differences in temperature, N availability, and TN:TP relation seem to be the driving parameters for interseasonal changes in the phytoplankton community in Peri Lagoon. The N:P ratio is an important determinant of the species composition of phytoplankton assemblages. Smith (1983) reported that cyanobacteria dominance is favored by a TN:TP ratio <29, which agrees with our findings in Peri Lagoon during the hot-rainy period (TN:TP median = 26.2). According to Pick and Lean (1987), TN alone would be a better predictor of cyanobacterial biomass than TN or TN:TP; however, *C. raciborskii* dominated at low TP concentration (19.2 µg L⁻¹ in the hot-rainy period and 15.6 µg L⁻¹ in the cold-dry period).

Bergström (2010) showed that the DIN:TP ratio could be a better indicator than the TN:TP ratio for N and P limitation of phytoplankton. The DIN:TP mass ratio corresponding to an estimated 50% probability for P limitation (or N limitation) is 2.2, and the ratios corresponding to 25 and 75% probabilities for P limitation (or 75 and 25% probabilities for N limitation) are 1.5 and 3.4, respectively. In this case, the DIN:TP ratio in Peri Lagoon was 1.5 during the hot-rainy period and 2.5 during the cold-dry period, which suggests N limitation during the hot-rainy period. The progress of the RUE in shallow German lakes tended to accompany the dominance of filamentous cyanobacteria during the summer under lower diversity, similar to the values found in the Peri coastal lagoon (Baptista 2012). The higher primary production as biovolume during the hot-rainy period is not explained by a considerable variation of dissolved nutrients and TN.

An absence of thermal stratification and readily available dissolved oxygen in Brazilian coastal lagoons were similarly recorded by previous studies. According to Petrucio (1998), water column homogeneity is often recorded in tropical coastal lagoons due to lower depth and exposure to winds, which allow greater movement and water oxygenation. The same pattern of vertical distribution was recorded by Leite and Fonseca (2002) in lakes located in Rio Grande do Sul State and by Soares et al. (2009) in Minas Gerais State. The rarity of other phytoplankton groups such as Chlorophyceae, Euglenophyceae, and Bacillariophyceae due to the dominance of *C. raciborskii* was recorded by Bouvy et al. (1999) in the northeast of the country.

Characteristics of *C. raciborskii* and functional groups of phytoplankton

The morphology of the *C. raciborskii* filaments in Peri Lagoon is considered anomalous (Laudares-Silva 1999). Because heterocytes are not present in all filaments and the akinete forms are absent, the field populations of Peri are difficult to identify, similar to those described in Paranoá Lake by Branco and Senna (1991). The coiled form of filaments was recorded by Bouvy et al. (1999) in northeast Brazil, together with scarce akinetes and heterocytes. In a review of the genus *Cylindrospermopsis*, Komárková (1998) confirmed that *C. raciborskii* is a common species in freshwater plankton in the form of straight trichomes. The presence of coiled forms of filaments in natural populations seems to be present mainly in turbulent ecosystems with limited dissolved nutrients.

Akinete formation may be triggered by cold temperatures or large temperature fluctuations and requires high levels of reactive P (Moore et al. 2005). In tropical or subtropical waters, *C. raciborskii* is perennial and akinetes rarely develop (Padišák 2003). This type of “resting cell” was not found in the Peri coastal lagoon. Heterocytes were more frequent in the hot-rainy period when N was more limited.

The adaptive advantages of *C. raciborskii* in Peri Lagoon may also be maintained by the lack of thermal stratification. According to Reynolds et al. (2002), *C. raciborskii* is associated with the S₁ functional group in terms of life strategies (warm mixed layers) and represents shallow, turbid, and dissolved nutrient-limited water, as found in Peri Lagoon. The L₃ functional group refers to...
originally to the *Peridinium–Woronichinia* genera, which attempts to accommodate assemblages involving *P. inconspicuum* and other cyanobacteria. The biomass-conserving canopy dinoflagellates genera, with their high biovolume and lower growth, are common when free nutrients have been exhausted (Reynolds 1997). Several species of Dinophyceae are motile species, able to migrate between the well-illuminated epilimnion and nutrient-rich hypolimnion when nutrients become scarce, similar to the buoyancy regulation of *C. raciborskii*.

Little is known about the diversity of dinoflagellates in Brazilian continental waters (Gomes et al. 2010). *C. raciborskii* has been reported to co-occur with *Peridinium* spp., mainly in warm, mesotrophic systems under nutrient limitation (Borics et al. 2000, 2005). *P. umbonatum* population dynamics in tropical areas occur in nutrient-poor conditions, mainly in small-sized lakes as shallow closed lagoons (Cardoso and Torgan 2007, Gomes et al. 2010).

Functional group S, represented by the genera *Pseudanabaena*, which can live on a minimal income of light and temperature, was more abundant during the cold-dry period. Silica concentrations (2.0 mg L\(^{-1}\)) were not shown to limit diatom biomass, so the low diversity of this group may be explained by higher temperatures. The widespread diatom *Aulacoseira* (group P) was the most abundant diatom in Peri Lagoon and is common under turbid conditions (Hutchinson 1967) and in turbulent environments in tropical lakes (Huszar et al. 1998). Functional group C species (colonist-invasive; Reynolds 1988), represented by small cells of Chlorophyceae susceptible to zooplankton grazing and dominant under low intensity of disturbance, were found at low biovolume in Peri Lagoon.

**Disturbance and equilibrium relation**

Constant mixing events representing disturbances (Connell 1978) were not sufficient in Peri Lagoon to interrupt species dominance and steady state. Because this type of disturbance is not strongly conducive to the maintenance of high species diversity, dominance by pioneer superior competitors may lead to competitive exclusion and reduced species diversity. Note that the homogeneous, well-mixed conditions assumed in the competitive exclusion principle hardly ever exist in the real world (Scheffer et al. 2003). Higher persistence by pioneer species under selective conditions seemed to better explain the occurrence of steady states in tropical waters (Soares et al. 2009).

Reynolds (1993) stated that a continuous disturbance represents a form of environmental constancy in which successive generations build up populations analogous to habitat colonists. According to Chorus and Schlag (1993), a permanent circulation can create low disturbance status, complemented by the small variation of abiotic conditions. The longer disturbance conditions persist, the poorer the survival of sensitive groups and the better the survival of tolerant groups. In a varying environment, however, each species has favorable periods and more species can coexist.

Hutchinson (1961) suggested that plankton communities may not be in equilibrium at all due to weather-driven fluctuations (Scheffer et al. 2003). Some investigations indicate that the presence of nonseasonal variations in tropical lakes may lead to more frequent steady-state conditions than in temperate ones. Steady-state conditions are more probable and longer lasting in tropical regions because of the smaller ranges of physical changes. Our current study does not support models that associate greater diversity with greater primary productivity and use of limiting resources.

**Conclusions**

Steady state occurs mainly under less pronounced abiotic changes (i.e., nutrient concentration and temperature), frequently leading to low diversity. The dominance of cyanobacteria such as *C. raciborskii* decreases the diversity of other species as a consequence of its more effective exploitation of resources. Mixing events during periods of dominance by cyanobacterial species do not represent disturbances in the sense of Connell (1978) because they do not interrupt the species performance and do not change the diversity. The status of low disturbance created by permanent water column circulation decreases diversity, especially in the case of monodominance. Because disturbances did not change species composition in Peri Lagoon, its phytoplankton community may represent a nonsuccessional change. *C. raciborskii* should probably be classified as a tropical species that takes advantage of the progressive warming of waterbodies.

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Low disturbances favor steady state: case of cyanobacterial monodominance in a Brazilian coastal lagoon


