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ECOLOGIA DO FITOPLÂNCTON NA LAGOA DO PERI: INFLUÊNCIA DA VARIABILIDADE CLIMÁTICA INTERANUAL SOBRE A LIMNOLOGIA E A DINÂMICA DA COMUNIDADE DE CIANOBACTÉRIAS

Tese submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do Grau de Doutor em Ecologia.

Orientador: Prof. Dr. Mauricio Mello Petrucio

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"**Ecologia do fitoplâncton na Lagoa do Peri: influência da variabilidade climática interanual sobre a limnologia e a dinâmica da comunidade de cianobactérias**"

Por

Eduardo Vetromilla Fuentes

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“A nossa capacidade de infligir caos a nós mesmos e ao mundo no qual nós vivemos é virtualmente ilimitada... Porém, tragicamente, a degradação gradual de um planeta habitável pode no fim ser apenas uma punição.”
(Robert E. Ricklefs, 1973)

SUMÁRIO

RESUMO

O foco principal deste estudo foi conhecer a influência da variabilidade climática interanual sobre a ecologia da comunidade fitoplanctônica de um lago costeiro subtropical destinado ao abastecimento público de água. Espera-se que períodos de anomalia negativa da precipitação pluviométrica promovam redução do nível hidrológico capaz de interferir na ressuspensão de sedimentos e na disponibilidade de nutrientes deste ambiente, resultando em mudanças na dominância e na abundância das populações de cianobactérias. Coletas mensais foram realizadas entre Abril/2012 e Maio/2013, com o objetivo de avaliar a dinâmica temporal das variáveis limnológicas e da comunidade fitoplanctônica. Dados prévios (Julho/2009 a Março/2012) foram obtidos de estudos anteriores. Foi observada forte relação entre a precipitação e o nível hidrológico do sistema. Apesar de apresentar condições predominantes de mistura vertical, a redução do nível hidrológico em resposta a redução da precipitação em 2012 resultou no aumento da estabilidade térmica da coluna d'água. Foi observada a dominância monoespecífica da cianobactéria *Cylindrospermopsis raciborskii* nos primeiros três anos do estudo, com redução da biomassa total em períodos mais frios. Esse padrão foi modificado e a monodominância dessa espécie foi interrompida durante o período de nível hidrológico reduzido. Os resultados sugerem a intensificação da ação do vento e da irradiação solar sobre os processos de ressuspensão de sedimentos e de estratificação diurna neste período, provavelmente em resposta à redução da profundidade média do sistema. Tais mudanças promoveram o aumento da disponibilidade de fósforo inorgânico dissolvido, da biomassa total e da dominância da cianobactéria bêntica *Pseudanabaena catenata*. Este estudo evidencia a importância da variabilidade interanual da precipitação sobre a ecologia do fitoplâncton da Lagoa do Peri. Além de contribuir para a melhor compreensão sobre o funcionamento limnológico deste ambiente complexo de elevada importância econômica e social, este estudo se justifica diante do atual cenário de mudanças climáticas, onde alterações nos regimes regionais de precipitação são esperadas.

Palavras-chave: Cianobactérias. Climatologia. Ecologia de Águas Continentais. Ecologia do Fitoplâncton.

ABSTRACT

The main goal of this study was to know the influence of interannual climate variability on the ecology of phytoplankton of a subtropical coastal lake used for human supply. It is expected that periods of negative anomaly in rainfall can promote decrease in water level able to interfere in resuspension of sediments and in the nutrient internal load of the system, resulting in changes of dominance and abundance of cyanobacterial populations. Monthly samples were taken from April 2012 to May 2013, in order to assess the temporal dynamics of limnological variables and phytoplankton community. Previous data (July 2009 to March 2012) were obtained from previous studies. The results showed strong relation between rainfall and water level in the system. Despite showing predominant conditions of vertical mixing, the decrease of water level in response to the rainfall reduction in 2012 resulted in increased thermal stability of the water column. Monospecific dominance of the cyanobacterium *Cylindrospermopsis raciborskii* was observed over the first three years of study, with decreasing total biomass in colder periods. This pattern was modified and the monodominance of this species was interrupted during the period of lower water level. The results suggest the intensification of wind and solar irradiation influence on the processes of sediment resuspension and daytime stratification of water column during this period, probably in response to lower average depth in the system. These changes promoted increased availability of dissolved inorganic phosphorus, increased total biomass, and increased biomass and dominance of the benthic cyanobacterium *Pseudanabaena catenata*. This study highlights the importance of interannual variability of rainfall on the phytoplankton ecology of Peri Lake. Besides contributing to a better understanding of the limnological functioning of this complex environment of high economic and social importance, this study is justified given the current scenario of climate change where changes are expected in regional rainfall patterns.

Keywords: Cyanobacteria. Climatology. Freshwater Ecology. Phytoplankton Ecology.

INTRODUÇÃO GERAL

Já é bastante conhecida a importância do clima e sua variabilidade natural como principal fator modulador das condições limnológicas em ambientes lacustres (TALLING, 2001). De forma geral, tanto o regime de mistura, tempo de retenção, transparência e disponibilidade de luz quanto a disponibilidade de nutrientes na água são fortemente influenciadas pelos elementos climáticos, tais como a radiação solar, o vento e a precipitação pluviométrica. Atualmente, já existe consenso de que, em ambientes aquáticos tropicais e subtropicais, os processos de dinâmica ecológica do fitoplâncton estão mais fortemente relacionados às variações sazonais no regime de precipitação pluviométrica do que às oscilações da temperatura e radiação solar, aspectos esses mais relevantes em regiões temperadas (HUSZAR; REYNOLDS, 1997; DOS SANTOS; CALIJURI, 1998; LIRA; BITTENCOURT-OLIVEIRA; MOURA, 2009; CHELLAPPA et al., 2009).

Lagos rasos são considerados mais suscetíveis às condições climáticas, especialmente os ambientes costeiros (KJERFVE; MAGILL, 1989; TALLING, 2001). Por exemplo, eventos de mistura promovida pelo vento podem resultar em aumento da carga interna de nutrientes por ressuspensão de sedimentos (DE SOUZA CARDOSO; DA MOTTA MARQUES, 2009). Por sua vez, tais processos podem influenciar a dinâmica do fitoplâncton de formas diversas, e por vezes contrastantes, tais como retardando o aumento da biomassa pela redução da disponibilidade de luz por aumento da turbidez, ou promovendo esse aumento por transporte de espécies tipicamente bênticas para o plâncton (PADISÁK; TÓTH; RAJCZY, 1990; ISTVÁNOVICS; OZSTOICS; HONTI, 2004).

Além disso, tais efeitos podem ser fortemente influenciados por flutuações do nível hidrológico em resposta à variabilidade interanual da precipitação (JEPPESEN et al., 2015). Por exemplo, reduções extremas do nível hidrológico durante períodos de estiagem prolongada podem resultar em tempos de retenção da água mais prolongados, bem como na alteração do regime de mistura, o que pode ser favorável a ocorrência de florações de cianobactérias (MCGREGOR; FABBRO, 2000). Adicionalmente, o aumento da biomassa de cianobactérias pode resultar em redução da transparência da água e da disponibilidade de luz subaquática, tornando o ambiente mais seletivo e reestruturando a diversidade fitoplanctônica no sentido de favorecer espécies adaptadas ao sombreamento (PAERL; HUISMAN, 2008).

Previsões climáticas indicam que o aumento gradual nas temperaturas globais pode causar mudanças nos regimes regionais de precipitação pluviométrica (PARRY et al., 2007). Tais mudanças podem promover alterações físicas e químicas em ecossistemas de água doce e resultar em alterações na frequência e intensidade de florações algais. No entanto, os mecanismos que produzem essas mudanças são complexos e dependem fortemente da dinâmica local de fatores bióticos e abióticos (O'NEIL et al., 2011;. REICHWALDT; GHADOUANI, 2012).

Enquanto as previsões de aumento da precipitação nas regiões subtropicais permanecem no campo da especulação, vários estudos mostram que a variabilidade da precipitação na América do Sul está intimamente ligada (via teleconexões) com o fenômeno El Niño Oscilação Sul (ENSO), de forma interanual (GRIMM; NATORI, 2006; GRIMM, 2011), e com a Oscilação Decadal do Pacífico (ODP) de forma interdecadal (KAYANO; ANDREOLI, 2007). Anomalias fortes e consistentes de precipitação no sul do Brasil foram associadas às fases fria (La Niña) e quente (El Niño) do ENSO (GRIMM; FERRAZ; GOMES, 1998), e essas podem ser reforçadas se combinadas com as fases de mesmo sinal do ODP (ANDREOLI; KAYANO, 2005).

Diversos trabalhos têm sugerido o papel importante da ENSO sobre o funcionamento e a resposta fitoplanctônica de ambientes lacustres (BOUVY et al., 1999, 2000). Em geral, esses estudos reportam que a redução do nível hidrológico em consequência de períodos de estiagem prolongada sob influência do ENSO resultou em aumento da eutrofização, da biomassa de cianobactérias e da frequência de florações em reservatórios do Nordeste brasileiro.

MONITORAMENTO DO FITOPLÂNCTON NA LAGOA DO PERI

O monitoramento limnológico da qualidade da água e da biomassa fitoplanctônica são ferramentas importantes para a gestão e conservação da qualidade da água em corpos d'água utilizados para abastecimento público. Isso se faz especialmente importante em ecossistemas dominados por cianobactérias, devido à gravidade dos problemas econômicos e de saúde pública causados pela proliferação excessiva de espécies tóxicas (CHORUS; BARTRAM, 1999; MCGREGOR; FABBRO, 2000). Conhecer os processos ecológicos que favorecem a elevação da biomassa de cianobactérias é um desafio para pesquisadores e gestores de água. As observações frequentes realizadas por programas de monitoramento contínuo podem levar a uma melhor compreensão da dinâmica do fitoplâncton e dos mecanismos que impulsionam a abundância e a variabilidade da estrutura dessa comunidade (KEDDY; WEIHER, 1999; ROJO; ÁLVAREZ-COBELAS, 2003).

O Laboratório de Ecologia de Águas Continentais da Universidade Federal de Santa Catarina (LIMNOS/UFSC), sob a coordenação do Prof. Dr. Mauricio Mello Petrucio e a contribuição de seu grupo de colaboradores, tem desenvolvido vários estudos e mantido um programa de monitoramento limnológico na Lagoa do Peri (Ilha de Santa Catarina, Brasil) desde março de 2007. A estrutura e a dinâmica temporal e espacial (vertical e horizontal) dos parâmetros da qualidade da água foram avaliadas entre Março/2008 e Setembro/2009, em cinco pontos e em diferentes profundidades. Os autores classificaram o lago como oligotrófico quanto à concentração de nutrientes, e meso-eutrófico quanto à transparência e a concentração de clorofila-*a*, de acordo com índices de Toledo et al. (1983) e Salas e Martino (1991). Os resultados evidenciaram a importância da influência dos ventos na promoção de homogeneidade vertical e horizontal das variáveis observada ao longo de todo o estudo, bem como das mudanças nos regimes de temperatura e precipitação pluviométrica na variação temporal da qualidade da água (HENNEMANN; PETRUCIO, 2011).

Com relação ao fitoplâncton, estudos anteriores reportaram a elevada produtividade fitoplanctônica e o predomínio de cianobactérias na Lagoa do Peri, em especial da espécie potencialmente tóxica *Cylindrospermopsis raciborskii* (LAUDARES-SILVA, 1999; KOMÁRKOVÁ-LEGNEROVÁ; LAUDARES-SILVA; SENNA, 1999; GRELLMANN, 2006). Os estudos realizados pelo grupo de colaboradores do LIMNOS/UFSC têm mostrado que esses resultados persistem (TONETTA; PETRUCIO; LAUDARES-SILVA, 2013;

SILVEIRA, 2013), trazendo novos entendimentos e também novos questionamentos acerca dos fatores direcionadores da dinâmica espacial e temporal desta comunidade.

No primeiro estudo (TONETTA; PETRUCIO; LAUDARES-SILVA, 2013), amostras mensais (Junho/2009 a Janeiro/2011) de fitoplâncton foram coletadas em quatro profundidades distintas de um ponto central da Lagoa do Peri (profundidade média ~ 9 m), e analisadas conjuntamente com as variáveis abióticas. Os resultados mostraram ausência de variação vertical na coluna d'água, e ocorrência de variação temporal das variáveis estudadas. O ambiente foi considerado limitante ao crescimento fitoplanctônico por baixa disponibilidade de luz e nutrientes, selecionando a ocorrência de populações de cianobactérias filamentosas. A comunidade fitoplanctônica foi representada por 31 espécies, sendo Cyanobacteria (com 87,7% da densidade total) o grupo mais representativo, seguido de Chlorophyta (11,8% da densidade total). *Cylindrospermopsis raciborskii* foi a espécie predominante (em densidade) durante quase todo o período estudado, sendo substituída por *Limnothrix* sp. em período de redução da velocidade do vento e aumento da temperatura e da concentração de fósforo. O estudo aponta que as várias espécies filamentosas de Cyanobacteria registradas neste ambiente mostraram diferentes correlações com as variáveis amostradas, e sugere que algumas espécies podem coexistir, e outras competirem pelo mesmo recurso. As principais variáveis responsáveis pela variação temporal observada na comunidade fitoplanctônica foram temperatura e nutrientes.

No outro estudo (SILVEIRA, 2013), realizado no mesmo ponto e nas mesmas profundidades, em período subsequente ao primeiro (Março/2011 a Fevereiro/2012), a autora mostra que Cyanobacteria foi o grupo mais expressivo em toda a série temporal, contribuindo em média com 83,2% da biomassa total do fitoplâncton, representado especialmente por espécies filamentosas. Nos períodos quentes, o grupo esteve constituído, sobretudo, por *C. raciborskii*, que chegou a constituir mais de 87% da biomassa relativa em Abril/2011. Já em meses frios, registraram-se períodos de codominância entre *C. raciborskii* e a cianobactéria bêntica *Pseudanabaena catenata* Lauterborn, com a segunda representando, em média, mais de 20% da biomassa relativa entre Agosto e Outubro/2011. Na subsuperfície, *C. raciborskii* teve contribuição expressivamente maior do que as outras espécies em todos os meses amostrados, embora em Outubro/2011, *P. catenata* tenha alcançado valores próximos ao da primeira espécie (4,1 mg L^{-1} e 3,4 mg L^{-1}, respectivamente). A Lagoa do Peri apresentou mistura total da coluna d'água em períodos cujo fitoplâncton apresentou menores biomassas. Em suma, a dinâmica temporal do fitoplâncton da Lagoa do Peri demonstrou ser direcionada majoritariamente pela condição de mistura permanente da massa d'água e pelo padrão de variação de temperatura da água.

Ambos os estudos descritos apontaram condições similares de mistura completa e predomínio de cianobactérias filamentosas, além da relação da variabilidade sazonal da biomassa algal com a temperatura e os nutrientes. Apesar disso, a composição e a estrutura da comunidade fitoplanctônica apresentaram diferenças marcantes entre os períodos estudados. Tais observações levantam a hipótese dos resultados estarem refletindo a variabilidade interanual das condições hidrológicas, provavelmente direcionada por fatores externos relacionados ao clima, e essa possa ser a causa principal da diferença observada entre os estudos.

O regime de mistura foi mais bem explorado no segundo trabalho, e os resultados apresentados sugerem que o lago não se apresenta permanentemente misturado conforme sugerido pelo estudo anterior. Ademais, nenhuma atenção foi dada ao papel do nível hidrológico e da contribuição da precipitação pluviométrica para essa variável em ambos os estudos. Tampouco foram avaliados possíveis processos de ressuspensão de sedimentos e sua influência sobre os nutrientes, a turbidez da água e a composição dos sólidos suspensos orgânicos e inorgânicos. Considerando tratar-se de um lago sabidamente influenciado pela ação do vento, é possível considerar que lacunas no conhecimento sobre o funcionamento do mesmo foram deixadas pelos estudos. Igualmente, apenas de posse de dados de série temporal mais longa se tornaria possível identificar a existência de variabilidade interanual das condições hidrológicas e da resposta fitoplanctônica a tais mudanças.

Em vista da importância da Lagoa do Peri como manancial para o abastecimento público da população do entorno, este estudo visou contribuir para o desenvolvimento de pesquisas em andamento, através da proposição de metodologia de estudo que levou em consideração a importância da variabilidade climática interanual, dentro do panorama atual de mudanças climáticas globais. O conhecimento da resposta ecológica do fitoplâncton da Lagoa do Peri a eventuais mudanças de ordem climatológica pode ser de grande contribuição para futuras medidas de manejo que visem à sustentabilidade e a preservação deste ecossistema.

Com base na fundamentação teórica e no conhecimento prévio existente, este estudo testou as seguintes hipóteses: i. o aumento da biomassa fitoplanctônica e da frequência de florações algais está associado à redução do nível hidrológico; ii. a redução do nível hidrológico resulta no aumento da disponibilidade de nutrientes, promovendo mudanças na abundância das populações e na dominância de espécies da comunidade fitoplanctônica.

OBJETIVOS

OBJETIVO GERAL DA TESE

Conhecer a influência da variabilidade climática interanual sobre o funcionamento interno de um lago costeiro subtropical, e suas consequências sobre a ecologia deste sistema e, em especial, da comunidade fitoplanctônica

OBJETIVOS DOS CAPÍTULOS

Capítulo I

Título: *"Water level decrease and increased water stability promotes phytoplankton growth in a mesotrophic subtropical lake"*

- Caracterizar as condições regionais de temperatura do ar, velocidade e direção do vento e precipitação pluviométrica, baseado em cinco anos de observações diárias
- Avaliar o papel do vento, temperatura do ar, precipitação pluviométrica e de fatores internos sobre o nível hidrológico, regime de mistura, transparência e disponibilidade de luz na coluna d'água
- Estabelecer a relação entre o clima e as condições favoráveis ao desenvolvimento da biomassa fitoplanctônica e ao aumento da frequência de eventos de floração algal

Capítulo II

Título: *"Change in rainfall regime breaks monodominance of Cylindrospermopsis raciborskii (Cyanobacteria) in a shallow subtropical lake"*

- Conhecer a dinâmica da comunidade fitoplanctônica, os períodos de maior disponibilidade e a origem (aporte externo ou ciclagem interna) dos nutrientes inorgânicos dissolvidos, baseado em quatro anos de monitoramento mensal

- Investigar os efeitos de um evento de redução do nível hidrológico sobre as condições limnológicas, a biomassa das populações de cianobactérias e a estrutura da comunidade fitoplanctônica

MATERIAL E MÉTODOS

ÁREA DE ESTUDO

A Lagoa do Peri localiza-se na porção sudeste da Ilha de Santa Catarina (27º44’S; 048º31’W). O ambiente é considerado como lago costeiro, e destina-se principalmente ao lazer e ao abastecimento público de água do sul e grande parte da costa leste da Ilha de Santa Catarina (Florianópolis/SC) (Figura 1). A população da ilha está estimada em torno de 461 mil habitantes (IBGE, 2014), e acredita-se que ela dobre devido ao turismo local, resultando em aumento da demanda sobre o sistema público de abastecimento hídrico durante a temporada de verão. Entretanto, o sistema local de captação hídrica para abastecimento público está dimensionado para a vazão média de 0,2 m^3 s^{-1} (LISBOA; SILVA; PETRUCIO, 2011). O lago é abastecido pelo aporte oriundo da bacia hidrográfica, principalmente através dos rios Cachoeira Grande e Ribeirão Grande, e seu escoamento se dá por fluxo unidirecional através do Rio Sangradouro. Os dados morfométricos disponíveis (Tabela 1) foram gerados anteriormente a execução de obra realizada para aumentar a capacidade de acúmulo do lago, a qual elevou o nível do sangradouro para 2.44 m. O nível mínimo de escoamento do lago se dá através de escada de peixes posicionada a 1.93 m acima do nível do mar. O clima da região é subtropical, com precipitações pluviométricas durante todo o ano, porém mais elevadas entre os meses de outubro e março (HENNEMANN; PETRUCIO; 2011).

OBTENÇÃO DE DADOS CLIMATOLÓGICOS E DADOS PRÉVIOS

Dados diários de temperatura média, máxima e mínima do ar, velocidade média, máxima e direção do vento e precipitação pluviométrica acumulada, do período compreendido entre Julho/2009 e Maio/2013, foram fornecidos pelo Instituto de Controle do Espaço Aéreo (ICEA), referentes aos registros realizados no Aeroporto Internacional Hercílio Luz (27º40’S; 048º33’W). Dados diários de nível hidrológico e precipitação pluviométrica acumulada na Lagoa do Peri foram fornecidos pela Companhia Catarinense de Águas e Saneamento (CASAN).

Dados limnológicos e de fitoplâncton da Lagoa do Peri correspondentes ao período compreendido entre Julho/2009 e Março/2012 foram obtidos de estudo prévios (TONETTA; PETRUCIO; LAUDARES-SILVA, 2013; SILVEIRA, 2013).

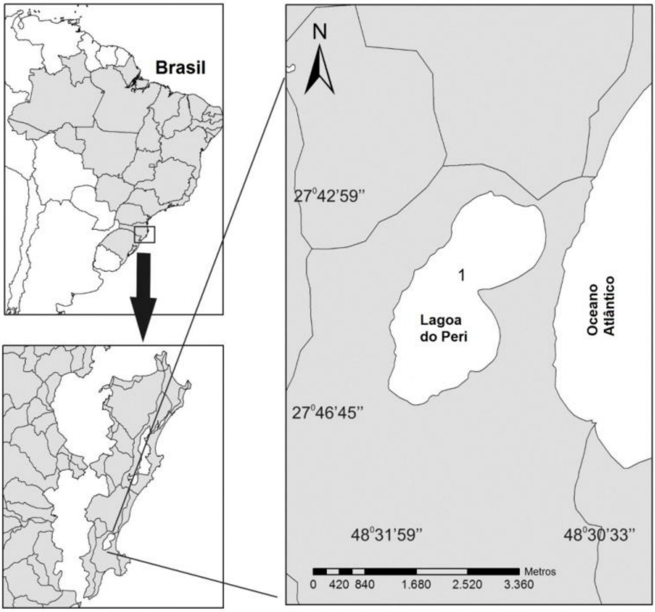

Figura 1. Localização da Lagoa do Peri (Ilha de Santa Catarina, Brasil) e posição aproximada do ponto de amostragem (adaptado de Fontes et al., 2011). **1** – ponto amostral.

Tabela 1. Dados morfométricos da Lagoa do Peri (Ilha de Santa Catarina, Brasil), obtidos ao nível linimétrico de 1,68 metros acima do nível do mar. Fonte: CONAGE, 1998.

Área ($\times 10^6$ m²)	5,07
Volume total ($\times 10^6$ m³)	21,2
Profundidade média (m)	4,2
Profundidade máxima (m)	11

MEDIÇÕES DE CAMPO

As medidas de campo foram realizadas mensalmente no período compreendido entre Abril/2012 e Maio/2013. As variáveis determinadas *in situ* foram temperatura (^{o}C) e condutividade elétrica ($\mu S\ cm^{-1}$), mediante uso de sonda WTW™, modelo Multi350i. A transparência da água foi obtida através da leitura da profundidade de extinção de disco de Secchi. A velocidade de rajada de vento foi obtida *in situ* através do anemômetro portátil Instrutherm™, modelo TAD 500.

AMOSTRAGEM

As amostragens foram realizadas no período compreendido entre Abril/2012 e Maio/2013. Foram realizadas coletas mensais no ponto central do lago (Fig. 1), em quatro profundidades (subsuperfície, profundidade de extinção do disco de Secchi, limite da zona eufótica e zona afótica). A escolha do ponto de amostragem se deu visando a continuação dos estudos anteriores e levou em consideração seus resultados que reportaram homogeneidade espacial das condições limnológicas e da comunidade fitoplanctônica do lago (HENNEMANN; PETRUCIO; 2011; TONETTA; PETRUCIO; LAUDARES-SILVA, 2013). As coletas foram realizadas com garrafa van Dorn de 3 L. Amostras destinadas à análise do fitoplâncton (alíquota de 100 mL) foram coletadas na subsuperfície e preservadas com lugol acético, adicionado na proporção de 1:100 (CHORUS; BARTRAM, 1999). A preservação por lugol acético foi utilizada por facilitar a sedimentação das amostras devido ao aumento que o mesmo promove no peso específico das células.

NUTRIENTES E CLOROFILA-*A*

Amostras de água não-filtrada foram coletadas para determinação das concentrações de fósforo total e nitrogênio total (VALDERRAMA, 1981). Amostras filtradas em membrana AP40 (Millipore™) foram utilizadas na determinação do fósforo solúvel reativo (STRICKLAND; PARSONS, 1960), nitrogênio amoniacal ($N\text{-}NH_4$ + $N\text{-}NH_3$), nitrito ($N\text{-}NO_2$) e nitrato ($N\text{-}NO_3$) (MACKERETH; HERON; TALLING, 1978). O nitrogênio inorgânico dissolvido foi considerado a soma das concentrações de nitrogênio inorgânico analisadas. A concentração de clorofila-*a* (µg L^{-1}) foi estimada utilizando-se o método proposto por Nusch (1980), empregando a extração com álcool etílico.

FITOPLÂNCTON

O fitoplâncton foi analisado em microscópio óptico com ocular de medição, onde foram observadas características morfológicas dos organismos, utilizadas no enquadramento taxonômico dos mesmos em chaves de identificação. A identificação dos táxons foi baseada em literatura especializada para cada grupo taxonômico: Bacillariophyta – Krammer e Lange-Bertalot (1986, 1991); Chlorophyta – Prescott et al. (1981) e Komárek e Fott (1983); Cyanobacteria – Komárek e Anagnostidis (1989; 2000; 2005); Dinophyta – Popovsky e Pfiester (1990); Chrysophyta, Cryptophyta, Euglenophyta e Xanthophyta – John, Whitton e Brook (2003).

A densidade fitoplanctônica (ind mL^{-1}) foi estimada segundo Utermöhl (1958) em microscópio invertido. O volume de amostra sedimentada foi definido de acordo com a concentração de algas e/ou detritos, sendo as amostras diluídas em água destilada e deionizada (quando necessário) e sedimentadas em cubetas de 5 mL. O tempo de sedimentação foi de pelo menos três horas para cada centímetro de altura da câmara (MARGALEF, 1983). Os indivíduos (células, colônias, cenóbios, filamentos) foram enumerados em campos aleatórios (UHELINGER, 1964), em número suficiente para alcançar 100 indivíduos da espécie mais freqüente, sendo o erro inferior a 20%, a um coeficiente de confiança de 95% (LUND; KIPLING; LECREN, 1958). A contagem do fitoplâncton por indivíduos ao invés de por células foi utilizada para fins de continuidade dos métodos empregados nos estudos prévios. Para as cianobactérias filamentosas, tricomas com número de células superior a quatro foram contados e medidos separadamente de tricomas menores. Para colônias e cenóbios, foi feita estimativa da média de células por indivíduo (30 indivíduos) e as medições das células.

A determinação do biovolume fitoplanctônico (mm^3 L^{-1}) foi feita pelo produto entre a densidade populacional de cada espécie e o volume médio do indivíduo, sempre que possível considerando as dimensões médias de cerca de 30 indivíduos. O volume de cada espécie foi calculado a partir de modelos geométricos aproximados à forma dos indivíduos: esferas, cilindros, cones, paralelepípedos, pirâmides, elipsóides e outros (SUN; LIU, 2003). O cálculo do volume médio de cenóbios e colônias considerou o produto dos volumes celulares pelas médias de células por indivíduo, e o cálculo do volume médio dos tricomas considerou as diferentes medições por tamanho.

A biomassa específica foi expressa em mg (peso fresco) mL^{-1}, assumindo a densidade das células fitoplanctônicas de 1 mg = 1 mm^3. A dominância específica foi estimada a partir da contribuição relativa de cada população para a biomassa total. As espécies que alcançaram contribuição relativa superior a 50% da biomassa total em pelo menos uma das amostragens (dominância monoespecífica; LOBO; LEIGHTON, 1986) foram analisadas individualmente e separadas do restante dos dados de outras espécies. A lista completa das espécies presentes nas amostras mensais de fitoplâncton está descrita em anexo (Anexo A).

PROCESSAMENTO E ANÁLISE DOS DADOS

A velocidade do vento foi avaliada de acordo com a escala de vento de Beaufort (BYERS, 1944), a qual varia entre o nível zero (calmo) ao nível 12 (furacão). A intensidade de precipitação pluviométrica foi obtida pela média anual (mm dia^{-1}), e a frequência foi determinada pela média de dias chuvosos (> 0.01 mm dia^{-1}) por mês. A profundidade da zona afótica foi considerada como profundidade média entre a zona eufótica e a profundidade máxima. A razão zona eufótica/profundidade máxima foi usada como indicativo de disponibilidade de luz na coluna d’água (JENSEN et al., 1994).

A ocorrência de termoclinas foi determinada de acordo com Reynolds (1984), baseada nas diferenças de densidade da água (picnoclina) entre as profundidades amostradas, e a densidade da água foi estimada pela temperatura (WEAST, 1989). Os perfis térmicos foram classificados como termoclina inexistente (picnoclina da subsuperfície à zona afótica < 0.02 kg m^3 m^{-1}), termoclina diurna (picnoclina > 0.02 kg m^3 m^{-1} apenas no primeiro metro de profundidade) ou camada de mistura diurna (picnoclina > 0.02 kg m^3 m^{-1} após o primeiro metro de profundidade), baseado em Imberger e Hambling (1985). Resultados negativos de picnoclina (termoclina inversa) foram convertidos a zero para análises estatísticas.

Para avaliar a variabilidade interanual dos dados, o intervalo de 12 meses (anos) foi considerado como o período entre março e fevereiro dos anos consecutivos no primeiro capítulo, e entre julho e junho no segundo capítulo. A variabilidade interanual foi avaliada através de Análise de Variância Simples (ANOVA one-way) e a comparação entre médias foi feita através do Teste de Tukey (*post hoc*), utilizando-se dados diários e mensais de todas as profundidades (quando disponíveis). Para evitar problemas com normalidade de dados e *outliers*, a estatística F foi testada por permutações (Monte Carlo), utilizando o pacote {lmPerm} no software R (R DEVELOPMENT CORE TEAM, 2010). Esta técnica permite que a significância dos resultados da ANOVA seja testada a partir de distribuição gerada através de permutação aleatória dos dados, dispensando assim o uso da distribuição normal para esta finalidade. Correlações entre variáveis meteorológicas, limnológicas e biológicas foram determinadas através do Coeficiente de Correlação Linear de Pearson (r), utilizando as médias mensais de todas as profundidades (quando disponíveis). O nível mínimo de significância dos resultados estatísticos foi de 95% ($P \leq 0.05$).

CAPÍTULO I

Water level decrease and increased water stability promotes phytoplankton growth in a mesotrophic subtropical lake.
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Water level decrease and increased water stability promotes phytoplankton growth in a mesotrophic subtropical lake

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Abstract. Global warming and climate variability can promote changes in freshwater ecosystems that may result in increased frequency of algal blooms. These effects, however, depend strongly on local factors. Peri Lake is a cyanobacteria-dominated shallow lake that has experienced a strong reduction in water level, as well as increased occurrence of algal blooms. The goal of this study was to determine the influence of water level on phytoplankton biomass in Peri Lake. We hypothesize that increased algal blooms are associated with reduction in water level, possibly in response to changes in rainfall patterns. We measured meteorological, physical, and chemical variables over five years, as well as chlorophyll-*a* levels. We observed a strong reduction in total rainfall in the last year of the study, in which lake water flow nearly ceased. Phytoplankton biomass increased despite lack of evidence of water heating or eutrophication. Our results suggest that changes in rainfall regime alter lake characteristics such as retention time and water stability (i.e., increased occurrence of diurnal stratification events), producing favorable conditions for cyanobacterial biomass growth; these effects perhaps better explain increases in algal biomass in this system than do temperature or nutrient availability alone.

Additional keywords: daytime stratification, filamentous cyanobacteria, Lagoa do Peri, mixing regime, monitoring.

Introduction

Lakes and reservoirs are regularly monitored in long-term studies in order to provide a better understanding of the impacts of external phenomena and natural or anthropogenic pressure (e.g., global warming, changes in rainfall, increased water demand, and urban occupation of water basins) on the function of these systems. Cyanobacteria-dominated aquatic environments have received special attention because of the risk of water contamination and its severe potential consequences for human health. The currently developing climate change scenario predicts increased frequency in the occurrence of toxic cyanobacterial blooms, mainly as a result of the positive effect of water heating on biomass accumulation of these organisms (McGregor and Fabbro 2000; Paerl and Huisman 2008).

Climate predictions indicate that the gradual increase in global temperatures may cause changes in regional rainfall regimes (Parry *et al.* 2007). Such modifications can promote physical and chemical changes in freshwater ecosystems, which may result in changes in the frequency and intensity of algal blooms. However, the mechanisms that produce these changes are complex, and depend strongly on local dynamics of biotic and abiotic factors (O'Neil *et al.* 2011; Reichwaldt and Ghadouani 2012).

Two hypothetical scenarios of changes in rainfall patterns are proposed, each with distinct anticipated impacts on cyanobacterial biomass dynamics (Reichwaldt and Ghadouani 2012). One scenario predicts an increase in rainfall intensity, which promotes increased intake of water and nutrients. This situation could favor increased cyanobacterial biomass by means of eutrophication (Heisler *et al.* 2008); however, heavy runoff associated with increased rainfall may oppose such effects (Bouvy *et al.* 2003; Figueredo and Giani 2009). The other scenario predicts reduced frequency of rainfall events (i.e., increase in the number of days without rainfall) and hence, reduction in water level and increase in retention time and thermal stability (Bouvy *et al.* 1999; An and Jones 2000). This situation may favor cyanobacteria with high phosphorus affinity and storage capacity, and the ability to remain in suspension (Reynolds and Walsby 1975; Posselt *et al.* 2009). In the latter case, increase in the biomass of these organisms can result in increased turbidity and light attenuation (Scheffer *et al.* 1993; Mischke 2003), making the environment more selective and restructuring phytoplankton diversity to favor shade-adapted species.

While the predicted increase in rainfall (e.g., due to climate change, Parry *et al.* 2007) in the subtropics remains speculative, studies show that rainfall variability in South America is closely linked (via teleconnections) with the El Niño Southern Oscillation (ENSO; Grimm and Natori 2006; Grimm 2011) in an interannual manner, and with the Pacific Decadal Oscillation (PDO, Kayano and Andreoli 2007) in an interdecadal manner. Strong and consistent rainfall anomalies in southern Brazil were found to be associated with warm/cold (El Niño/La Niña) phases of ENSO (Grimm *et al.* 1998), and these anomalies may become strengthened if combined with same signal (positive/negative) phases of the PDO (Andreoli and Kayano 2005).

Subtropical environments, particularly those near the coast, are strongly influenced by weather. Weather is the predominant force in determining limnological conditions such as nutrient input, variations in water level, mixing regime and water retention time, and interactions between these factors strongly affect cyanobacterial biomass dynamics (Kjerfve and Magill 1989; de Souza Cardoso and da Motta Marques 2009). Additionally, climate-induced changes in thermal regime have been recognized as a factor that positively influences cyanobacteria dominance (Wilhelm and Adrian 2008; Wagner and Adrian 2009).

Peri Lake on Santa Catarina Island, Brazil, is a subtropical, freshwater, shallow lake that is constantly monitored due to its use for public water supply. Previous on-site studies (Hennemann and Petrucio 2011, Tonetta *et al.* 2013) have reported mesotrophic nutrient conditions (total phosphorus ~15 µg L^{-1}, total nitrogen ~745 µg L^{-1}, according OECD 1982), with low concentrations of dissolved nutrients (soluble reactive phosphorus ~2.5 µg L^{-1}, dissolved inorganic nitrogen ~24 µg L^{-1}). Predominance of filamentous cyanobacteria has been observed in this site for more than a decade (Komárková *et al.* 1999, Baptista and Nixdörf 2014). In recent years (2012-2013) there has been a strong reduction in the water level in this system, as well as increased occurrence of algal blooms. We hypothesize that the increase in algal blooms is associated with the observed reduction in water level, as a possible response to changes in regional rainfall patterns. The aims of this study were: a) to determine the influence of water level on phytoplankton biomass, and b) to evaluate interannual behavior of meteorological variables, in particular rainfall regime, and its impact upon limnological conditions in this environment.

Methods

Study area

Peri Lake (27º 42'–46'S; 048º 30'–32'W) is a natural coastal lake located in the southeastern region of Santa Catarina Island (Florianópolis-SC, Brazil). The regional climate is humid subtropical (Cfa, according to the Köppen climate classification), with stronger winds during the austral spring (September to November; Fuentes *et al.* 2013) and rainfall occurring throughout the year, although more intense in the hottest periods (Hennemann and Petrucio 2011). The water intake system for supply purposes is configured for a mean flow of 0.2 $m^3 s^{-1}$ (Lisboa *et al.* 2011).

Data and sampling

On-site data were collected daily on rainfall (rainfall station ~230 m from the margin) and water level of the lake (March 2008 to February 2013). Rainfall, average air temperature, average wind speed and prevailing wind direction were also collected daily from the weather station located at Hercílio Luz International Airport (27°40'S; 048°33'W). Monthly sampling of limnological variables was performed between March 2008 and February 2013 (n=60) in the central region of the lake, always during the morning (8a.m.–12p.m.). Water temperature, electrical conductivity, chlorophyll-*a* (Lorenzen 1967) and total phosphorus (Valderrama 1981) concentrations were determined at four depths: subsurface (~0.5m), Secchi disk extinction, limit of the photic zone, and aphotic zone. Maximum wind gust speed was measured on site during sampling. Algal blooms were determined visually by surface water color, which becomes greenish due to algal proliferation.

Data analysis

Wind speed was evaluated according to the Beaufort Wind Scale (Byers 1944), which varies from level zero (calm) to level 12 (hurricane). Rainfall intensity was assessed by the annual mean (mm day^{-1}), and rainfall frequency was determined by the average number of days with rainfall ($\geq$ 0.01 mm day^{-1}) per month. The euphotic zone was considered to be 2.7 times the value of Secchi depth (Cole 1994). Aphotic zone depth was considered the average depth between the euphotic zone and the maximum depth. The euphotic zone/maximum depth ratio was used as an indicator of light availability in the water column (Jensen *et al.* 1994). The occurrence of thermoclines was determined according to Reynolds (1984), based on differences in water density ($\Delta\rho w$) between the sampled depths, and water density was estimated from temperature (Weast 1989). The thermal profiles were classified as non-existent thermocline (when $\Delta\rho w$ from subsurface to aphotic zone < 0.02 kg m^3 m^{-1}), diurnal thermocline (when $\Delta\rho w$ > 0.02 kg m^3 m^{-1} only in the first meter of depth) or diurnal mixed layer (when $\Delta\rho w$> 0.02 kg m^3 m^{-1} after the first meter of depth), based on Imberger (1985). Interannual variations in data and comparisons between means (using monthly data from all depths, when available) were analyzed by one-way ANOVA with Tukey's post-hoc test ($P \leq 0.05$). To avoid problems with non-normal data or outliers, the F-statistics were tested by permutations, using {lmPerm} package in R (R Development Team Core 2010). Our 12-month intervals were considered to be between March and February of consecutive years. Correlations between climatic and environmental variables were determined using Pearson's correlation coefficient (*r*).

Results

Meteorological analysis

The data series from the weather station showed a monthly pattern for air temperature with seasonal characteristics typical of subtropical regions of the Southern Hemisphere (Fig. 1). Daily average temperature ranged between 9.4 º C and 30.6 º C, with differences between years (Table 1) and an increase of 0.7 º C between 2011-2012 and 2012-2013. Wind speed was more intense between the end of the winter and the beginning of the warm season. Winds from the north and south quadrants were more frequent (see Supplementary material, Fig S1), with higher frequency of intermediate (> 3 < 5 m s^{-1}) and strong winds (> 5 m s^{-1}). Wind speeds ranged between calm (< 0.3 m s^{-1}) and fresh breeze (8.0 to 10.7 m s^{-1}). Mean wind speed increased from light breeze (1.6 to 3.3 m s^{-1}) between 2008-2011 to gentle breeze (3.4 to 5.4 m s^{-1}) between 2011-2013, with significant differences between the study years (Table 1). In contrast, average wind gust speed was not significantly different between years, increasing from light air (0.3 to 1.5 m s^{-1}) in 2008-2009 to gentle breeze between 2009 and 2012, and decreasing to light breeze in 2012-2013 (Table 1).

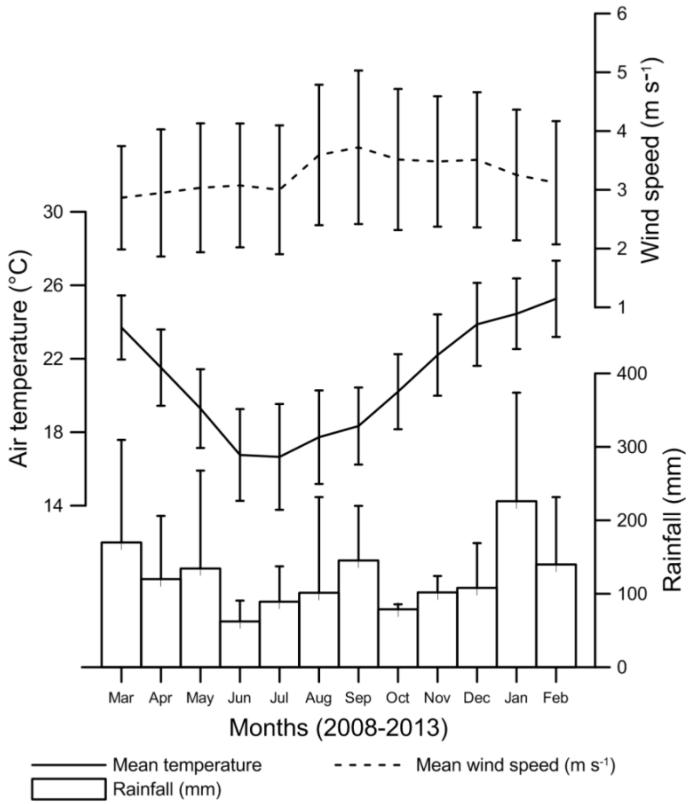

Fig. 1. Monthly variation (Mar 2008 to Feb 2013) in mean air temperature, wind speed and total rainfall at Hercílio Luz International Airport (Florianópolis-SC, Brazil). Vertical bars indicate standard error of the mean.

Peri Lake on-site rainfall data time series failures (308 cases out of 1821) were replaced with data recorded at the airport weather station. The monthly rainfall recorded at the on-site rainfall station showed a strong and significant correlation (r= 0.83, n=52; P<0.05) with airport station data. On average, rainfall was highest in summer (December to February; mean = 158.0 mm) and fall (March to May; mean = 148.5 mm), intermediate in spring (September to November; mean = 108.8 mm), and lowest in winter (June to August; mean = 84.3 mm). Total rainfall was lowest in 2012-2013 (Table 1). The number of days without rainfall increased from 195 (53.4%, 2010-2011) to 222 (60.8%, 2012-2013), and the proportion of days with rainfall above 10 mm day^{-1} decreased from 18.3% to 12.1% in the last three years (Fig. 2).

Limnological analysis

Water level ranged between 2.19 m and 3.23 m, with differences between years. The lowest values were observed in 2012-2013, averaging 2.38 ± 0.08 m (Table 1), in which water flow nearly ceased in the lake, greatly reducing outflow volume. Water temperature varied between 14.5 ° C and 29.0 ° C (mean = 22.6 ± 3.6 ° C), and was similar between years.

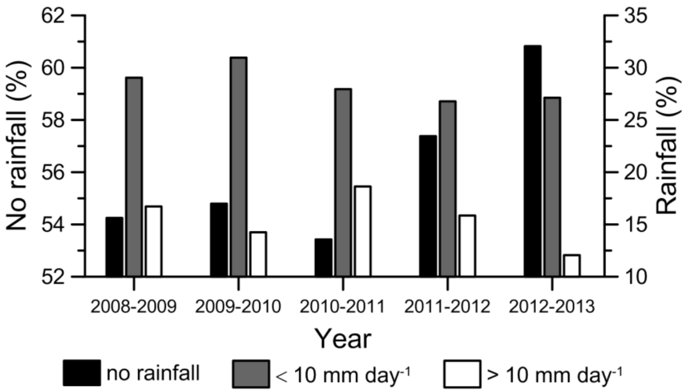

Fig. 2. Interannual variation (%) in rainfall intensity in Peri Lake.

Table 1. Annual means (min–max) of meteorological and limnological variables in Peri Lake, and significance results (F and P) of one-way ANOVA between years, from March 2008 e February 2013. Within columns, mean values with different superscript letters differ significantly (P , 0.05; Tukey's post hoc test). ASL, above sea level

Variables	*n*	Years (March to February)					*F*	*P*
		2008–09	2009–10	2010–11	2011–12	2012–13		
Meteorological								
Air temperature (°C)	1801	20.6 (9.8–26.8)^{a}	20.8 (10.3–30.6)^{ab}	20.9 (9.9–28.1)^{ab}	20.7 (9.4–28.5)^{a}	21.4 (11.9–29.7)^{b}	7.27	<0.01
Wind speed (m s^{-1})	1823	3.3 (1.3–7.3)^{ab}	3.2 (0.8–6.8)^{ab}	3.1 (1.2–7.1)^{a}	3.4 (1–8.4)^{b}	3.4 (1–7.2)^{b}	5.55	0.02
Wind gust speed (m s^{-1})	59	1.5 (0–4.7)^{a}	3.7 (0–9.7)^{a}	5 (0–9.1)^{a}	4.1 (0–10)^{a}	3 (0–8.6)^{a}	1.22	0.27
Rainfall intensity (mm day^{-1})	801	12.6 (0.1–142.2)^{a}	10.4 (0.1–125.1)^{a}	13.6 (0.1–133.2)^{a}	12.1 (0.1–88.2)^{a}	9.5 (0.1–95.9)^{a}	0.88	0.35
Rainfall frequency (days month^{-1})	60	13.9 (4–25)^{a}	13.8 (9–21)^{a}	14.2 (5–22)^{a}	13 (7–19)^{a}	11.9 (8–16)^{a}	1.42	0.24
Total rainfall (mm)	–	2110	1711	2305	1892	1363	–	–
Rain-days year^{-1}	–	167	165	170	156	143	–	–
Limnological								
Water level (m ASL)	1673	2.8 (2.51–3.23)^{a}	2.76 (2.58–3.03)^{b}	2.84 (2.60–3.1)^{c}	2.78 (2.58–3.08)^{ab}	2.38 (2.19–2.67)^{d}	769.3	<0.01
Water temperature (°C)	240	22.9 (18.7–27.9)^{a}	23.1 (17.4–28.8)^{a}	22.3 (18.5–28.5)^{a}	22.1 (14.5–29)^{a}	22.9 (16.9–28.3)^{a}	0.30	0.58
Electrical conductivity (µS cm^{-1})	229	76.5 (68.6–88.2)^{a}	69.2 (60.5–78)^{b}	68.3 (57.1–76.6)^{b}	65 (57–86)^{c}	66.7 (57–73.6)^{bc}	96.28	<0.01
Total phosphorus (µg L^{-1})	234	15.5 (9.3–26.5)^{a}	13.2 (8.7–19.7)^{a}	12.4 (6.8–39.1)^{a}	15 (11.3–21.2)^{a}	13.6 (7.2–28.9)^{a}	0.78	0.38
Chlorophyll-*a* (µg L^{-1})	240	18.8 (8.5–32)^{a}	17.9 (4.3–24.6)^{a}	19.4 (10.7–26.2)^{a}	28.3 (8–54.5)^{b}	32.6 (17.1–59.8)^{c}	143	<0.01
Secchi depth (m)	60	1.1 (0.8–1.3)^{a}	1 (0.8–1.2)^{a}	1,1 (0.9–1.4)^{a}	0.8 (0.6–1.1)^{b}	0.8 (0.5–1)^{b}	32.21	<0.01
Euphotic zone/maximum depth ratio	60	0.41 (0.33–0.48)^{ab}	0.35 (0.29–0.45)^{b}	0.43 (0.28–0.56)^{a}	0.31 (0.18–0.42)^{bc}	0.28 (0.17–0.42)^{c}	23.18	<0.01

Non-existent thermoclines were most common (43.3%), followed by diurnal thermocline and diurnal mixed layer (30.0% and 26.7%, respectively) (Fig. 3). The sum of non-existent and diurnal thermoclines (73.3%) was indicative of the prevailing absence of stratification. However, the yearly occurrence of a diurnal mixed layer increased from 16.7% (2009-2011) to 41.7% in the last year (Fig. 3).

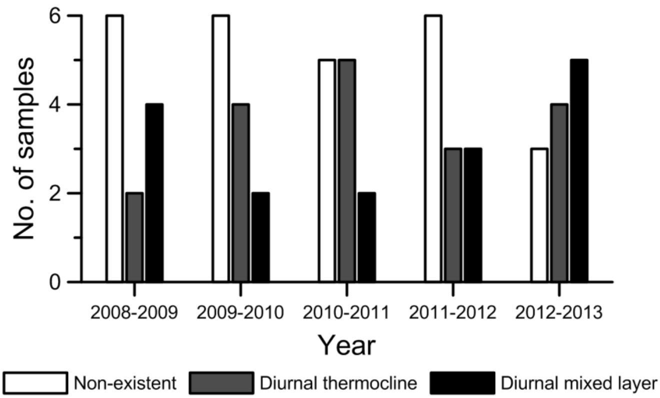

Fig. 3. Interannual variation (n=60) of thermal profiles observed in Peri Lake. Profiles are based on differences in water density (Δρw): Non-existent thermocline (Δρw < 0.02 kg m^3 m^{-1} from subsurface to aphotic zone depth); diurnal thermocline (Δρw > 0.02 kg m^3 m^{-1} only in the first meter of depth); diurnal mixed layer (Δρw > 0.02 kg m^3 m^{-1} after the first meter of depth).

Electrical conductivity ranged between 57.0 and 88.2 µS cm^{-1} (mean = 69.3 ± 6.4 µS cm-1), and was highest in 2008-2009 (Table 1). Total phosphorus ranged between 6.8 and 39.1 µg L^{-1} (mean = 13.9 ± 4.5 µg L^{-1}), and was similar between years (Table 1). The values of total phosphorus were mostly within the range of mesotrophic lakes (10-35 µg L^{-1}).

Chlorophyll-*a* increased significantly in the last two years (Table 1). Concentrations ranged from 4.3 µg L^{-1} to 59.8 µg L^{-1} (mean = 23.4 ± 8.8 µg L^{-1}); the annual average increased from 19.4 µg L^{-1} (2010-2011) to 32.6 µg L^{-1} (2012-2013). In contrast to previous years in which they rarely occurred, algal bloom formations were observed in 50% of samples taken in 2012-2013.

Secchi depth was lowest in the last two study years, with mean values decreasing from 1.1 m to 0.8 m over the study period (Table 1). This led to a lower euphotic zone/maximum depth ratio; we observed an average 15% reduction in the proportion of the euphotic layer relative to the water column in the last three years (Table 1).

Correlations between meteorological and limnological variables

Air temperature showed a strong correlation with water temperature (r=0.84, n=60; $P \leq 0.05$). Wind speed also correlated significantly with wind gust speed, although weakly (r=0.34, n=59; $P \leq 0.05$). No significant correlations were observed between wind speed and limnological variables. Thermocline absence was associated with higher wind gust speed and lower surface temperatures. The opposite happened for diurnal mixed layers (Fig. 4*a*–*b*). Diurnal thermocline data (n=18) were omitted from this graph, as they represent an intermediate profile between stratified and mixing conditions.

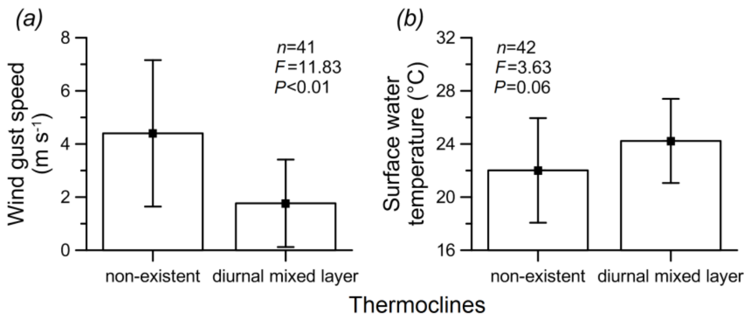

Fig. 4. Variation (Mar 2008 to Feb 2013) in (*a*) mean wind gust speed and (*b*) surface water temperature related to non-existent themocline ($\Delta\rho w < 0.02$ kg m^3 m^{-1} from subsurface to aphotic zone depth) and diurnal mixed layer ($\Delta\rho w > 0.02$ kg m^3 m^{-1} after the first meter of depth) occurrence in Peri Lake. Vertical bars indicate standard deviation of the mean.

Daily variation in water level was positively correlated with daily rainfall (r=0.67, n=1465; $P \leq 0.05$). This correlation increased when weekly water level variation and accumulated precipitation were taken into consideration (r=0.79, n=1465; $P \leq 0.05$). For monthly data (n=56), water level was positively correlated with Secchi depth (r=0.37; $P \leq 0.05$) and the euphotic zone/maximum depth ratio (r=0.44; $P \leq 0.05$).

Chlorophyll-*a* was negatively correlated with water level (r=-0.33; $P \leq 0.05$; Fig. 5), Secchi depth (r=-0.67; $P \leq 0.05$), and the euphotic zone/maximum depth ratio (r=-0.58; $P \leq 0.05$), and positively correlated with water temperature (r=0.41; $P \leq 0.05$).

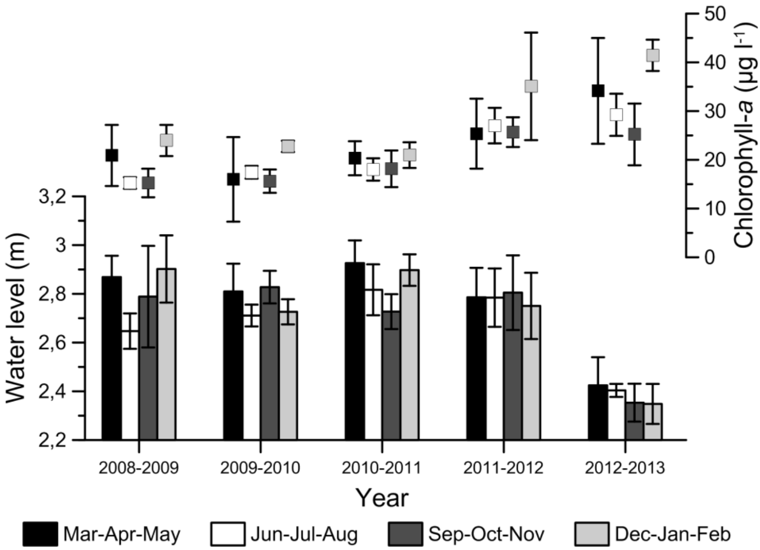

Fig. 5. Interannual variation in chlorophyll-*a* concentration and water level in Peri Lake. Vertical bars indicate minimum and maximum values.

The positive correlation between electrical conductivity and the optical variables Secchi depth (r=0.30; $P \leq 0.05$) and euphotic zone/maximum depth ratio (r=0.27; $P \leq 0.05$) indicated that periods of greater transparency coincided with higher ionic charges. No significant correlations were observed between total phosphorus and limnological or meteorological variables.

Lake water quality (i.e., in terms of increased algal biomass and decreased transparency) decreased in the last two years (2011-2013) (Table 1), with an increase in chlorophyll-*a* concentration mainly in summer (Fig. 5). Total phosphorus concentration decreased significantly compared to previous period (2008-2011, Fig. 6*a*), while the number of days without rain increased (Fig. 6*b*). Additionally, we observed that chlorophyll-*a* concentration was most related to diurnal mixed layer occurrence during the summer (Fig. 7).

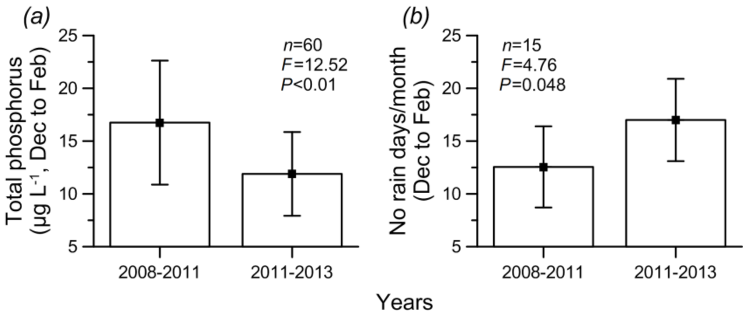

Fig. 6. Variation in (*a*) mean total phosphorus concentrations and (*b*) number of rain days (per month) in summer (December to February) of the first three (2008–2011) and last two (2012–2013) years in Peri Lake.Vertical bars indicate standard error of the mean.

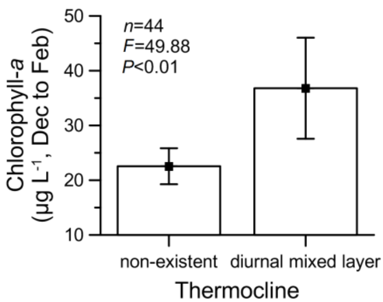

Fig. 7. Variation in mean chlorophyll-*a* concentrations in summer (December to February) related to non-existent themocline ($\Delta\rho w < 0.02$ kg m^3 m^{-1} from subsurface to aphotic zone depth) and diurnal mixed layer ($\Delta\rho w > 0.02$ kg m^3 m^{-1} after the first meter of depth) occurrence in Peri Lake. Vertical bars indicate standard error of the mean.

Discussion

Our results suggest that changes in lake characteristics (i.e., increased retention time and water stability) due to changes in rainfall regime produce favorable conditions for cyanobacterial biomass growth, and that these effects perhaps better explain algal biomass increase in this system than do temperature or nutrient availability alone.

Although the frequency and intensity of rainfall was similar throughout the study, we observed a strong reduction in total rainfall in the last year, as a result of fewer rain days in the summers of 2011-2012 and 2012-2013. Reduction in water level was the most obvious impact of reduced total rainfall, and was mainly caused by decreased supply in the water basin.

The water level decrease may be an environmental response to the interannual variability in rainfall related to a significant ENSO event occurring in the last three years of the study. This La Niña event, the strongest since 1970s, lasted from late 2010 to early 2012 and was considered the main cause of both severe drought in northeastern Brazil, and of intense rainfall and flooding in Amazonia during the austral summer and fall of 2012 (Marengo *et al.* 2013). Historically, strong and consistent negative anomalies of rainfall in southeastern South America (~23ºS to 35ºS) occur beginning in October, and extend through the summer and fall of La Niña years (Grimm *et al.* 1998; Grimm and Tedeschi 2009). This ENSO event is considered the probable cause for the decrease of total rainfall and number of rain days observed in 2012-2013.

In the present study, the thermal profile of Peri Lake showed a strong tendency towards vertical thermal homogeneity of the water column. Daytime stratification is apparently a recurring phenomenon in this environment, and its increased occurrence in the last years of the study seems to be related to the decrease in water level. Lower water level greatly reduces lake outflow volume, resulting in increased retention time; it also reduces the wind fetch of the lake, which likely also contributed to more stable water column conditions.

Although air temperature increased significantly over the study years, water temperature did not; this suggests that the direct effects of temperature rise are not a major factor causing the increased biomass. Additionally, electrical conductivity (i.e., ionic dissolved compounds) tended to decrease over the course of the study, and total phosphorus concentrations decreased in the last two summers when mean chlorophyll-*a* concentrations were highest; these observations may refute a hypothesis of eutrophication effects on algal biomass.

Recent studies have reported cyanobacterial dominance in Peri Lake, where filamentous species predominated with a relative density above 80% between June 2009 and February 2012 (Silveira 2013; Tonetta *et al.* 2013). Cyanobacteria have traits that confer a competitive advantage in conditions of water column stability and light stress (buoyancy and photoacclimation, respectively), and in times of inorganic phosphorus scarcity (accessing organic phosphorus with phosphatases). This may help to explain cyanobacterial dominance in mesotrophic environments (Carey *et al.* 2012).

According to a recent review (Reichwaldt and Ghadouani 2012), the few existing studies investigating effects of changes in rainfall regime on cyanobacterial biomass indicate that a decrease in rainfall can favor biomass proliferation given sufficient nutrient availability and stratification (Bouvy *et al.* 2003), or increased water retention time (Bouvy *et al.* 1999; An and Jones 2000). In a long-term study in the polymictic Müggelsee Lake (Berlin, Germany), Wagner and Adrian (2009) observed that the number of stratification events tended to increase throughout the years, and that this increase was induced by changes in climate; this resulted in enhanced cyanobacterial dominance under a broad range of total phosphorus thresholds. The authors concluded that prolonged thermal stratifications events, rather than direct temperature effects, enhanced the dominance of filamentous cyanobacteria, especially those capable of buoyancy and nitrogen fixation.

Our study concludes that a strong relationship exists between water level and phytoplankton biomass, and that the observed variability in climate and environmental conditions resulting from changes in water level were beneficial to phytoplankton development. This points to a worrying scenario, wherein mesotrophic and naturally disturbed (shallow) environments may be susceptible to increased algal blooms and prevalence of toxic algae. This justifies the need for careful monitoring and proper management of these resources. Such measures should aim to maintain ideal water level, as it exerts influence on both water retention time and mixing regime, and seems to be an important factor in phytoplankton performance. As Peri Lake is the main source of drinking water in this region, the first aim should be to continue to keep eutrophication low, and also to reduce water uptake for public drinking supply during periods of less rainfall, since the cost of water treatment (by removing algal biomass) and the human health risk will increase.

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Supplementary material

Water level decrease and increased water stability promotes phytoplankton growth in a mesotrophic subtropical lake

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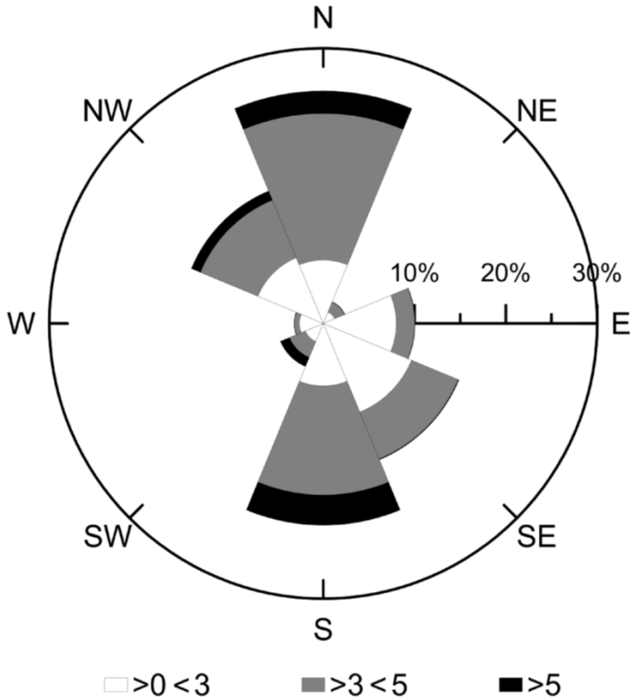

Fig. S1. Frequency distribution (%) of mean wind speed (m s^{-1}) and prevailing direction (2008–13) in Hercílio Luz International Airport (Florianópolis-SC, Brazil).

CAPÍTULO II

Change in rainfall regime breaks monodominance of *Cylindrospermopsis raciborskii* (Cyanobacteria) in a shallow subtropical lake

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Change in rainfall regime breaks monodominance of *Cylindrospermopsis raciborskii* (Cyanobacteria) in a shallow subtropical lake

Eduardo V. Fuentes, Mônica H. Silveira, Denise Tonetta and Mauricio M. Petrucio

Abstract

Water level fluctuations due to interannual climate variability may influence ecological function in shallow lakes. This study investigated effects of changing rainfall patterns on algal community structure and biomass dynamics in a cyanobacteria-dominated lake. We hypothesized that water level decrease increases nutrient availability, promoting shifts in population growth that alter species dominance. Meteorological, physical, and chemical properties, and phytoplankton abundance were measured between July 2009 and May 2013. Decreased rainfall in 2012 resulted in two distinct hydrological periods (i.e., higher vs. lower water levels), each period with distinct water chemistry responses. Our results suggest a seasonal pattern of phytoplankton dynamics related to water temperature variability and characterized by year-round monospecific dominance of *Cylindrospermopsis raciborskii* during higher water levels. However, the 2012 water level decrease likely resulted in stronger wind influence on resuspension processes, altering dissolved nutrient availability and increasing benthic species recruitment to phytoplankton populations. These factors may have favored the increase in *Pseudanabaena catenata* biomass, breaking *C. raciborskii* monodominance in the last year of the study. Considering the changes in rainfall regime expected with climate change, continued monitoring of mixing regime and resuspension processes in cyanobacteria-dominated shallow lakes will be fundamental for proper management of water quality.

Keywords: filamentous cyanobacteria, water supply system, low dissolved nutrients, community changes, adaptive traits, Peri Lake

Introduction

Phytoplankton biomass monitoring is an important tool for management and preservation of water quality in water bodies used for human supply. This is particularly true for ecosystems dominated by cyanobacteria due to the severity of health and economic problems caused by excessive proliferation of toxic species (Chorus and Bartram 1999; McGregor and Fabbro 2000). Recognizing the ecological processes that favor increase of cyanobacterial biomass is a challenge for aquatic researchers, and the frequent observation promoted by monitoring programs may increase our understanding of phytoplankton dynamics and the underlying mechanisms driving variability in phytoplankton abundance and community structure (Keddy and Weiher 1999; Rojo and Álvarez-Cobelas 2003).

Some filamentous cyanobacteria of Nostocales and Oscillatoriales are able to form perennial populations, and can become dominant in tropical and subtropical lakes (Reynolds *et al*. 2002; Soares *et al.* 2013). In shallow lakes, greater competitive ability for light and nutrients (Mischke and Nixdorf 2003) and adaptation to stressful conditions (Padisák *et al.* 2003) seems to be the main physiological and evolutionary traits allowing these organisms to persist in long-term dominance despite the temporal variability inherent in seasonal and hydrological cycles of these ecosystems (Figueredo and Giani 2009; Soares *et al.* 2009). While some species of Nostocales and Oscillatoriales share physiological and adaptive traits and may coexist under various conditions, their populations typically respond differently to environmental gradients (Rojo and Álvarez-Cobelas 1994; Bonilla *et al*. 2012).

Among the filamentous bloom-forming cyanobacterial species showing perennial dominance in tropical and subtropical shallow lakes, one of the most successful (or at least, best documented) is *Cylindrospermopsis raciborskii* (Woloszynska) Seenaya & Subba Raju. The global expansion of *C. raciborskii* (Nostocales) has been attributed to several of its physiological characteristics, including facultative diazotrophy (i.e., N_2 fixation) and mixotrophy (i.e., use of dissolved organic phosphorus) (Posselt 2009; O'Neil *et al*. 2011; Moisander *et al.* 2012), high affinity for phosphorus and ammonia (Padisák 1997; Burford and O'Donohue 2006), high heat and shade tolerance

(Briand *et al*. 2002), near neutral buoyancy (Kehoe 2010), resistance to herbivory by toxicity (Wilson *et al.* 2006) and allelopathic interference (Figueredo et al. 2007). These characteristics make them highly adaptable, strongly competitive, and may favor long periods of dominance under a variety of environmental conditions (Bormans *et al*. 2004; Antenucci *et al*. 2005). However, these characteristics make it hard to define any clear ecological preferences in this species, and to date there is no consensus among researchers regarding the primary mechanisms allowing widespread occurrence of this species (Bonilla *et al*. 2012).

Shallow lakes are often more responsive to weather conditions, which strongly influence nutrient input, water level, and mixing regime in these systems (Talling 2001). For example, wind-induced mixing events can result in increased internal nutrient load via sediment resuspension (Cardoso and Marques 2009), and in turn, this process may influence phytoplankton dynamics in complex and contrasting ways (e.g., reduction of light availability due to increased turbidity hindering algal growth; algal biomass increasing due to transport of benthic species to plankton) (Padisák *et al.* 1990; Istvánovics *et al*. 2004). These effects may also be strongly influenced by fluctuations in water level in response to interannual variability in rainfall (Jeppesen *et al.* 2015). For example, extreme water level reductions during extended drought periods may result in prolonged hydraulic residence times and altered mixing regimes, which may result in favorable conditions for cyanobacterial blooms (McGregor and Fabbro 2000). Increase in cyanobacterial biomass may also result in decreased water transparency and light penetration, making the environment more selective and restructuring phytoplankton diversity to favor shade-adapted species (Paerl and Huisman 2008).

Peri Lake is a subtropical, freshwater, shallow lake used for human water supply. Filamentous cyanobacteria (especially *C. raciborskii*) have been reported as dominant organisms in the lake since 1999 (Komárková *et al*. 1999, Tonetta *et al.* 2013; Silveira 2013; Baptista and Nixdörf 2014). An increase in phytoplankton biomass and algal blooms was also reported in a recent study, which suggests that changes in lake characteristics (i.e., decreased water level and increased water stability) due to changes in interannual rainfall variability have produced favorable conditions for phytoplankton growth (Fuentes and Petrucio 2015). The present study investigates the effects of changing rainfall patterns on algal community structure and biomass dynamics. We hypothesize that changes in environmental conditions (especially the decrease in water level) may result in increased nutrient availability and stimulate the growth of other populations, altering species dominance.

Materials and Methods

Peri Lake (27º 42'–46'S; 048º 30'–32'W) is a natural coastal lake located in the southeastern region of Santa Catarina Island (Florianópolis, Santa Catarina, Brazil). The regional climate is humid subtropical, with stronger winds during the austral spring and rainfall occurring throughout the year (Fuentes and Petrucio 2015). On-site rainfall and lake water level were collected daily from July 2009 to May 2013. Missing rainfall data were replaced with daily recordings from the Hercílio Luz International Airport weather station (27°40'S; 048°33'W). Maximum wind gust speed, water temperature, total phosphorus and nitrogen, soluble reactive phosphorus, and dissolved inorganic nitrogen (as the sum of nitrite, nitrate and ammonium) concentrations were determined monthly on site. Limnological sampling was performed in the mornings (8a.m.–12p.m.) in the central region of the lake, at four different depths: subsurface (~0.5 m); Secchi depth; limit of the euphotic zone (2.7 times Secchi depth, Cole 1994); and aphotic zone (average depth between the euphotic zone and the maximum depth). Phytoplankton samples were collected monthly at the subsurface. Phytoplankton densities were determined by sedimentation (Utermöhl 1958), and biovolumes were estimated using formulas for the geometric shapes of species (Sun and Liu 2003). To compute the wet weight biomass, we assumed the specific gravity of 1 mg = 1 mm^3. Species that attained monospecific dominance (Lobo and Leighton 1986) with relative contribution > 50% of total biomass at least once were analyzed individually and separated from the remaining species data. Water stability was estimated based on maximal differences in water density of pycnocline ($\Delta\rho$) between the sampled depths, and water density was estimated from temperature (Weast 1989). Pycnocline $\Delta\rho$ results greater than 20×10^{-3} Kg m^{-3} m^{-1} were considered indicative of more stable water column conditions (Reynolds 1997). Pycnocline $\Delta\rho$ negative results (inverse pycnocline) were converted to zeroes for statistical analyses. To assess interannual variability, 12-month intervals were chosen between July and June of consecutive years for statistical analysis. Variation among years (using daily and monthly data from all depths, when available) was analyzed by one-way ANOVA with Tukey's post-hoc test. To avoid issues with non-normal data or outliers, F-statistics were tested by permutations using the {lmPerm} package in R (R Development Team Core 2010). Correlations between variables were determined using Pearson's correlation coefficient (r), using monthly data. Results were considered significant at $P \leq 0.05$.

Results

Climate, physical and chemical analysis

Although well distributed throughout the year (mean monthly = 152.8 ± 90.8 mm), rainfall tended to be higher during the austral summer (January to March) (Fig. 1). This pattern differed in the summer of 2012, with an average decrease of 43% compared to other study years (monthly mean during summer of previous years = 245.7 mm). Similarly, rainfall decreased by 48% during the 2012 austral winter (July to September; monthly mean during winter of previous years = 169.2 mm) (Fig. 1). These decreases resulted in a 33% overall reduction in 2012 annual rainfall (mean = 1,382 mm) compared to 2010 and 2011 (mean = 2,075 mm). Water level ranged between 2.19 and 3.10 m (Fig. 1), with significant differences between years (n=1316; F=816.7, $P \leq 0.01$). When water levels were below 2.50 m (April 2012 to February 2013) (Fig. 1), a strong reduction in outflow volume was observed due to the spillway level of the lake (2.44 m).

Wind gust speed ranged from zero to 10 m s^{-1} (mean = 3.9 ± 3.1 m s^{-1}) (Fig. 2), and was similar between years. Water temperature varied between 14.5 °C and 29.0 °C (mean = 22.5 ± 3.6 °C) (Fig. 2), and was similar between years. The water column stability index (pycnocline $\Delta\rho$) ranged from zero to 128.9 $\times 10^{-3}$ Kg m^{-3} m^{-1} (mean = 37.1 ± 37.7 $\times 10^{-3}$ Kg m^{-3} m^{-1}). As expected, the water stability followed the variation of water temperature, and tended to be higher during warmer periods (October to February), especially at lower wind speeds (Fig. 2).

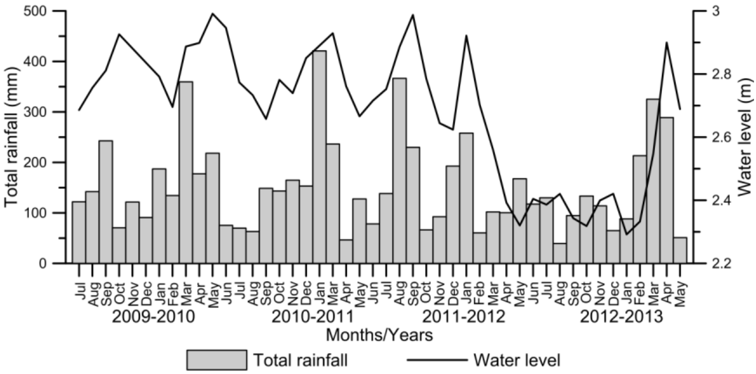

Fig. 1. Monthly rainfall variation and mean water level in Peri Lake (Jul 2009 to May 2013).

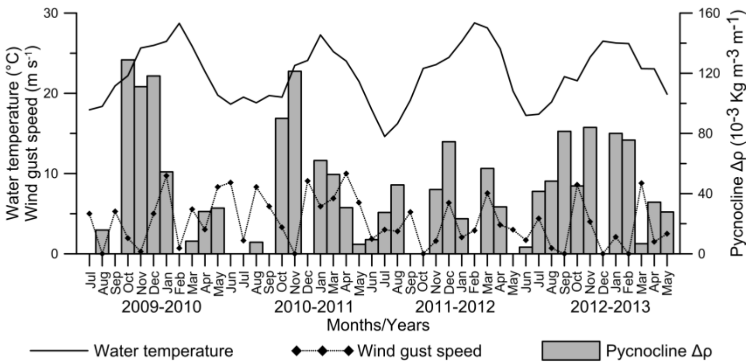

Fig. 2. Variation in water temperature, wind gust speed and water density gradient (pycnocline Δρ) during samplings in Peri Lake (Jul 2009 to May 2013).

Total phosphorus ranged between 6.4 and 28.9 µg L^{-1} (mean = 12.9 ± 4.3 µg L^{-1}), and was similar between years (Fig. 3 *a*). Total nitrogen ranged between 90.6 and 1752.6 µg L^{-1} (mean = 609.3 ± 350.3 µg L^{-1}), and was different between years (Fig. 3 *b*). The highest concentrations of total phosphorus (mean = 23.9 ±

3.3 µg L^{-1}) and total nitrogen (mean = 1581.6 ± 103.9 µg L^{-1}) occurred from August to September 2012. Soluble reactive phosphorus ranged between 0.1 and 10.5 µg L^{-1} (mean = 2.8 ± 2.1 µg L^{-1}), and was different between years (Fig 3 *c*). The highest average concentrations were observed in the last year of the study. Dissolved inorganic nitrogen ranged between 1.9 and 55.3 µg L^{-1} (mean = 18.5 ± 9.9 µg L^{-1}), and was different between years (Fig 3 *d*). Lowest average concentrations were observed during the last year of the study.

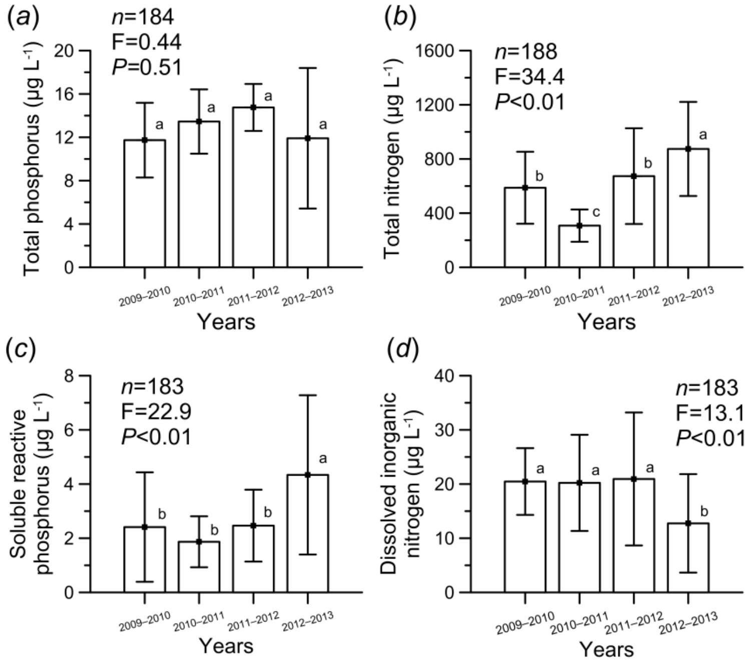

Fig. 3. Interannual variation (2009–2013) in *(a)* total phosphorus, *(b)* total nitrogen, *(c)* soluble reactive phosphorus and *(d)* dissolved inorganic nitrogen concentrations in Peri Lake. Vertical bars indicate standard error of the mean. Different lower case letters indicate significant differences in mean values between years (*P* <0.05; Tukey's post-hoc test).

Phytoplankton analysis

The group of filamentous cyanobacteria species from orders Oscillatoriales and Nostocales were predominant during the study period, with relative biomasses above 70% (mean = 90.8%). There were six Oscillatoriales species: *Pseudanabaena catenata* Lauterborn, *Limnothrix redekei* (Goor) Meffert, *Limnothrix* sp., *Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová & Cronberg, *Planktolyngbya circumcreta* (G.S.West) Anagnostidis & Komárek, and *Planktolyngbya* sp., and two Nostocales species (*Cylindrospermopsis raciborskii* and *Dolichospermum* sp.). Two species presented monospecific dominance: *C. raciborskii* (41 of 46 samples) and *P. catenata* (October 2012). They were also co-dominant on three sample dates (October 2011, August to September 2012) (Fig. 4), and *L. redekei* was co-dominant with *C. raciborskii* on one sample date (May 2013).

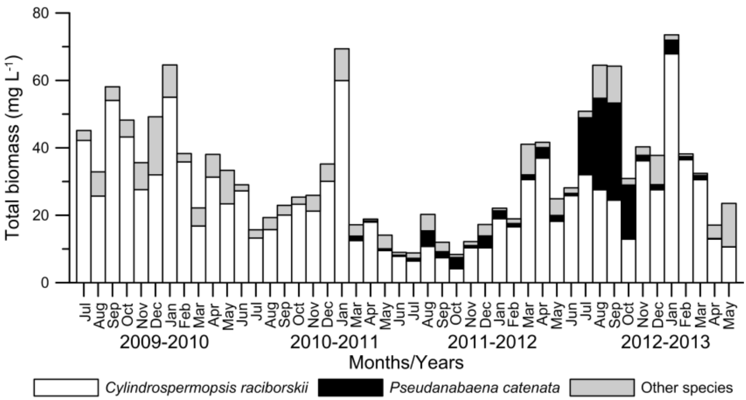

Fig. 4. Monthly variation in Peri Lake total phytoplankton biomass (Jul 2009 to May 2013).

Total biomass ranged between 8.4 and 73.5 mg L^{-1} (mean = 32.5 ± 17.2 mg L^{-1}), and was similar between years (Fig. 5 *a*). Peaks in phytoplankton biomass typically occurred in January, with a tendency to decrease from January to June and increase from July to December (Fig. 4); this pattern differed in 2012 (Fig. 4). *C. raciborskii* biomass ranged between 4.1 and 67.8 mg L^{-1}

(mean = 25.2 ± 14.6 mg L^{-1}). *C. raciborskii* relative biomass (mean = 77.2 ± 15.9 %) varied significantly between years (Fig 5 *b*). The second most abundant species was *P. catenata*, which ranged in biomass from zero to 28.8 mg L^{-1} (mean = 2.7 ± 6.4 mg L^{-1}). Its biomass tended to be higher from July to October, especially in 2012 (Fig. 4), and its overall relative contribution to total phytoplankton biomass (mean = 7.8 ± 13.4 %) differed between years (Fig. 5 *c*). The biomass of the remaining species ranged between 0.5 (April 2011) and 17.2 (December 2009) mg L^{-1} (mean = 4.5 ± 3.8 mg L^{-1}), showed no variation between years (Fig. 5 *d*), and had relative contributions to total biomass between 1.8 and 54.9 % (mean = 14.9 ± 10.3 %).

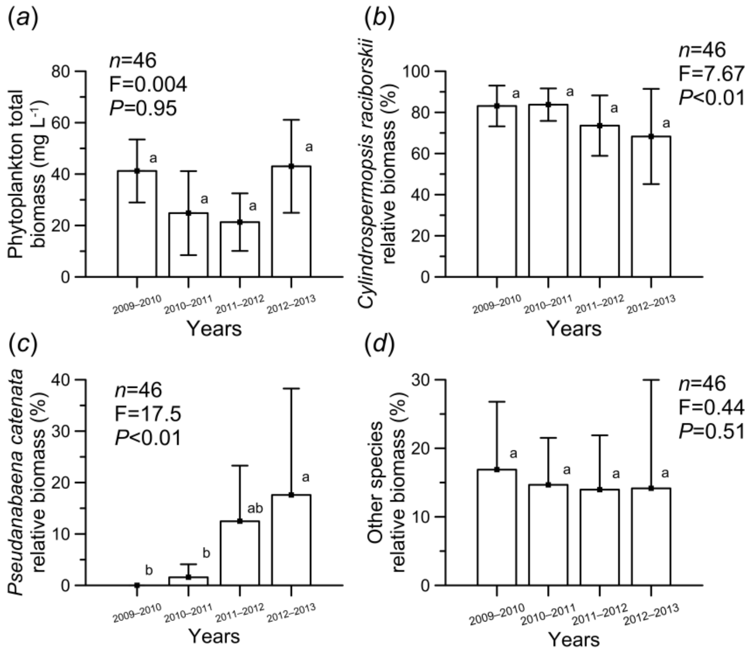

Fig. 5. Interanual variation in *(a)* total biomass of phytoplankton and relative biomasses of *(b) C. raciborskii*, *(c) P. catenata*, and *(d)* remaining species in Peri Lake. Vertical bars indicate standard error of the mean. Different lower case letters indicate significant differences in mean values between years (*P* <0.05; Tukey's post-hoc test).

Correlations between environmental variables and phytoplankton

As expected, water level was positively correlated with total rainfall (Table 1). The decrease in rainfall in 2012 resulted in two distinct periods with respect to water level (higher and lower), which in turn resulted in different responses in water chemistry. Higher water level (2009-2011) yielded no difference in total phosphorus concentrations and maintained low concentration of soluble reactive phosphorus (Fig. 3 *a*, *c*). Wind gust speed was negatively correlated with soluble reactive phosphorus and total nitrogen (Table 1), which varied greatly between years and showed no clear tendency toward increase until 2012 (Fig. 3 *b*). Dissolved inorganic nitrogen was indirectly related to greater rainfall; this was probably due to higher external loading, as the increase was positively correlated with increase in water level (Table 1).

Table 1. Pearson's correlations (P <0.05) between phytoplankton and environmental variables in Peri Lake. TR, total rainfall; WL, water level; WT, water temperature; Δρ, pycnocline density gradient; TP, total phosphorus; TN, total nitrogen; SRP, soluble reactive phosphorus; DIN, dissolved inorganic nitrogen.

Variables	**TR**	**WL**	**WT**	**Δρ**	**TP**	**TN**	**SRP**	**DIN**
Wind gust speed						-0.36[b]	-0.33[b]	
Water level	0.34[d]					-0.48[e]		0.66[f]
Total biomass		-0.42[b]		0.38[a]		0.41[b]		
C. raciborskii biomass			0.35[a]					
C. raciborskii dominance					-0.36[b]	0.37[b]	-0.61[b]	
P. catenata biomass		-0.49[d]			0.57[b]	0.56[b]	0.53[b]	-0.39[c]
P. catenata dominance		-0.38[d]			0.48[b]		0.35[b]	
Other species biomass				0.34[a]			0.57[b]	
Other species dominance							0.49[b]	

[a] , *n*=46; [b] , *n*=45; [c] , *n*=44; [d] , *n*=43; [e] , *n*=42; [f] , *n*=41

Total and dissolved nutrient availability changed significantly in the last year of the study. While dissolved inorganic nitrogen decreased (Fig. 3 *d*), soluble reactive phosphorus (Fig. 3 *c*) and total nitrogen (Fig. 3 *b*) increased significantly. As already mentioned, total phosphorus also showed the highest concentrations during 2012. The decrease of water level was related to increased total nitrogen (Table 1). Total biomass was positively correlated with total nitrogen, and biomass increase was directly related to increase in water stability and water level decrease (Table 1).

C. raciborskii biomass was positively correlated with increasing water temperature, and dominance (i.e., relative contributions to total biomass) was inversely related to phosphorus availability (Table 1). *P. catenata* biomass increased in response of changes in nutrient availability, resulting in increased total biomass (Fig. 5 *a*, *c*). *P. catenata* biomass was positively correlated with total phosphorus, soluble reactive phosphorus and total nitrogen, and inversely correlated with water level and dissolved inorganic nitrogen (Table 1). The biomasses of the remaining species were positively correlated with increased water stability and soluble reactive phosphorus availability (Table 1).

Discussion

Our results suggest a seasonal pattern of environmental and biological responses in Peri Lake. This variability is likely related to seasonal variability in water temperature due to increase in daily light availability and solar heating of waters during warmer periods. This system is characterized by the all-year monodominance of *Cylindrospermopsis raciborskii*, with increased total biomass during warmer periods. However, the decrease in water level observed in 2012 may have resulted in stronger influence of external factors (e.g., solar irradiance and wind) at the bottom and in littoral areas of the lake, altering dissolved nutrient availability and increasing benthic species recruitment to phytoplankton populations through resuspension processes. These seem to be the main factors favoring increase in *Pseudanabaena catenata* biomass and breaking the dominance of *C. raciborskii* in the last year of the study.

Effects of climate variability on physical and chemical conditions

Mixing regimes in subtropical coastal lakes are strongly influenced by wind (Kjerfve and Magill 1989; Cardoso and Marques 2009). Winds whose predominant direction is in line with the geographical profile of the lake and with annual average speeds above 3 m s^{-1} hamper the formation of stable stratification in Peri Lake (Fuentes and Petrucio 2015). In this study, the mixing regime of the lake was characterized mainly by lower water stability; this was particularly true between 2009 and 2011 due to higher wind speeds and higher rainfall. Nevertheless, daytime stratifications are recurring phenomena in this system, and these events became more frequent during periods of lower water level and lower outflow volume (Fuentes and Petrucio 2015).

The thermal response of lakes to climate variability depends on lake morphometry and trophic state (Nõges *et al.* 2011). Despite Peri Lake being more subjected to wind mixing as a polymictic and functionally shallow system (*sensu* Padisák and Reynolds 2003), its low water transparency (Secchi depth ~ 1 m) makes it susceptible to diurnal stratifications, especially during periods of weaker winds and higher temperatures. Peri Lake transparency decreased during periods of increased algal biomass (i.e., during higher trophic states). This may have reduced light penetration and trapped large amounts of solar irradiance in upper layers, resulting in the increased vertical density gradients (i.e., increased water column stability) observed in 2012-2013 (Fuentes and Petrucio 2015). On the other hand, changes in nutrient concentrations during lower water levels seem to be due to stronger influence of wind mixing through resuspension processes at night, and increased phytoplankton growth rate during daytime stratification periods.

Wind-induced sediment resuspension is the most important transport process in wind-exposed shallow lakes (Istvánovics *et al.* 2004). Resuspension events are often followed by changes in internal phosphorus load and increased soluble reactive phosphorus concentration, which may stimulate algal growth (Søndergaard *et al.* 1992; Cardoso and Marques 2009). Simultaneously, transport of benthic species may temporarily increase the biomass of phytoplankton (Padisák *et al.* 1990). Increase in internal phosphorus load and biomass of benthic species during lower water levels are indicative of increased wind-induced resuspension events. These events probably became more frequent and stronger due to the changes in morphometry of the lake (i.e., decrease in mean depth).

Drivers of variability in phytoplankton populations

Monospecific dominance in cyanobacteria was recently reviewed for Brazilian tropical and subtropical lakes (Soares *et al*. 2013), and was found to be most common at lower latitudes. *C. raciborskii* monodominance was more frequent in shallow systems with annual mixing and more eutrophic conditions. The authors reinforced that *C. raciborskii* is well adapted to both mixed and stable conditions, as observed in other water bodies (Burford *et al*. 2006; Berger *et al*. 2006). As *C. raciborskii* is apparently unaffected by water column stability, high phosphorus affinity and phosphorus storage capacity may give it adaptive advantage over other species (Istvánovics *et al.* 2000), especially under more stable conditions. Studies have suggested that the dominance of this species may be associated with its ability to deplete the dissolved phosphorus in the epilimnion under stable conditions with low nutrient concentration (Antenucci *et al*. 2005; Burford and O'Donohue 2006; Posselt *et al*. 2009). The monospecific dominance of *C. raciborskii* in Peri Lake represents an alternative situation for Brazilian lakes with respect to latitude and trophic state (*sensu* reports of Soares *et al.* 2013). The mean concentrations of soluble reactive phosphorus during periods when water levels were higher can be considered limiting for phytoplankton growth (< 3 µg L^{-1}, or < 0.1–0.2 µmol P L^{-1}, *sensu* Reynolds 2006). However, studies of Australian lakes suggest that low concentrations of dissolved inorganic phosphorus (< 0.06 µmol P L^{-1}) may be sufficient to promote the growth of *C. raciborskii* (Burford and O'Donohue 2006; Posselt *et al*. 2009). In the last year of the present study when soluble reactive phosphorus was more available, another filamentous cyanobacterium (planktonic *Limnothrix redekei*) attained higher biomass and dominance during higher water levels (May 2013). This may explain the negative correlation between *C. raciborskii* dominance and phosphorus availability.

Steady-state communities in the natural environment are apparently strongly determined by K-strategist species (Naselli-Flores *et al*. 2003) such as filamentous cyanobacteria. A study conducted in shallow lake in a savanna (Lagoa Santa) had similar conditions to those observed in Peri Lake, with the prevalence of *C. raciborskii* throughout the year (Figueredo and Giani 2009). The authors suggested that constant mixing of the water column may have been responsible for the stability of the phytoplankton community. In this sense, Baptista and Nixdörf (2014) proposed that Peri Lake presents a non-successional phytoplankton community state, directed by competitive exclusion in low disturbance conditions due to permanent mixing of the water column. However, while the decrease in water level during 2012 was a clear response to interannual rainfall variability (Fuentes and Petrucio 2015), its consequences for lake function indicate its role as a disturbance event with regard to biomass dynamics and community structure. The tendency for phytoplankton biomass to decrease in warmer periods was modified during this year, and changes in community structure began in July 2012 (when *C. raciborskii* was still monodominant). The monospecific dominance of *C. raciborskii* was disrupted in August 2012, and the co-dominance between species remained until October 2012, when *P. catenata* attained monodominance over the phytoplankton community.

Internal nutrient cycling may increase when sublittoral strata (i.e., strata too deep to be impacted by internal waves at high water levels) become more subjected to resuspension due to boundary mixing under extreme reduction in water level (Jeppesen *et al.* 2015). Additionally, development of phytoplankton biomass may reduce underwater light penetration, negatively impacting benthic microalgae (Scheffer *et al.* 1997) at lower mean depths. Water level reduction favored increased water stability and algal biomass (as chlorophyll-*a* concentrations) in Peri Lake, particularly in the 2012-2013 sampling year (Fuentes and Petrucio 2015). These results were confirmed by correlations between total phytoplankton biomass, water level, and water stability. As shown by Barbosa and Pádisak (2002), daytime stratifications can influence phytoplankton community structure by allowing non-floating species to remain in suspension in the epilimnion for a longer period of time. This may have favored the biomass increase and dominance of *P. catenata*.

P. catenata is a benthic species frequently found in plankton as a dominant species and commonly coexisting with *C. raciborskii* (Padisák *et al*. 2003; Bouvy *et al*. 2003; Aragão-Tavares *et al*. 2013). However, to our knowledge the current study is the first record of *P. catenata* monodominance. Because its dominance has been recorded in such different habitats, *P. catenata* was often classified in different functional groups of phytoplankton (*sensu* Reynolds *et al*. 2002), such as **S1** (photoadapting solitary filamentous cyanobacteria), or **R** (hypo-metalimnion of deep and stratified oligo-mesotrophic lake cyanoprokariotes) (Moura *et al*. 2007; Naselli-Flores *et al*. 2003). The **MP** functional group was eventually created, which includes metaphytic, periphytic and epilithic specimens drifting plankton in frequently stirred-up, inorganic, turbid, shallow lakes; *P. catenata* was included as a representative species of this group (Padisák *et al*. 2007). A consensus is likely to be reached that *P. catenata* and *C. raciborskii* share ecological traits such as low light requirements and low sinking rates, and environmental preferences such as tolerance for mixing. Although *P. catenata* belongs to a different habitat, its year-round presence in plankton at low biomass clearly reflects the influence of mixing regime on phytoplankton community structure in wind-mixed Peri Lake.

An interesting observation is that *C. raciborskii* seems to be less competitive for soluble reactive phosphorus than *P. catenata*, which greatly increased its biomass when availability of this nutrient was higher. Lower competitive ability of *C. raciborskii* for nutrients has been previously suggested (Briand *et al.* 2002), and has been observed in comparison with other Oscillatoriales species, the planktonic *Planktothrix agardhii* (Gomont) Anagnostidis & Komárek (Bonilla *et al*. 2012). The authors observed lower performance of *C. raciborskii* compared to *P. agardhii* under low light and temperature conditions, confirming the different growth strategies of these species. However, facultative diazotrophy and mixotrophy in *C. raciborskii* (O'Neil *et al.* 2011) gives it an important advantage over other filamentous species and guarantees biomass maintenance when dissolved inorganic nutrients is limited (Figueredo *et al.* 2014). In the present study, *C. raciborskii* monodominance was restored after dissolved inorganic nutrients become strongly limiting to phytoplankton growth. Where conditions for phytoplankton growth are restrictive (i.e., in terms of dissolved nutrients concentrations) such as in Peri Lake, adaptive traits are more valuable than competitive traits, and species with strong adaptive traits seem to be capable of maintaining and even increasing biomass and dominance.

In conclusion, this study provided evidence that decreased water level results in morphological and hydrological changes that allow external factors (i.e., wind speed and solar heating of water) to promote stronger influence over lake physical and chemical conditions. Resuspension processes increased phosphorus availability and improved benthic species recruitment to plankton, driving changes in phytoplankton abundance and community structure when water level is lower. *C. raciborskii* monodominance was associated with warmer conditions and lower phosphorus availability. Given the changes in rainfall expected to occur with climate change, future environmental monitoring of lake mixing regime and resuspension processes is fundamental for proper management of water quality in drinking water sources, especially in shallow cyanobacteria-dominated systems such as Peri Lake.

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CONCLUSÕES FINAIS

O estudo presente mostrou que a Lagoa do Peri (Ilha de Santa Catarina, Brasil) é um ecossistema costeiro naturalmente perturbado sob o ponto de vista da estabilidade física. Sua conformação geográfica com a direção predominante do vento torna o ambiente suscetível à mistura completa da coluna d'água por ação dos ventos médios registrados na região. Hidrologicamente, o lago se mostrou fortemente dependente do aporte hídrico promovido pela precipitação pluviométrica, que por sua vez tem sido climatologicamente bem distribuída ao longo dos anos.

Por possuir o entorno relativamente bem preservado de atividades antrópicas, em comparação com outros ambientes costeiros da própria ilha, o lago apresenta concentrações baixas (oligo/mesotróficas) de nutrientes inorgânicos dissolvidos (fósforo e nitrogênio). No estudo, a disponibilidade do nitrogênio inorgânico dissolvido se mostrou relacionada à contribuição alóctone em períodos de níveis hidrológicos mais elevados (maiores montantes de precipitação pluviométrica), enquanto que o fósforo inorgânico dissolvido esteve relacionado a processos de ciclagem interna (ressuspensão de sedimentos).

A variabilidade climática interanual, especialmente da precipitação pluviométrica, se mostrou um fator importante para a ecologia desse sistema, uma vez que resultou em modificações morfológicas e hidrológicas suficientemente capazes de promover alterações significativas das condições físicas e químicas que resultaram em mudanças na estrutura e na dinâmica da comunidade fitoplanctônica presente. A resposta do nível hidrológico do sistema a esse fator externo leva a importantes considerações que não foram abordadas nesse estudo, tais como a necessidade de conhecer melhor questões relacionadas ao balanço hídrico da bacia hidrográfica, bem como o possível impacto do crescimento urbano do entorno sobre a situação das águas subterrâneas e do lençol freático.

Apesar de apresentar baixas concentrações de nutrientes dissolvidos, o lago apresenta biomassas fitoplanctônicas relativamente elevadas (eu/hipereutróficas) que influenciam claramente sobre a disponibilidade de luz subaquática. Este estudo reforça a importância deste fator sobre a estruturação da comunidade fitoplanctônica da Lagoa do Peri, uma vez que demonstra a predominância absoluta e perene de populações adaptadas a condições de sombreamento (cianobactérias filamentosas). Igualmente, questões relacionadas à perda de diversidade biológica pelo predomínio de condições restritivas ao crescimento fitoplanctônico não foram abordadas e sugerem estudos futuros, especialmente no campo experimental, já que esse trabalho, assim como outros anteriores realizados pelo Laboratório de Ecologia de Águas Continentais (LIMNOS/UFSC), pode vir a contribuir como fonte de informações destinadas a esse propósito.

Todos os resultados observados neste estudo sugerem que a comunidade fitoplanctônica da Lagoa do Peri encontra-se, sob o ponto de vista ecológico, em estágio sucessional maduro e em equilíbrio. Tal conclusão se dá pelo fato da ampla dominância de organismos tipicamente K-estrategistas, fortemente adaptados às condições de mistura e baixa disponibilidade de luz e nutrientes observadas no ambiente. Mesmo os eventos de perturbação externa observados nesse estudo não foram capazes de promover mudança da comunidade fitoplanctônica para estágios iniciais de sucessão ecológica, o que sugere elevada resiliência deste ecossistema a eventos de natureza externa, como a variabilidade climática sazonal e interanual.

Apesar disso, por ser um ambiente costeiro, raso e utilizado para abastecimento de água de significativa parcela populacional do município, mais importante se torna a necessidade de monitoramento e gestão adequada e constante deste recurso. Sob o ponto de vista da utilidade econômica e social, este estudo espera ter contribuído com informações e sugestões importantes, especialmente no que se refere ao monitoramento limnológico da qualidade de água, da dinâmica da comunidade fitoplanctônica e do aporte hídrico oriundo da precipitação pluviométrica na região, bem como quanto ao gerenciamento de volume de água estocada no sistema. As medidas sugeridas se fazem necessárias levando-se em consideração a condição de predomínio de uma espécie potencialmente tóxica da qual pouco ainda se sabe quanto aos mecanismos capazes de iniciar o processo de produção de toxinas pela mesma.

Levando-se ainda em consideração o atual cenário onde é esperado o aumento global da temperatura do ar, bem como mudanças nos regimes pluviométricos regionais, as medidas sugeridas se fazem ainda mais urgentes e necessárias. A comunidade científica precisa continuar envolvida com tais questionamentos e assim poder contribuir mais extensivamente, da mesma forma que o estado e a sociedade precisam estar cientes dessas informações e agir conjuntamente para a melhor preservação desses recursos.

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ANEXOS

Anexo A - Espécies encontradas nas amostras mensais de fitoplâncton na Lagoa do Peri (Abr/2012 a Mai/2013).

	abr/12	mai/12	jun/12	jul/12	ago/12	set/12	out/12	nov/12	dez/12	jan/13	fev/13	mar/13	abr/13	mai/13
Cyanobacteria														
Aphanocapsa conferta (West & G.S.West) Komárková-Legnerová & Cronberg							x	x	x	x				
Chroococales sp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Cylindrospermopsis raciborskii (Woloszynska) Seenayya & Subba Raju	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Limnothrix redekei (Goor) Meffert	x	x	x		x		x	x	x	x	x		x	x
Planktolyngbya limnetica (Lemmermann) Komárková-Legnerová & Cronberg	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Planktolyngbya sp.	x			x	x		x		x					x
Pseudanabaena catenata Lauterborn	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Bacillariophyta														
Aulacoseira ambigua					x	x			x					x
Fragillaria sp.			x						x					
Chlorophyta														
Actinastrum aciculare Playfair	x	x	x	x	x	x		x	x	x	x	x	x	x
Botryococcus braunii Kützing						x								
Cosmarium porteanum W.Archer	x		x	x	x			x	x					
Golenkinia paucispina West & G.S.West										x				
Monoraphidium irregulare (G.M.Smith) Komárková-Legnerová	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Oocystis lacustris Chodat												x		
Scenedesmus spinosus Chodat									x					
Staurastrum tetracerum Ralfs ex Ralfs		x	x				x		x		x	x	x	x
Staurastrum sp.							x	x		x				
Englenophyta														
Trachelomonas sp.								x						