

Denise Tonetta

DISSERTAÇÃO DE MESTRADO

**PRODUÇÃO PRIMÁRIA E RESPIRAÇÃO PELÁGICA EM UM  
LAGO COSTEIRO SUBTROPICAL (LAGOA DO PERI,  
BRASIL): VARIAÇÕES VERTICAL E TEMPORAL E SUAS  
RELAÇÕES COM A COMUNIDADE FITOPLANCTÔNICA**

Florianópolis  
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**UNIVERSIDADE FEDERAL DE SANTA CATARINA  
DEPARTAMENTO DE ECOLOGIA E ZOOLOGIA  
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA**

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BRASIL): VARIAÇÕES VERTICAL E TEMPORAL E SUAS  
RELAÇÕES COM A COMUNIDADE FITOPLANCTÔNICA**

Dissertação apresentada ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina, como parte dos requisitos para a obtenção do título de Mestre em Ecologia.

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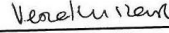
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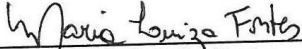
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Florianópolis, 13 de fevereiro de 2012.

A meus pais, Ivo e Marinêz, e a meu  
irmão Ivandro.

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"Sabemos que o que fizemos foi apenas uma gota  
d'água no oceano... Mas se não tivéssemos feito  
essa gota faltaria".

(Madre Tereza de Calcutá)

## RESUMO

Lagos costeiros são ambientes que apresentam características particulares quanto a sua dinâmica, estado trófico, morfologia e interação das comunidades biológicas. Em geral, são ambientes rasos submetidos à intensa ação dos ventos. A lagoa do Peri localizada na ilha de Santa Catarina (27°44'S e 48°31'W) é um sistema costeiro subtropical de água doce com 5,7 km<sup>2</sup> de área e 4,2 m de profundidade média. De acordo com a literatura, apresenta homogeneidade horizontal e vertical para clorofila *a* e nutrientes, característica oligotrófica para a concentração de nutrientes e presença de cianobactérias. Com o objetivo de verificar a ocorrência de autotrofia e heterotrofia na lagoa do Peri, determinaram-se as taxas de produção primária (bruta e líquida) e de respiração fitoplanctônica através de incubações em garrafas claras e escuras durante 24 horas no outono, inverno, primavera e verão. Incubações em garrafas claras e escuras, também foram conduzidas bimensalmente, em quatro profundidades em uma estação central da lagoa, para avaliar a variação vertical das taxas de produção primária (bruta e líquida) e de respiração bem como sua relação com a comunidade fitoplanctônica. Condições de heterotrofia foram encontradas no outono, quando as maiores taxas de respiração ocorreram devido ao aumento da disponibilidade de matéria orgânica e fósforo total. Condições de autotrofia ocorreram no verão devido às maiores taxas de produção primária líquida, favorecida pelas maiores temperaturas e luz. As taxas de produção primária, respiração e a densidade dos grupos fitoplanctônicos, em geral, não apresentaram variação vertical, em função da homogeneização promovida pelos ventos incidentes na lagoa do Peri. Condições limitantes de luz e nutrientes, para o crescimento fitoplanctônico, foram os fatores atribuídos as menores taxas de produção primária encontradas neste ambiente em relação a outros ambientes tropicais e subtropicais. A densidade fitoplanctônica e condições de temperatura e luz favoreceram a produção primária na primavera e no verão. Cyanobacteria e Chlorophyta foram os grupos mais importantes da comunidade fitoplanctônica, em termos de densidade e diversidade, com destaque para *Cylindrospermopsis raciborskii* que dominou na maior parte do período de estudo. Assim, a lagoa do Peri apresentou alternância entre períodos autotróficos e heterotróficos em função das diferentes condições ambientais e as taxas de produção primária foram menores que em outros ambientes, variando em função das variáveis bióticas e abióticas.



**Palavras-chave:** Lago costeiro subtropical. Metabolismo aquático. Produção primária. Respiração. Fitoplâncton. *Cylindrospermopsis raciborskii*.

## ABSTRACT

Coastal lakes are environments with distinct characteristics when it comes to dynamics, trophic state, morphology, and the interaction of biological communities. They are generally shallow environments subjected to intense winds. Peri lagoon located on the island of Santa Catarina (27°44'S and 48°31'W) is a subtropical coastal system of freshwater with an area of 5.7 km<sup>2</sup> and average depth of 4.2 m. According to literature, it is horizontally and vertically homogenous for chlorophyll *a* and nutrients, oligotrophic characteristics for nutrient concentration and presence of Cyanobacteria. In order to verify the occurrence of autotrophy and heterotrophy in the Peri lagoon, primary production (gross and net) and respiration rates were determined by incubating in light and dark bottles over a period of 24 hours in the fall, winter, spring and summer. Incubations in light and dark bottles were also conducted every two months, at four depths in the central part of the lagoon, in order to evaluate the vertical variation in primary production rates (gross and net) and respiration and the relationship to the phytoplankton community. Heterotrophic conditions were found in autumn, where the highest rates of respiration were found due to an increased availability of organic matter and total phosphorus. Autotrophic conditions occurred in the summer due to higher rates of net primary production, favored by higher temperatures and light availability. In general, the primary production rates, respiration and phytoplankton group density, did not show vertical variation due to the homogenization promoted by winds in the Peri lagoon. Light and nutrients limitation were attributed to the lower rates of primary production found in this environment than other ones. However, phytoplankton density, temperature and light conditions favored the primary production rates in spring and summer. Cyanobacteria and Chlorophyta were the most important groups of the phytoplankton community in terms of density and diversity, especially *Cylindrospermopsis raciborskii*, which was dominant during the majority of the study period. Thus, the Peri lagoon had alternating autotrophic and heterotrophic periods due to different environmental conditions and the primary production rates were lower than other tropical environments, depending on biotic and abiotic variables.

**Keywords:** Coastal subtropical lagoon. Aquatic metabolism. Primary production. Respiration. Phytoplankton. *Cylindrospermopsis raciborskii*.

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## 1 INTRODUÇÃO GERAL

Lagos costeiros são ambientes aquáticos lênticos que se distribuem ao longo da costa, podendo receber influência direta ou indireta do ambiente marinho (Kennish e Paerl, 2010). Sua conexão com o mar pode ser feita por um ou mais canais ou podem estar separadas deste por barreiras (Kjerfve, 1994). Ocupam, no mundo todo, aproximadamente 13% da costa. Ao redor dos continentes ocupam 17,9% da África, 17,6% da América do Norte, 13,8% da Ásia, 12,2% da América do Sul, 11,4% da Austrália e 5,3% da Europa (Barnes, 1980). No Brasil, os lagos costeiros estão distribuídos desde o Sul até o Nordeste, sendo em maior número no Rio de Janeiro e no Rio Grande do Sul (Esteves, 1998).

Esses ambientes apresentam grande importância ecológica por constituírem interfaces entre áreas costeiras, águas interiores e águas marinhas, abrigando elevada biodiversidade. Apresentam grande heterogeneidade em relação às características morfológicas, geológicas e hidrológicas (Medina-Gómez e Herrera-Silveira, 2006). Tamanho, morfologia, balanço hidrológico, salinidade, profundidade e ventos são alguns fatores que influenciam os processos físicos e químicos desses sistemas, alterando sua dinâmica que responde rapidamente às alterações ambientais (Kjerfve, 1994; Kennish e Paerl, 2010).

São sistemas fortemente utilizados para fins comerciais, através da exploração de seus recursos, abastecimento público, área de lazer, local de despejo de efluentes, entre outros. Isso os torna vulneráveis aos processos antrópicos, dentre eles a eutrofização, que altera a dinâmica dos lagos costeiros e seu valor ecológico.

Um estudo sobre a antecipação das mudanças climáticas e seus efeitos (IPCC, 2007) mostra que as alterações ambientais podem afetar os ambientes aquáticos, elevando a temperatura, a emissão de CO<sub>2</sub>, alterando a salinidade, turbidez, hidrodinâmica e morfologia, e assim afetando as comunidades biológicas (Lloret et al., 2008; Tadolnéké, 2010). Como já considerado por Goldman (1988), a produção primária é uma das melhores variáveis para elucidar como os sistemas aquáticos respondem às mudanças ambientais.

Lagos tropicais e subtropicais, costeiros ou não, exibem diferenças dos lagos temperados pela menor variação intra e intersazonal devido à menor variação da incidência luminosa e temperatura, em função de sua posição geográfica (Melack, 1979; Esteves et al., 1984), propiciando maiores taxas de produção nestes ambientes (Lewis, 1996; Esteves, 2011). Assim, se há grande

disponibilidade de nutrientes, em função do aporte vindo dos ambientes terrestres e marinhos e da penetração de radiação na coluna d'água, ocorre rápida síntese de matéria orgânica (Lewis, 1996; Kjerfve, 1994). Caso contrário, em condições de oligotrofia e turbidez, os lagos podem apresentar baixos valores de produção primária e maiores taxas de respiração (Wondie et al., 2007).

De acordo com Esteves (2011), muitas abordagens se desenvolveram no estudo dos lagos, desde os trabalhos pioneiros de Forbes (1887), sobre o lago como um microcosmo e de Forel (1892), sobre como as comunidades aquáticas se integram, passando por estudo de transferência de calor por Birge (1897) e de conceitos de estados tróficos, propostos por Naumann (1919; 1930) e Thienemann (1926). Atualmente o foco dos estudos volta-se para sua importância no ciclo do carbono. Apesar de esses ecossistemas ocuparem apenas cerca de 3% da área continental mundial (Downing et al., 2006), seu metabolismo é relevante por participar intensamente dos processos de transporte, transformação, estocagem e exportação de CO<sub>2</sub> para a atmosfera (Cole et al., 2000; Cole et al., 2007).

Toda produção primária dentro de um ecossistema aquático provém da energia de substâncias orgânicas que os organismos autotróficos fixam a partir da matéria inorgânica, por meio da fotossíntese e que é incorporada em biomassa (Cole, 1994; Howarth et al., 1996; Caraco e Cole, 2002), ficando disponível para os níveis superiores da cadeia trófica. Já a respiração é o processo de oxidação/mineralização dessa matéria orgânica, efetuada por organismos heterotróficos, principalmente bactérias e zooplâncton, e também realizada pelos autotróficos, em determinados períodos.

Neste ciclo, os processos de fotossíntese e mineralização, juntamente com a quimiossíntese, são as principais vias pelas quais a matéria orgânica pode ser produzida ou consumida (Cole et al., 2000), sendo a soma desses processos correspondente à produção total ou bruta do ecossistema aquático (Falkowski et al., 2008).

A produção primária é controlada por fatores como luz, temperatura, nutrientes e interação dos organismos presentes na comunidade planctônica (Lewis, 2011). Já a respiração é regulada principalmente pela disponibilidade de matéria orgânica dissolvida (Del Giorgio e Peters, 1994; Hanson et al., 2003). Essa dependência de tantos fatores é responsável pela variação interanual da produção primária e pela ampla escala de variação entre os ambientes (Coloso et al., 2011). Além disso, em sistemas rasos, a produção primária pode ser maior,

devido ao acoplamento entre os processos que ocorrem na coluna d'água e no sedimento (Cole e Cloern, 1987; Jassby et al., 1990).

A disponibilidade de nutrientes e as interações na cadeia trófica determinam se um ambiente será uma fonte ou sumidouro de carbono (Arst et al., 2008). Nitrogênio e fósforo estão relacionados com a autotrofia – taxa de produção primária maior que respiração, enquanto o carbono orgânico dissolvido controla a heterotrofia dos lagos – taxa de respiração maior que produção primária (Odum, 1956; Cole et al., 2000; Del Giorgio e Duarte, 2002; Hanson et al., 2003; Duarte e Prairie, 2005; Dodds e Cole, 2007; Staehr e Sand-Jensen, 2007). Lagos oligotróficos tendem a ser heterotróficos e as taxas de respiração são subsidiadas por matéria orgânica alóctone (Falkowski, 1994; Lennon, 2004; Marotta et al., 2009).

Em ambientes brasileiros, Roland et al. (2010), apresentaram cinco reservatórios supersaturados de CO<sub>2</sub> e Marotta et al. (2010) evidenciaram que a entrada de matéria alóctone, carregada pelo aporte de água continental, promove a supersaturação de CO<sub>2</sub> em lagos costeiros. Para lagos rasos da América do Sul, a saturação de CO<sub>2</sub> apresentou correlação positiva com a temperatura, sugerindo que o aquecimento das águas permite maior exportação desse gás para a atmosfera (Kosten et al., 2010).

O metabolismo de um ambiente aquático é regulado pela atividade de todos os organismos que o compõe, especialmente por organismos fitoplanctônicos, perifíton, bactérias autotróficas e heterotróficas, zooplâncton, macrófitas, entre outros, que são os responsáveis pelos processos de produção primária, ciclagem de nutrientes e decomposição da matéria orgânica (Ducklow, 2008).

A comunidade fitoplanctônica representa um grupo polifilético de organismos procariontes e eucariontes, fotossintetizantes, que varia em tamanho, forma e demanda de nutrientes. São organismos que flutuam livremente em águas pelágicas, estando susceptíveis a ação dos ventos e correntes aquáticas ou apresentando movimentos limitados, tendo papel determinante na produção de matéria orgânica e oxigênio dos ambientes aquáticos (Reynolds, 2006).

Muitos aspectos do fitoplâncton relacionados à sua ecologia, fisiologia, morfologia e estruturação das comunidades vem sendo estudados, notando-se uma permanente variabilidade em escalas temporais e espaciais (Teubner, 2003; O'Sullivan e Reynolds, 2004).

As taxas de crescimento das populações fitoplanctônicas são reguladas pelos controles ascendente (recursos) e descendente (predação) (Reynolds, 2006; Huszar et al., 1990; Krebs, 1994). Além

disso, temperatura, clima, salinidade, dentre outros, que não são constantes no tempo e no espaço (Hillmer et al., 2008; Liu et al., 2010) modulam aqueles controles (Reynolds, 1980; Álvarez-Góngora e Herrera-Silveira, 2006; Becker et al., 2010).

Em ambientes tropicais e subtropicais a dinâmica da comunidade fitoplanctônica e das taxas de produção primária, apesar de apresentarem baixo coeficiente de variação temporal, são direcionadas principalmente pelas condições ambientais de chuva e luz, além da disponibilidade de nutrientes (Melack, 1979; Cardoso e Motta Marques, 2003). Compreender os fatores que regulam a dinâmica da comunidade fitoplanctônica e as taxas de produção primária em uma lagoa costeira subtropical permite fazer previsões sobre seu comportamento e a resposta desses ambientes às mudanças ambientais.

No Brasil, estudos da comunidade fitoplanctônica abrangem todos os tipos de ecossistemas aquáticos lênticos, desde reservatórios, estuários, lagos, lagos de inundação e costeiros (Huszar e Esteves, 1988; Laudares-Silva, 1999; Melo e Huszar, 2000; Cardoso e Motta Marques, 2004; Crosseti et al., 2007; Dantas et al., 2008; Fonseca e Bicudo, 2008; Moura et al., 2011).

Apesar dos estudos sobre metabolismo aquático terem seu início com o trabalho de Odum (1956), só recentemente esse assunto vêm recebendo mais atenção, sendo ainda poucos os estudos em sistemas aquáticos tropicais e subtropicais. No Brasil, os trabalhos vêm sendo desenvolvidos recentemente por Marotta (2009; 2010) e Roland (2010).

Em uma síntese sobre produção fitoplanctônica realizada por Bassoli (2006) a maioria dos dados encontrados esteve relacionada a lagos, lagos de inundação e reservatórios, onde a produtividade foi inferior a  $300 \text{ mg C m}^{-2} \text{ dia}^{-1}$ . A autora demonstrou ainda que o auge de publicações ocorreu na década de 1990, que poucos dados de produtividade em lagos costeiros foram publicados em anos recentes e que os ambientes analisados eram em sua maioria pouco produtivos.

A lagoa do Peri é um lago costeiro subtropical, de água doce, que apresenta homogeneidade espacial para clorofila *a* e nutrientes. Vem apresentando elevadas densidades de cianobactérias, principalmente *Cylindrospermopsis raciborskii* (Woloszinska) Seenayya et Subba-Raju, e característica oligotrófica para a concentração de nutrientes (Komárková et al., 1999; Laudares-Silva, 1999; Grellmann, 2006; Hennemann e Petrucio, 2011). Com base na literatura e nesses conhecimentos prévios, sobre a lagoa do Peri, elaboramos as seguintes hipóteses para este estudo:

1. As taxas de produção primária e respiração pelágica não variam temporalmente em um ambiente subtropical (capítulo 1),
2. A lagoa do Peri é um ambiente predominantemente heterotrófico (capítulo 1),
3. As taxas de produção primária pelágica e respiração apresentam variação vertical, relacionando-se diretamente com a comunidade fitoplanctônica (capítulo 2),
4. As taxas de respiração pelágica são maiores que as taxas de produção primária em um ambiente com baixa concentração de nutrientes e dominado por cianobactérias (capítulo 2).

## 1.1 OBJETIVOS

### 1.1.1 Objetivo Geral

Estimar as taxas de produção primária e respiração pelágica da lagoa do Peri, verificando sua relação com a comunidade fitoplanctônica e as variáveis abióticas.

### 1.1.2 Objetivos Específicos

1. Estimar as taxas de produção primária e respiração pelágica da lagoa do Peri, em quatro períodos, sob diferentes condições ambientais (capítulo 1),
2. Verificar se há predominância de heterotrofia neste ambiente (capítulo 1),
3. Verificar a existência de variação vertical nas taxas de produção primária, respiração e comunidade fitoplanctônica (capítulo 2),
4. Relacionar as taxas de produção primária e respiração com a comunidade fitoplanctônica e com as variáveis abióticas (capítulo 2).

## 2 ÁREA DE ESTUDO

O Parque Municipal da Lagoa do Peri (PMLP) é uma das oito áreas de proteção ambiental da ilha de Santa Catarina e compreende um dos últimos remanescentes de mata Atlântica deste local. Foi criado para preservar o maior manancial de água doce da ilha – a Lagoa do Peri, que vem sendo utilizada pela Companhia Catarinense de Águas e Saneamento (CASAN), desde o ano 2000, para abastecimento da população local. O PMLP foi regulamentado pela Lei Municipal 1.828/81, decretado pela Lei nº 091/82 e está localizado no sudeste da ilha de Santa Catarina com aproximadamente 1.500 hectares de área florestal (CECCA, 1997).

A lagoa do Peri (Figura 1), localizada entre as latitudes sul 27°42'59" e 27°46'45" e as longitudes oeste 48°30'33" e 48°31'59", está situada a 3 m acima do nível do mar, com o qual se conecta através de um canal de sentido único lagoa→mar (Canal Sangradouro). A lagoa apresenta área superficial de 5,7 km<sup>2</sup>, comprimento máximo de 4 km, largura média de 1,7 km, profundidade média de 4,2 m e profundidade máxima de 11 m. Os rios Cachoeira Grande e Ribeirão Grande são os principais tributários da lagoa, a qual tem seu volume calculado em 21,2 milhões de metros cúbicos de água (Laudares-Silva, 1999; Oliveira, 2002).

Desde meados de 1990, vem sendo registrada a presença da cianobactéria potencialmente tóxica *Cylindrospermopsis raciborskii* na lagoa do Peri, e vem se evidenciado o aumento na sua densidade e períodos de dominância (Komárková et al., 1999; Laudares-Silva, 1999; Grellmann, 2006). Este lago apresenta natureza turbulenta, típica de ambientes polimíticos e a zona eufótica geralmente é menor que a zona de mistura, sendo, portanto limitado por luz (Laudares-Silva, 1999). Um estudo sobre o estado trófico classificou a lagoa do Peri como oligotrófica para a concentração de nutrientes e meso-eutrófica para a transparência e concentração de clorofila *a* (Hennemann e Petrucio, 2011).

A lagoa do Peri é rodeada por uma cadeia montanhosa de mata Atlântica, nas porções norte, oeste e sul, e separada do mar por uma região de restinga na porção leste. Este ambiente vem sendo local de diversos estudos sobre a qualidade da água, as comunidades fitoplanctônica, zooplantônica, ictiológica e de insetos aquáticos, além de estudos sobre decomposição de matéria orgânica nos rios tributários da lagoa.

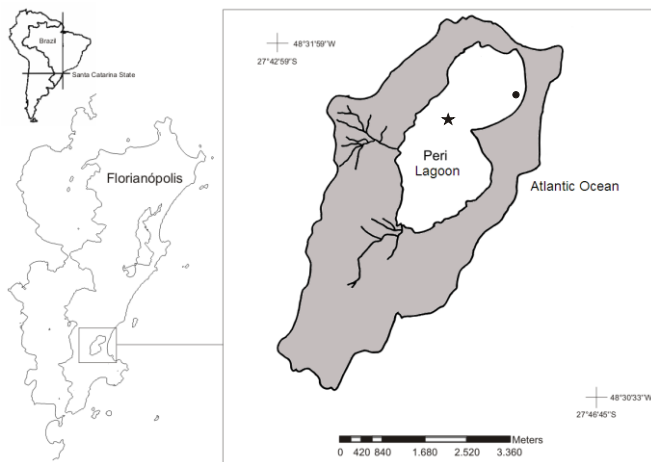


Figura 1 – Mapa e localização geográfica da lagoa do Peri, ilha de Santa Catarina, Brasil, modificado de Hennemann e Petrucio (2011), evidenciando os pontos amostrados durante o período de estudo. Círculo representa o local amostrado para o estudo desenvolvido no capítulo 1 e estrela o local das amostragens em perfil vertical no estudo desenvolvido no capítulo 2.

### 3 MATERIAL E MÉTODOS

#### 3.1 PRODUÇÃO PRIMÁRIA E RESPIRAÇÃO PELÁGICA

As taxas de produção primária e respiração na região pelágica da lagoa do Peri foram determinadas utilizando o método de incubação *in situ* em garrafas claras e escuras, com determinação do oxigênio dissolvido, seguindo o método de Winkler (Wetzel e Likens, 2000).

No capítulo 1, foram amostrados dias representativos de cada estação do ano: outono (23 de maio de 2010), inverno (1 de agosto de 2010), primavera (30 de setembro de 2010) e verão (13 de janeiro de 2011). As incubações foram conduzidas na margem nordeste da lagoa, durante 24 horas. Todas as garrafas foram inicialmente incubadas a uma profundidade de aproximadamente 20 cm na coluna d'água, no início da manhã (9:00 horas). A cada intervalo de tempo (3, 6, 9, 15, 21 e 24 horas de incubação), um conjunto de duas garrafas claras e duas escuras foi retirado da lagoa e o oxigênio dissolvido determinado por titulação. Adicionalmente, duas garrafas foram preenchidas e fixadas no início dos experimentos para determinar a concentração inicial do oxigênio dissolvido.

Para determinar a taxa de produção primária líquida (NPP) utilizou-se a concentração do oxigênio dissolvido da garrafa clara após a incubação e subtraiu-se da concentração do oxigênio dissolvido determinada inicialmente.

Para determinar a taxa de respiração (R) utilizou-se a concentração do oxigênio dissolvido determinada inicialmente, subtraindo-se da concentração do oxigênio dissolvido da garrafa escura, após o tempo de incubação.

A taxa de produção primária bruta (GPP) foi determinada como a soma da variação do oxigênio dissolvido na garrafa clara e a variação do oxigênio dissolvido na garrafa escura.

Os valores de produção primária e respiração obtidos em  $\text{mg O}_2 \text{ L}^{-1} \text{ h}^{-1}$  foram convertidos em  $\text{mg C m}^{-3} \text{ h}^{-1}$  usando o coeficiente fotossintético (PQ=1,2) para encontrar o valor de carbono fixado e o coeficiente respiratório (RQ=1,0) para encontrar o valor de carbono oxidado, ambos propostos por Wetzel e Likens (2000), de acordo com as fórmulas abaixo:

$$\text{GPP (mg C m}^{-3} \text{ h}^{-1}) = [(\text{O}_2 \text{ LB}) + (\text{O}_2 \text{ DB})](1000)(0.375)/(\text{PQ})(t)$$

$$\text{NPP (mg C m}^{-3} \text{ h}^{-1}) = [(\text{O}_2 \text{ LB}) - (\text{O}_2 \text{ IB})](1000)(0.375)/(\text{PQ})(t)$$

$$\text{R (mg C m}^{-3} \text{ h}^{-1}) = [(\text{O}_2 \text{ IB}) - (\text{O}_2 \text{ DB})](1000)(0.375) (\text{RQ})/(t)$$



Onde: LB= garrafa clara, DB= garrafa escura, IB= garrafa inicial, t= tempo de incubação.

No capítulo 2, as estimativas de produção primária e respiração foram efetuadas bimensalmente, de junho/09 a dezembro/10, em quatro profundidades de uma estação central da lagoa do Peri, com profundidade máxima em média de 8,4 m, determinadas de acordo com a incidência de radiação, a partir da leitura visual do disco de Secchi (Figura 2).

A incubação para profundidade 1 foi realizada na superfície, que correspondeu a 100% da radiação fotossinteticamente ativa (PAR) incidente. A incubação para a profundidade 2 foi realizada na profundidade do desaparecimento visual do disco de Secchi, que correspondeu a 10% da PAR (aproximadamente 1,0 m). Para a profundidade 3 foi calculada três vezes a profundidade 2, que correspondeu a aproximadamente 1% da PAR incidente (aproximadamente 3,0 m). E a profundidade 4 foi determinada pela distância intermediária entre o fundo e a profundidade 3, considerada como zona afótica (aproximadamente 6,0 m).

Amostras de água em cada profundidade foram coletas com garrafa de Van Dorn, sendo preenchidas duas garrafas claras e duas escuras, além de duas garrafas adicionais, para determinar a concentração inicial do oxigênio dissolvido em cada profundidade. As garrafas foram incubadas nas profundidades correspondentes, por um período de 3 a 5 horas, determinando-se a concentração do oxigênio dissolvido após esse período. As incubações sempre ocorreram no período da manhã, com início em torno das 10:00 horas.

### 3.2 METABOLISMO PELÁGICO

Autotrofia e heterotrofia da lagoa do Peri foram estimadas em quatro períodos: outono (23 de maio de 2010), inverno (1 de agosto de 2010), primavera (30 de setembro de 2010) e verão (13 de janeiro de 2011), através da concentração de oxigênio dissolvido em uma garrafa clara incubada *in situ* por 24 horas, na subsuperfície da parte nordeste da lagoa do Peri. O valor obtido foi expresso em  $\text{mmol O}_2 \text{ m}^{-2} \text{ dia}^{-1}$ . Quando o valor foi negativo o sistema foi considerado heterotrófico (taxa de respiração maior que a produção primária) e quando positivo (taxa de respiração menor que a produção primária) o sistema foi considerado autotrófico (Staeher et al., 2010).

A autotrofia e a heterotrofia também foram estimadas através da concentração de CO<sub>2</sub> em água livre, pelo método pH-alcalinidade (Stumm e Morgan, 1996). Para isto, foram medidos alcalinidade, pH, salinidade, ventos e temperatura da água às 9:00, 12:00, 15:00, 18:00, 24:00, 6:00 e 9:00 horas em cada período amostrado. As concentrações de CO<sub>2</sub> foram calculadas após correção para altitude, temperatura e força iônica (Cole et al., 1994). Fluxos de carbono entre ar e água foram estimados considerando a velocidade pistão (Cole e Caraco, 1998) e o fator de enriquecimento químico (Wanninkhof e Knox, 1996). Esses resultados foram expressos em mmol C m<sup>-2</sup> dia<sup>-1</sup>. Quando o valor foi negativo o sistema foi considerado autotrófico e quando positivo o sistema foi considerado heterotrófico.

### 3.3 COMUNIDADE FITOPLANCTÔNICA

Juntamente com as estimativas de produção primária bimensal (capítulo 2), foram coletadas amostras de fitoplâncton total. Essas amostras foram coletadas com auxílio da garrafa de Van Dorn, em quatro profundidades sob diferentes incidências luminosas, fixadas com formalina, em concentração final de 1,6% e mantidas sob refrigeração. A identificação dos indivíduos foi feita em microscópio óptico com auxílio de literatura específica.

Para as estimativas de densidade (indivíduos mL<sup>-1</sup>), subamostras de 5 mL foram sedimentadas durante 24 horas, em câmaras Utermöhl com solução de Lugol. Em microscópio invertido, toda a comunidade fitoplanctônica foi contada até atingir 400 indivíduos da espécie dominante (Hasle, 1978), obtendo-se precisão de 10% para um intervalo de confiança de 95%. Cada célula, filamento ou colônia foi considerado um indivíduo.

As espécies abundantes e dominantes foram estimadas de acordo com Lobo e Leighton (1986). Foi considerada abundante quando a densidade da espécie foi maior que a densidade média da amostra e foi considerada dominante quando a espécie apresentou densidade maior que 50% da densidade total da amostra.

### 3.4 VARIÁVEIS ABIÓTICAS

Paralelamente às estimativas de produção primária, algumas variáveis foram amostradas *in situ*: radiação fotossinteticamente ativa (PAR) com auxílio de radiômetro (Li-cor 250A) com sensor esférico, intensidade de ventos com anemômetro (Instrutherm TAD 500) e

temperatura do ar, com termômetro de mercúrio. Os valores de precipitação foram obtidos junto a EPAGRI/CIRAM (Centro de Informações de Recursos Ambientais e de Hidrometeorologia de Santa Catarina).

As variáveis limnológicas medidas *in situ* foram a temperatura da água, pH, condutividade e oxigênio dissolvido, com auxílio de sonda (YSI-85), nos períodos/meses e profundidades amostradas.

Em laboratório foram determinadas a alcalinidade total por titulação (Mackereth et al., 1978) e as concentrações de nitrogênio e fósforo totais (Valderrama, 1981) em amostradas de água não filtradas. Nitrito (Golterman et al., 1978); fósforo solúvel reativo (Strickland e Parsons, 1960) e nitrogênio amoniacal (Koroleff, 1976) foram determinados em amostras de água filtradas em filtros de 0,7  $\mu\text{m}$  de porosidade.

Para estimar as concentrações de clorofila *a*, 500 mL de água foram filtrados em filtros de fibra de vidro AP40 Millipore de 47 mm de diâmetro e 0,7  $\mu\text{m}$  de abertura do poro. A extração foi feita com acetona 90%, com correção para feopigmentos (Lorenzen, 1967). As amostras de água filtradas e não filtradas, para análise de nutrientes e os filtros utilizados para extração de clorofila foram mantidos sob congelamento a  $-20^{\circ}\text{C}$  até a realização das análises.

### 3.5 ANÁLISES ESTATÍSTICAS

A estatística descritiva foi usada para avaliar o conjunto de dados, obtido durante o período de amostragem, através da determinação dos valores mínimo, máximo, média e desvio padrão. Análises de variância para os efeitos tempo de incubação, período, profundidade e meses amostrados, foram utilizadas para verificar diferença significativa entre os dados. Correlação de Spearman foi utilizada para relacionar as variáveis bióticas e abióticas com as taxas de produção primária bruta e líquida e respiração, sendo as últimas consideradas variáveis dependentes.

Análise de regressão múltipla (*stepwise*) foi aplicada para taxas de produção primária e respiração, a fim de verificar as variáveis independentes mais importantes. Para estimar a relação entre determinadas variáveis foi utilizada a análise de regressão linear, com as taxas de produção primária e respiração como variáveis dependentes.

Os dados foram transformados quando necessário e as variáveis redundantes foram excluídas quando apropriado. Todas as análises foram feitas através *software* Statistica 7 (StatSoft®).

## 4 CAPÍTULO 1

### HETEROTROFIA E AUTOTROFIA EM UMA LAGOA COSTEIRA SUBTROPICAL

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## Heterotrophy and autotrophy in a subtropical coastal lagoon

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### Abstract

In order to assess the importance of the environmental drivers on metabolic processes in a subtropical lagoon, pelagic primary production and respiration were investigated in an subtropical coastal lagoon by incubating light and dark bottles for up to 24 hours in autumn, winter, spring and summer. In parallel, ecosystem metabolism was estimated from free-water CO<sub>2</sub> and O<sub>2</sub> in bottles. We hypothesized that i) production and respiration rates would not vary between seasons in a subtropical environment and ii) such an environment would not undergo changes between autotrophic and heterotrophic metabolism, remaining constantly heterotrophic. Our findings were not consistent with these hypotheses, because primary production and respiration varied significantly between seasons, demonstrating the existence of environmental variability in the subtropical system, and showing an alternative pattern from heterotrophy during autumn and winter to autotrophy during spring and summer, by variations in CO<sub>2</sub> and O<sub>2</sub> concentrations. The greatest biological activity was observed between three and six hours of incubation, with the highest gross primary production and respiration rates in the autumn (69.8 and 63.4 mg C m<sup>-3</sup> h<sup>-1</sup>, respectively). The highest net primary production rate (31.6 mg C m<sup>-3</sup> h<sup>-1</sup>) was detected in the summer. Nutrient concentrations, precipitation and photosynthetic active radiation were the main driving forces of the temporal variation in the subtropical lagoon, determining whether its metabolism was heterotrophic or autotrophic.

Keywords: Subtropical coastal lagoon. Primary production. Respiration. Aquatic metabolism.

## Introduction

Coastal lakes have high physical, chemical and biological variability over both the spatial and temporal scales. Gross primary production (GPP), respiration (R) and net primary production (NPP) are also known to vary widely across aquatic ecosystems and to display large temporal variations within ecosystems. Nutrients and photosynthetic active radiation are the major regulators of primary production rates, affecting planktonic organisms (Arst and others 2008; Wondie and others 2007; Tilahun and Ahlgren 2010), while R is regulated by dissolved organic matter (Del Giorgio and Peters 1994; Hanson and others 2003).

The pelagic metabolism of an ecosystem is equal to the difference between how much is produced and consumed [ $NEP=GPP-R$ ] (Odum 1956). The majority of aquatic environments are typically heterotrophic ( $NEP<0$ ), supersaturated in carbon dioxide ( $CO_2$ ), rendering lakes as an important conduit of this gas to the atmosphere. Autotrophic environments ( $NEP>0$ ) can support an export or accumulation of organic material within the ecosystem (Del Giorgio and others 1997; Duarte and Agustí 1998; Cole and others 2002; Cole and others 2007; Kosten and others 2010). Heterotrophic and autotrophic activities play important role in dynamics of aquatic environments and  $CO_2$  emissions (Roland and others 2010).

Terrestrial organic carbon can play an important role in lakes, where it partially supports aquatic food webs, metabolism and contributes to the prevalent  $CO_2$  saturation of lake waters at both daily and annual time scales (Sobek and others 2005; Marotta and others 2009).

On a global scale aquatic metabolism is useful for understanding carbon cycling and explicitly defining the role of ecosystems as sources or sinks of atmospheric  $CO_2$  (Del Giorgio and Duarte 2002; Staehr and Sand-Jensen 2007). Since, some ecosystems alternate between autotrophic and heterotrophic phases during the course of a year (Staehr and others 2010).

Around 75 % of the lakes in the world are lower than 1 km<sup>2</sup> (Downing and others 2006). The Peri lagoon, with 5.7 km<sup>2</sup> is representative of lakes of large extension, spatially homogeneous for chlorophyll *a* and nutrients, dominated by filamentous Cyanobacteria and located in the subtropics (Laudares-Silva, 1999; Grellmann, 2006; Hennemann and Petrucio 2011), where the studies of metabolism are scarce and restricted to some ecosystems (Carmouze and others 1991;

Thomaz and others 2001; Marotta and others 2009; Marotta and others 2010a; Roland and others 2010).

Aiming to improve the understanding of the plankton metabolism from subtropical environments and the relevance in the carbon cycle, we hypothesized that: i) primary production and respiration rates would not undergo temporal variation in a subtropical environment, due to the relatively minor climatic variations observed among seasons; and ii) the studied coastal lagoon would be permanently net heterotrophic, since is dominated for Cyanobacteria with lowest photosynthetic capacity and the lagoon is oligotrophic for nutrients concentrations.

## Materials and methods

### Study site

The Peri lagoon (Figure 1) is located at the southeast of Santa Catarina Island ( $27^{\circ}44'S$  and  $48^{\circ}31'W$ ), Brazil, into a protect area (Peri Lagoon Municipal Park). The lagoon has a surface area of 5.7 km<sup>2</sup> and average and maximum depths of 4.2 m and 11.0 m, respectively. Spatial homogeneity of nutrients and chlorophyll *a* and elevated densities of the Cyanobacteria *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba-Raju have been observed in the lagoon (Komárková and others 1999; Laudares-Silva, 1999; Grellmann, 2006). The lagoon was classified as oligotrophic for nutrients concentrations and meso-eutrophic for transparency and chlorophyll *a* (Hennemann and Petrucio 2011). The system has two main tributaries (Cachoeira Grande and Ribeirão Grande streams) and it does not exchange water with the ocean since it is at 3 m above sea level, which means it is a freshwater lagoon. Its water is used to human supply and the only anthropic activity allowed in the lagoon is recreational.

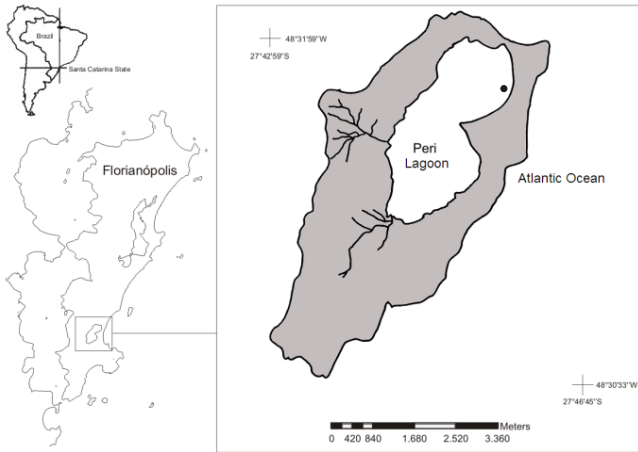


Figure 1: Map and location of the Peri lagoon, Santa Catarina Island, Brazil, showing the incubation station. Adapted from Hennemann and Petrucio (2011).

#### Bottle incubation and data collection

Pelagic metabolic rates were measured by incubation *in situ* of dark and light bottles (duplicate), with initial and final determination of dissolved oxygen by the Winkler method (Wetzel and Likens 2000). In each incubation time, a set of two dark and two light bottles were titrated to quantify dissolved oxygen.

All bottles were incubated at a shallow site, in the northeast of Peri lagoon on four different periods of the year: autumn (May 23, 2010), winter (August 1, 2010), spring (September 30, 2010) and summer (January 13, 2011). Net primary production (NPP, final concentration in light bottles minus initial concentration), respiration (R, initial concentration minus final concentration in dark bottles) and gross primary production (GPP, sum of dissolved oxygen variation in dark and light bottles) rates were determined after 3, 6, 9, 15, 21 and 24 hours of incubation. These incubation durations coincided with 12:00, 15:00, 18:00, 24:00, 6:00 and 9:00 h.

The results, in  $\text{mg O}_2 \text{ L}^{-1} \text{ h}^{-1}$ , were then converted to carbon consumption using the respiratory quotient ( $\text{RQ}=1.0$ ) and carbon productivity using the photosynthetic quotients ( $\text{PQ}=1.2$ ), thereby obtaining values for R, NPP and GPP in  $\text{mg C m}^{-3} \text{ h}^{-1}$  (Wetzel and Likens 2000).

The estimated NPP rates for each incubation interval were normalized for chlorophyll *a* concentration, thereby obtaining the



assimilation number – mg C (mg Chla h)<sup>-1</sup> – as described by Ryther and Yentsch (1957).

Pelagic metabolism were calculated from changes in dissolved oxygen in light bottles, after 24 hours of incubation, with negative results expression net heterotrophic conditions. The heterotrophic or autotrophic status of the Peri lagoon itself was also determined by measuring free-water CO<sub>2</sub>. The data of alkalinity, pH, salinity, wind velocity and water temperature collected at 9:00, 12:00, 15:00, 18:00, 24:00, 6:00 and 9:00 h were used to perform this calculation for all four collection dates. The pH-alkalinity method (Stumm and Morgan 1996) was used to calculate CO<sub>2</sub> concentrations after correction for temperature, altitude and ionic strength (Cole and others 1994), while CO<sub>2</sub> saturation was calculated on the basis of equilibrium with the atmosphere. Air-water carbon fluxes were estimated on the basis of piston velocity (Cole and Caraco 1998) and the chemical enhancement factor (Wanninkhof and Knox 1996). When these results were negative the system was defined as autotrophic and when positive, as heterotrophic.

#### Abiotic variables

The climatological variables were measured *in situ* at the following times of day: 9:00, 12:00, 15:00, 18:00, 24:00, 6:00 and 9:00 h. The variables were: photosynthetic active radiation (PAR), measured at the subsurface and at 50 cm in the water column using a radiometer (Li-cor 250A) with a spherical sensor. Wind velocity was estimated using an anemometer (Instrutherm TAD 500) and air temperature measured using a mercury thermometer. The light attenuation (k) was calculated as described by Wetzel and Likens (2000). Precipitation records were obtained from the Santa Catarina Environmental Resources and Hydrometeorology Information Centre (EPAGRI/CIRAM) and average precipitation for seven days prior to the start of each 24-hour sampling period was estimated.

Water samples were taken at subsurface in the northeast of Peri lagoon for determination of the limnological variables at the same time of climatological variables sampling. The variables water temperature, conductivity and dissolved oxygen were measured with a multiparameter probe (YSI-85), total alkalinity using Gran's titration method (Mackereth and others 1978) and pH with a Digimed pH meter (DM-22) with a precision of 0.01, immediately after collection. For chlorophyll *a* analysis (Chla), 500 mL of water was filtered using Millipore AP40 glass fibre (0.7 µm pore size and 47 mm diameter) and

kept frozen at  $-20^{\circ}\text{C}$ , followed by extraction using 90% acetone (Lorenzen 1967).

Water samples collected at the beginning of each period were frozen at  $-20^{\circ}\text{C}$  for determination of total nitrogen (TN) and total phosphorus (TP) as described by Valderrama (1981). Additionally, the TN:TP ratio was used to indicate which nutrient would potentially limit primary production in Peri lagoon. When TN:TP was less than 20, production was defined as N-limited, and when greater than 38 was defined as P-limited (Sakamoto 1966).

### Statistical analyses

Analysis of variance (Kruskal-Wallis) was conducted for the abiotic variables, GPP, NPP and R in order to evaluate differences between the four periods and incubation times. Spearman correlation coefficients were used to test for possible relationships between abiotic variables and primary production (gross and net) and respiration rates. Forward *stepwise* multiple linear regressions was used to identify the most influential abiotic variables, weighting each variable and its importance for GPP, NPP and R. *Software* Statistica 7 (StatSoft®) was used to conduct all analyses, redundant variables were excluded where appropriate and log transformed when necessary.

## Results

### Abiotic variables

All abiotic variables measured in Peri lagoon (Table 1) differed between the four periods ( $p < 0.05$ ). Mean water temperature and conductivity results were highest in the summer and lowest in the winter, whereas wind velocity was the opposite. Dissolved oxygen concentration was lower in the summer and higher in winter. The highest nitrogen results were observed in the summer and the lowest in the autumn, while phosphorus concentrations were lowest in winter and highest in the autumn. In the winter, spring and summer the TN:TP ratio classified the Peri lagoon as P-limited and the system was N-limited in the autumn.

Table 1: Mean, standard deviation (SD), minimum (min) and maximum (max) values for abiotic variables sampled in autumn (May/2010), winter (August/2010), spring (September/2010) and summer (January/2011) in Peri lagoon. Letters indicate statistic difference.

Variables	Autumn	Winter	Spring	Summer
	Mean – SD (min-max)	Mean – SD (min-max)	Mean – SD (min-max)	Mean – SD (min-max)
Water temperature (°C)*	20.7±0.44 <sup>a</sup> (20.2-21.4)	16.5±0.94 <sup>b</sup> (15.3-17.6)	21.1±1.04 <sup>a</sup> (20.2-22.9)	27.5±1.27 <sup>d</sup> (26.0-29.0)
Conductivity (µs cm <sup>-1</sup> )*	68.3±0.72 <sup>a</sup> (67.7-69.8)	57.2±0.94 <sup>b</sup> (55.9-58.3)	65.0±1.50 <sup>c</sup> (63.5-68.0)	74.5±2.75 <sup>d</sup> (70.8-77.5)
Dissolved oxygen (mg L <sup>-1</sup> )*	8.5±0.36 <sup>e</sup> (8.0-9.0)	9.4±0.13 <sup>b</sup> (9.2-9.6)	9.0 ±0.29 <sup>b</sup> (8.6-9.4)	7.4±0.21 <sup>c</sup> (7.2-7.7)
pH*	7.1±0.13 <sup>a</sup> (6.96-7.28)	7.2±0.05 <sup>a</sup> (7.18-7.34)	7.5±0.10 <sup>b</sup> (7.32-7.64)	7.5±0.33 <sup>b</sup> (6.87-7.8)
Alkalinity (mEq L <sup>-1</sup> )*	0.111±0.00 <sup>a</sup> (0.105-0.115)	0.123±0.01 <sup>b</sup> (0.108-0.133)	0.124±0.01 <sup>b</sup> (0.115-0.132)	0.123±0.01 <sup>b</sup> (0.115-0.129)
Wind (m s <sup>-1</sup> )*	0.3±0.50 <sup>a</sup> (0-1.3)	7.1±2.21 <sup>b</sup> (5.1-11.0)	2.4±1.80 <sup>c</sup> (0.5-5.8)	1.4±1.00 <sup>c</sup> (0-2.5)
TN (µg L <sup>-1</sup> )**	115.2±13.34 <sup>a</sup> (99.4-130.6)	538.8±4.55 <sup>b</sup> (534.9-544.9)	477.8±9.03 <sup>c</sup> (464.8-485.6)	673.4±15.17 <sup>d</sup> (654.2-691.3)
TP (µg L <sup>-1</sup> )**	18.2±1.05 <sup>a</sup> (17.3-19.5)	8.9±0.29 <sup>b</sup> (8.6-9.3)	15.8±1.42 <sup>c</sup> (13.9-17.3)	14.2±1.49 <sup>c</sup> (12.6-16.2)
Chlorophyll <i>a</i> (µg L <sup>-1</sup> )*	16.0±0.96 <sup>a</sup> (14.9-17.1)	15.6±2.64 <sup>a</sup> (10.7-18.7)	18.9±2.46 <sup>b</sup> (16.0-23.5)	18.2±2.88 <sup>b</sup> (12.8-21.9)

\*n=7 \*\*n= 4 in each period.

Mean precipitation, for seven days previously each period, ranged from 16.8 mm day<sup>-1</sup> in the autumn to 0.1 mm day<sup>-1</sup> in the winter, with 9.5 mm day<sup>-1</sup> in the spring and 3.0 mm day<sup>-1</sup> in the summer. Air temperature varied from 13°C in the winter to 26°C in the summer (Figure 2).

The results for PAR measured at the subsurface were similar for the autumn and winter, reaching higher values in summer. The highest light attenuation was observed in the autumn, due high precipitation (Table 2).

Gross primary production (GPP), net primary production (NPP) and respiration (R)

The GPP rates calculated over 24 hours (Figure 3, black bars) varied significantly between periods ( $p < 0.05$ ), where the lowest rates were observed in winter and spring and the highest rates in autumn and summer. Metabolic rates were greatest after 3 and 6 hours of incubation, with a significant difference between these durations and all other

incubation times ( $p < 0.05$ ). However, neither GPP and NPP nor R differed between incubations of three, six or nine hours ( $p > 0.05$ ).

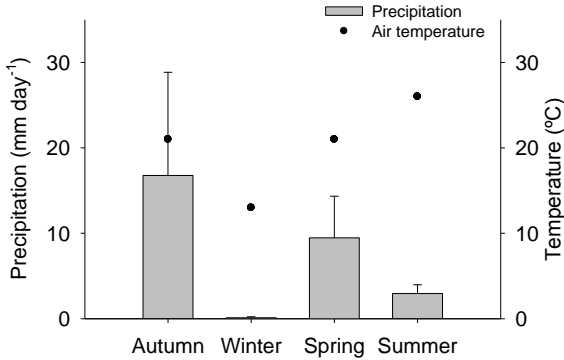


Figure 2: Mean precipitation and standard error of the seven days before sampling and air temperature during sampling period in autumn (May/2010), winter (August/2010), spring (September /2010) and summer (January/2011) in Peri lagoon.

Table 2: Photosynthetic active radiation – PAR – ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) measured in subsurface water column and light attenuation (k) calculated in autumn (May/2010), winter (August/2010), spring (September/2010) and summer (January/2011) in Peri lagoon.

Time	Autumn		Winter		Spring		Summer	
	PAR	k	PAR	k	PAR	k	PAR	k
09:00	147.6	1.65	155.0	0.53	369.9	1.62	312.2	0.47
12:00	124.1	1.21	130.5	0.84	300.1	0.32	736.0	0.17
15:00	143.2	1.64	153.1	0.41	85.0	0.20	609.9	0.38
18:00	-	-	-	-	-	-	62.3	0.40
24:00	-	-	-	-	-	-	-	-
06:00	-	-	-	-	19.8	0.67	-	-
09:00	79.1	1.16	63.6	0.50	144.8	0.18	123.5	0.79
Mean	123.5	1.42	125.5	0.57	183.9	0.60	368.8	0.44

- Lacking natural light

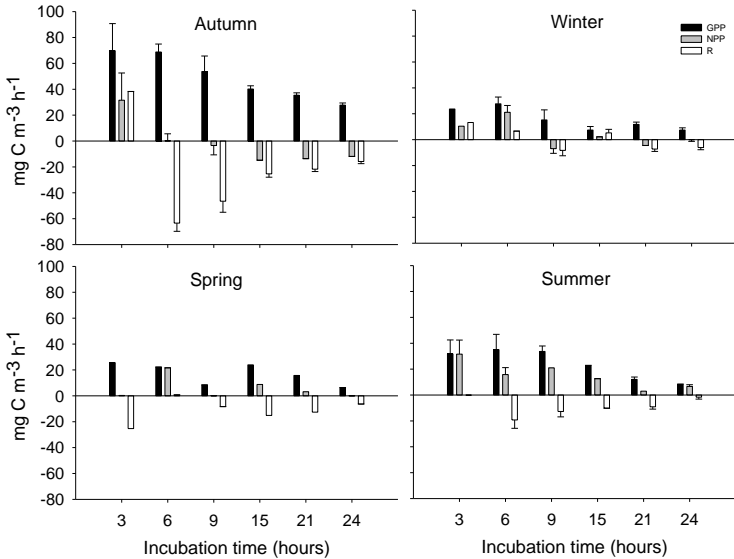


Figure 3: Mean values and standard error of GPP, NPP and R ( $\text{mg C m}^{-3} \text{ h}^{-1}$ ) at each incubation time in autumn 2010, winter 2010, spring 2010 and summer 2011, in Peri lagoon.

The highest estimated GPP value ( $69.8 \text{ mg C m}^{-3} \text{ h}^{-1}$ ) was for a 3-hour incubation period in the autumn, whereas the highest GPP in winter ( $27.7 \text{ mg C m}^{-3} \text{ h}^{-1}$ ) was detected after 6 hours of incubation. Peak GPP in spring was  $25.6 \text{ mg C m}^{-3} \text{ h}^{-1}$  after 3 hours of incubation and the peak value for the summer was  $35.1 \text{ mg C m}^{-3} \text{ h}^{-1}$  after 6 hours of incubation.

Net primary production (Figure 3, grey bars) and R (Figure 3, white bars) over 24 hours of incubation varied between periods ( $p < 0.05$ ), with the greatest NPP result observed in the summer and peak R observed in the autumn. Analysis of the whole 24 hour-incubation period revealed that NPP were higher during the initial hours of incubation and then tended to decrease as the incubation time increased ( $p < 0.05$ ) while R rates not showed significant difference between incubation time ( $p > 0.05$ ).

During the initial hours incubation, NPP reached maximum of  $31.5 \text{ mg C m}^{-3} \text{ h}^{-1}$  and was observed a non-photosynthetic carbon fixation, in the absence of light ( $38.2 \text{ mg C m}^{-3} \text{ h}^{-1}$ ), in the autumn. In the winter, NPP reached  $21.1 \text{ mg C m}^{-3} \text{ h}^{-1}$  and non-photosynthetic carbon fixation, in the absence of light, was also observed ( $6.5 \text{ mg C m}^{-3} \text{ h}^{-1}$ ). In the spring, NPP was  $0.3 \text{ mg C m}^{-3} \text{ h}^{-1}$  and R was  $25.3 \text{ mg C m}^{-3} \text{ h}^{-1}$ .

$\text{h}^{-1}$ . In the summer, NPP reached  $15.8 \text{ mg C m}^{-3} \text{ h}^{-1}$  and R was  $19.3 \text{ mg C m}^{-3} \text{ h}^{-1}$ .

The highest assimilation number was after 3 hours of incubation in autumn and summer ( $1.9$  and  $1.6 \text{ mg C (mg Chla h)}^{-1}$ , respectively) and after 6 hours of incubation in winter and spring ( $1.2$  and  $1.1 \text{ mg C (mg Chla h)}^{-1}$ , respectively).

The Spearman correlation coefficients for metabolic rates against all of the abiotic variables measured, revealed significant positive correlations of GPP and R with precipitation and total phosphorus. While there were positive correlations of NPP with water temperature, PAR and total nitrogen (Table 3).

Table 3: Spearman correlation coefficient for relationships between GPP, NPP, R and abiotic variables ( $n=24$ ,  $*p<0.05$ ). Abbreviations: water temperature (WT), photosynthetic active radiation (PAR), Precipitation (Prec.), total nitrogen (TN), total phosphorus (TP), conductivity (Cond.), chlorophyll *a* (Chla), alkalinity (Alk.), dissolved oxygen (DO) and light attenuation (k).

	GPP	NPP	R	WT	PAR	Prec.	TN	TP	Cond.	pH	Chla	Alk.	Wind	DO
GPP	1.0													
NPP	0.12	1.0												
R	0.45*	-0.51*	1.0											
WT	0.39	0.45*	0.26	1.0										
PAR	0.18	0.48*	-0.24	0.42*	1.0									
Prec.	0.58*	-0.25	0.58*	0.32	-0.04	1.0								
TN	-0.42*	0.48*	-0.38	0.27	0.13	-0.80*	1.0							
TP	0.58*	-0.25	0.58*	0.32	-0.04	1.00*	-0.80*	1.0						
Cond.	0.52*	0.37	0.34	0.95*	0.27	0.38	0.20	0.38	1.0					
pH	-0.24	0.55*	-0.04	0.53*	0.16	-0.15	0.55*	-0.15	0.42*	1.0				
Chla	-0.33	0.20	0.05	0.35	0.11	-0.10	0.41*	-0.10	0.30	0.65*	1.0			
Alk.	-0.52*	0.29	-0.44*	-0.09	0.20	-0.47*	0.46*	-0.47*	-0.23	0.48*	0.38	1.0		
Wind	-0.41*	0.27	-0.55*	-0.39	0.22	-0.80*	0.47*	-0.80*	-0.50*	0.06	-0.19	0.44*	1.0	
DO	-0.34	-0.14	-0.38*	-0.79*	-0.01	-0.31	-0.25	-0.31	-0.86*	-0.33	-0.32	0.17	0.61*	1.0
k	0.22	0.33	-0.19	0.21	0.63*	0.10	-0.09	0.10	0.15	0.01	-0.11	-0.11	0.03	-0.01

The *stepwise* multiple regression models explained 70% of the variance in GPP, 27% of the variance in respiration and 27% of variance

in NPP (Table 4). The abiotic variables more important for metabolic rates were total nitrogen and phosphorus concentration, water temperature and precipitation, reflecting the environmental variation observed between sampling periods, in a subtropical lagoon and the importance these variables for the aquatic organisms.

Table 4: *Stepwise* multiple regression analysis to GPP, NPP and R in all incubation time and periods. Partial *t*-values indicate the size of statistical effects of the independent variables ( $n=24$ ,  $p<0.05$ ). Variables were log transformed.

Gross Primary Production $F_{(5,18)}=11.612$ , $p<0.00004$ . Adjusted $R^2= 0.70$			
Independent variables	Regression coefficient	Partial <i>t</i>	p level
Intercept	15.29355	3.43268	0.002969
Total nitrogen	1.04580	-4.29125	0.000440
Water temperature	2.42013	4.26490	0.000466
Total phosphorus	14.38136	-3.39003	0.003263
Precipitation	1.70244	3.29153	0.004056
Respiration $F_{(3,20)}=3.8993$ , $p<0.02412$ . Adjusted $R^2= 0.27$			
Intercept	-1.54021	-1.38212	0.182177
Total phosphorus	2.28969	2.35976	0.028562
Net Primary Production $F_{(5,18)}=2.6806$ , $p<0.05573$ . Adjusted $R^2= 0.27$			
Intercept	0.66766	0.13279	0.895832
Water temperature	6.61008	2.73696	0.013544
Precipitation	-1.15192	-2.56711	0.019393

### Pelagic metabolism

Pelagic metabolism estimated by net dissolved oxygen variability after 24 hours incubation period in the light bottles produced a negative result in the autumn and in the winter, indicating more consume of the oxygen than production (heterotrophy) and positive in the spring and the summer (more production than consume, autotrophy).

Over measured the variation in free-water  $CO_2$ , the metabolism was predominantly heterotrophic in the autumn and the winter, when respiration rates were higher than primary production, indicating that  $CO_2$  is exported to the atmosphere. In contrast, the aquatic system acted as a carbon sink during spring and summer, since autotrophy

predominated, when primary production was higher than respiration (Table 5).

Table 5: Autotrophy and heterotrophy in the Peri lagoon estimated from O<sub>2</sub> concentration, after 24hours incubation, and CO<sub>2</sub> concentration in free-water in 24 hours.

Period	O <sub>2</sub> (mmol O <sub>2</sub> m <sup>-2</sup> day <sup>-1</sup> )	CO <sub>2</sub> (mmol C m <sup>-2</sup> day <sup>-1</sup> )	Status
Autumn	-9.53	3.07	Heterotrophic
Winter	-0.03	3.10	Heterotrophic
Spring	0.02	-2.05	Autotrophic
Summer	5.30	-12.56	Autotrophic

## Discussion

### Primary production and respiration rates

Our results showed significant changes in abiotic and metabolic variables, demonstrating the occurrence of temporal variation in the subtropics, however differences especially between summer and winter in our environment was smaller than those reported for temperate environments (Talling 1986; Lewis 2011).

We observed that GPP and R were positively associated with precipitation and total phosphorus. Precipitation was highly correlated with nutrients, negatively with total nitrogen and positively with total phosphorus, suggesting that this climatological variable drives production and respiration rates in different ways. This variable was important in the multiple regression models and determined the heterotrophy in Peri lagoon, as observed by Marotta and others (2010a) in other Brazilian ecosystems.

Correlations between GPP and R with phosphorus concentrations have been shown in other studies (Hanson and others 2003; Hagerthey and others 2010). However, it is expected that other variables, especially dissolved organic carbon, will be associated with R rates, since total phosphorus explained 27% of R in the multiple regression model.

As expected, NPP was the highest in summer under high light and temperature conditions. Both of these variables are important factors regulating primary production of the phytoplankton community, along with nutrient concentrations (Lewis 1974; Erikson and others 1998; Montero and others 2011). NPP was positively correlated with total nitrogen boosting primary production and autotrophy (Cole and others 2000; Dodds and Cole 2007).



High light intensity is not always related to an increase in phytoplankton productivity because in excess it causes photoinhibition. This is especially true to phytoplankton species with low light requirements, such as *Cylindrospermopsis raciborskii*, which is dominant in Peri lagoon (Padisák 1997; Komárková and others 1999; Laudaes-Silva, 1999; Greellmann, 2006). The UV radiation also affects the photosynthetic efficiency of autotrophs organisms (Sinha and others 1998).

The reduction in NPP rates during some incubation times in summer, when PAR intensity was greater than other periods, could be associated with photoinhibition. We also observed low assimilation number in the summer, providing further evidence of reduced photosynthetic efficiency, as has been observed by Wondie and others (2007) for Lake Tana (Ethiopia).

The Peri lagoon was P-limited during most of the sampling periods and the low assimilation number indicates that nutrient depletion is occurring (Curl and Small 1965). During autumn, when the Peri lagoon was N-limited, GPP was at least two times higher than during the other periods. The major input of allochthonous organic matter and low intensities of PAR in the water column, due low water transparency, limited primary production, stimulating R.

The lowest GPP rates in Peri lagoon were in spring, followed by winter and summer, and the highest rates were in the autumn. The highest GPP rate ( $69.7 \text{ mg C m}^{-3} \text{ h}^{-1}$ ) in Peri lagoon was lower than reported by Tilahun and Ahlgren (2010) for three lakes in Ethiopia (146, 249 and  $303 \text{ mg C m}^{-3} \text{ h}^{-1}$ ). When compared to other Brazilian subtropical coastal lakes the figure is more similar. For example, in Itapeva Lake, GPP varied from 38.8 to  $54.9 \text{ mg C m}^{-3} \text{ h}^{-1}$ , with respiration rates varying from  $49.9 \text{ mg C m}^{-3} \text{ h}^{-1}$  to  $131.1 \text{ mg C m}^{-3} \text{ h}^{-1}$  (Cardoso and Motta Marques 2009).

In all study periods, we observed the highest GPP, NPP, R and assimilation number over three to six hours of incubation, indicating high phytoplankton photosynthetic efficiency during short incubation time.

Negative NPP represents a state in which respiration is greater than photosynthesis, in light bottles, which generally results from terrestrial input of allochthonous organic matter (Cherbadgy and Propp 2008). Additionally, our observations about oxygen production in the absence of light can be related with detoxification of reactive oxygen species (ROS), such as  $\text{H}_2\text{O}_2$ , produced by microalgae (Pamatmat 1997; Pospisil and others 2007; Milne and others 2008). This shows us those

others sources of oxygen may be influencing the metabolism of Peri lagoon, however is necessary more studies for identification these process.

#### Autotrophic and heterotrophic status

The metabolism of the Peri lagoon estimated from free-water and dissolved oxygen measurements, after incubation in bottles for 24 hours, indicated net heterotrophy in autumn and winter and net autotrophy in spring and summer. In two subtropical lagoons Carmouze and others (1991) found seasonal shift between net autotrophy and heterotrophy. Heterotrophic and autotrophic subtropical coastal systems were also found by Thomaz and others (2001). Recently some tropical lakes has been studied and found acting as consistent CO<sub>2</sub> sources to the atmosphere (Marotta and others 2009; Marotta and others 2010b).

Transitions between autotrophic and heterotrophic are mostly know to be controlled by changes in limnological conditions, especially phosphorus, dissolved organic carbon, light attenuation and living organisms inhabiting the system (Carmouze and others 1998; Thomaz and others 2001; Hanson and others 2003; Dodds and Cole 2007; Loeb1 and others 2007; Hagerthey and others 2010; Montero and others 2011).

We found that in Peri lagoon the precipitation influenced metabolism through its effect on terrestrial inputs of nutrients, especially phosphorus. It can also influence the organic matter, CO<sub>2</sub> and hydraulic residence time, which can reflect in carbon sedimentation and mineralization (Algesten and others 2003; Lennon 2004; Marotta and others 2009), favoring the heterotrophic metabolism. The importance of allochthonous material to the lakes metabolism has been demonstrated in 12 Brazilian lakes by increases in CO<sub>2</sub> after the rainy period (Marotta and others 2010a).

The autotrophic metabolism recorded in spring and summer was favored by temperature, transparency, light conditions and high total nitrogen concentration, especially in summer. Moreover, in the summer Peri lagoon provides enough carbon as organic material to supply the food chain, while in autumn it requires allochthonous organic matter sources, exporting inorganic carbon to the atmosphere.

It can be concluded that primary production and respiration rates varied temporally in a subtropical system, in response to changing abiotic variables and heterotrophy and autotrophy alternate coupled with these changes.

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### References

- Algesten G, Sobek S, Bergstrom A, Agren A, Tranvik LJ, Jansson M. 2003. Role of lakes for organic carbon cycling in the boreal zone. *Global Change Biology* 10:141-147.
- Arst H, Nõges T, Nõges P, Paavel B. 2008. Relations of phytoplankton *in situ* primary production, chlorophyll concentration and underwater irradiance in turbid lakes. *Hydrobiologia* 599:169-176.
- Cardoso LS, Motta Marques D. 2009. Hydrodynamics-driven plankton community in a shallow lake. *Aquat Ecol* 43:73-84.
- Carmouze JP, Knoppers B, Vasconcelos P. 1991. Metabolism of a subtropical Brazilian lagoon. *Biogeochemistry* 14:129-148.
- Carmouze JP, Farias B, Bernardes MC, Kuroshima KN. 1998. Benthic influence on the metabolism of a shallow tropical lagoon (Lagoa da Barra, Brazil). *Hydrobiologia* 373/374:89-100.
- Cherbadgy II, Propp LN. 2008. Photosynthesis and respiration of a deep-water periphyton community (Macclesfield Bank, South China Sea). *Russian Journal of Marine Biology* 34:301-308.
- Cole JJ, Caraco NF, Kling GW, Kratz TK. 1994. Carbon-dioxide supersaturation in the surface waters of lakes. *Science* 265:1568-1570.
- Cole JJ, Caraco NF. 1998. Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF<sub>6</sub>. *Limnol Oceanogr* 43:647-656.

Cole JJ, Pace ML, Carpenter SR, Kitchell JF. 2000. Persistence of net heterotrophy lakes during nutrient addition and food web manipulations. *Limnol Oceanogr* 45:1718-1730.

Cole JJ, Carpenter SR, Kitchell JF, Pace ML. 2002. Pathways of organic carbon utilization in small lakes: Results from a whole-lake  $^{13}\text{C}$  addition and coupled model. *Limnol Oceanogr* 47:1664-1675.

Cole JJ, Prairie YT, Caraco NF, McDowell WH, Tranvik LJ, Striegl RG, Duarte CM, Kortelainen P, Downing JA, Middelburg JJ, Melack J. 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. *Ecosystems* 10:171-184.

Curl H, Small LF. 1965. Variations in photosynthetic assimilation ratios in natural, marine phytoplankton communities. *Limnol Oceanogr Suppl* 10:67-73.

Del Giorgio PA, Peters RH. 1994. Patterns in planktonic P:R ratios in lakes: influence of lake trophic and dissolved organic carbon. *Limnol Oceanogr* 39:772-787.

Del Giorgio PA, Cole JJ, Cimbleris A. 1997. Respiration rates in bacteria exceed plankton production in unproductive aquatic systems. *Nature* 385:148-151.

Del Giorgio PA, Duarte CM. 2002. Respiration in the open ocean. *Nature* 420:379-384.

Dodds WK, Cole JJ. 2007. Expanding the concept of trophic state in aquatic ecosystems: It's not just the autotrophs. *Aquatic Sciences* 69:427-439.

Downing JA and others. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. *Limnol Oceanogr* 51:2388-2397.

Duarte CM, Agustí S. 1998. The  $\text{CO}_2$  balance of unproductive aquatic ecosystems. *Science* 28:234-236.

Erikson R, Hooker E, Mejia M, Zelaya A, Vammen K. 1998. Optimal conditions for primary production in a polymictic tropical lake (Lake Xolotlán, Nicaragua). *Hydrobiologia* 382:1-16.

Greellmann C. 2006. Aspectos da morfologia e da ecologia de *Cylindrospermopsis raciborskii* (Woloszinska) Seenayya et Subba-Raju e da produção de cianotoxinas na lagoa do Peri, Florianópolis, SC, Brasil. Dissertação. Universidade de Santa Catarina.

Hagerthey SE, Cole JJ, Kilbane D. 2010. Aquatic metabolism in the Everglades: Dominance of water column heterotrophy. *Limnol Oceanogr* 55:653-666.

Hanson PC, Bade DL, Carpenter SR. 2003. Lake metabolism: Relationships with dissolved organic carbon and phosphorus. *Limnol Oceanogr* 48:1112-1119.

Hennemann MC, Petrucio MM. 2011. Spatial and temporal dynamic of trophic relevant parameters in a subtropical coastal lagoon in Brazil. *Environ Monit Assess* doi: 10.1007/s10661-010-1833-5.

Komárková J, Laudares-Silva R, Senna PAC. 1999. Extreme morphology of *Cylindrospermopsis raciborskii* (Nostocales, Cyanobacteria) in the Lagoa do Peri, a freshwater coastal lagoon, Santa Catarina, Brazil. *Algological Studies* 94:207-222.

Kosten S, Roland F, Motta Marques DML, Van Nes EH, Mazzeo N, Sternberg LSL, Scheffer M, Cole JJ. 2010. Climate-dependent CO<sub>2</sub> emissions from lakes, *Global Biogeochem. Cycles* 24 GB2007 doi:10.1029/2009GB003618.

Laudares-Silva R. 1999. Aspectos limnológicos, variabilidade especial e temporal na estrutura da comunidade fitoplanctônica da Lagoa do Peri, Santa Catarina, Brasil. 216f. Tese (Doutorado) Universidade Federal de São Carlos.

Lennon JT. 2004. Experimental evidence that terrestrial carbon subsidies increase CO<sub>2</sub> flux from lake ecosystems. *Oecologia* 138:584-591.

Lewis WM. 1974. A revised classification of lakes based on mixing. *Ca J Fis Aquat Sci* 40:1779-1787.

Lewis WM. 2011. Global primary production of lakes: 19<sup>th</sup> Baldi Memorial Lecture. *Inland Waters* 1:1-28.

Loebl M, Dolch T, van Beusekom JEE. 2007. Annual dynamics of pelagic primary production and respiration in a shallow coastal basin. *Journal of Sea Research* 58:269-282.

Lorenzen CJ. 1967. Determination of chlorophyll and pheopigments: Spectrophotometric equations. *Limnol Oceanogr* 12:343-346.

Mackereth FJH, Heron J E, Talling JF. 1978. *Water Analysis: some revised methods for limnologists*. Freshwater Biological Association, Scientific Publication 36.

Marotta H, Paiva LT, Petrucio MM. 2009. Changes in thermal and oxygen stratification pattern coupled to CO<sub>2</sub> outgassing persistence in two oligotrophic shallow lakes of the Atlantic Tropical Forest, Southeast Brazil. *Limnology* 10:195-202.

Marotta H, Duarte CM, Pinho L, Enrich-Prast A. 2010a. Rainfall leads to increased pCO<sub>2</sub> in Brazilian coastal lakes. *Biogeosciences* 7:1607-1614.

Marotta H, Duarte CM, Meirelles-Pereira F, Bento L, Esteves FA, Enrich-Prast A. 2010b. Long-term CO<sub>2</sub> variability in two shallow tropical lakes experiencing episodic eutrophication and acidifications events. *Ecosystems* 13:382-392.

Milne A, Davey MS, Worsfold PJ, Achterberg EP, Taylor AR. 2008. Real-time detection of reactive oxygen species generation by marine phytoplankton using flow injection–chemiluminescence. *Limnology and Oceanography Methods* 7:706-715.

Montero P, Daneri G, González H, Iriarte JL, Tapia FJ, Lizárraga L, Sanchez N, Pizzaro O. 2011. Seasonal variability of primary production in a fjord ecosystem of the Chilean Patagonia: Implications for the

transfer of carbon within pelagic food webs. *Continental Shelf Research* 31:202-215.

Odum EP. 1956. Primary production in flowing waters. *Limnol Oceanogr* 1:102-117.

Padisák J. 1997. *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba-Raju, and expanding, highly adaptive cyanobacteria: Worldwide distribution and review of its ecology. *Archiv für Hydrobiologie* 107:563-593.

Pamatmat MM. 1997. Non-photosynthetic oxygen production and non-respiratory oxygen uptake in the dark: a theory of oxygen dynamics in plankton communities. *Marine Biology* 129:735-746.

Pospisil P, Snyrychová I, Naus J. 2007. Dark production of reactive oxygen species in photosystem II membrane particles at elevated temperature: EPR spin-trapping study. *Biochimica et Biophysica Acta* 1767:854-859.

Ryther JH, Yentsch CS. 1957. The estimation of phytoplankton production in the ocean from chlorophyll and light data. *Limnol Oceanogr* 2:281-286.

Roland F, Vidal LO, Pacheco FS, Barros NO, Assireu A, Ometto JPHB, Cimberis ACP, Cole JJ. 2010. Variability of carbon dioxide flux from tropical (Cerrado) hydroelectric reservoirs. *Aquatic Sciences* 72:283-293.

Sakamoto M. 1966. Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. *Archiv für Hydrobiologie* 62:1-28.

Sinha RP, Klisch M, Groniger A, Hader DP. 1998. Ultraviolet-absorbing/screening substances in cyanobacteria, phytoplankton and macroalgae. *J Photochem Photobiol. B: Biol* 47:83-94.

Sobek S, Tranvik LJ, Cole J. 2005. Temperature independence of carbon dioxide supersaturation in global lakes. *Global Biogeochemical Cycles* 19:GB2003.

Staehr PA, Sand-Jensen K. 2007. Temporal dynamics and regulation of lake metabolism. *Limnol Oceanogr* 52:108-120.

Staehr PA, Sand-Jensen K, Raun AL, Nilsson B, Kidmose J. 2010. Drivers of metabolism and net heterotrophy in contrasting lakes. *Limnol Oceanogr* 55:817-830.

Stumm W, Morgan JJ. 1996. *Aquatic chemistry: chemical equilibria and rates in natural waters*. Wiley-Interscience, New York.

Talling JF. 1986. The seasonality of phytoplankton in African lakes. *Hydrobiologia* 138:139-160.

Thomaz SM, Enrich-Prast A, Gonçalves JF, Santos AM, Esteves FA. 2001. Metabolism and gaseous exchanges in two coastal lagoons from Rio de Janeiro with distinct limnological characteristics. *Brazilian Archives of Biology and Technology* 44:433-438.

Tilahun G, Ahlgren G. 2010. Seasonal variations in phytoplankton biomass and primary production in the Ethiopian Rift Valley lakes Ziway, Awassa and Chamo – The basis for fish production. *Limnologia* 40:330-342.

Valderrama JC. 1981. The simultaneous analysis of total nitrogen and phosphorus in natural waters. *Marine Chemistry* 10:1109-1122.

Wanninkhof R, Knox M. 1996. Chemical enhancement of CO<sub>2</sub> exchange in natural waters. *Limnol Oceanogr* 41:689-697.

Wetzel RG, Likens GE. 2000. *Limnological Analyses*. Springer-Verlag New York. 150p.

Wondie A, Mengistu S, Vijverberg J, Dejen E. 2007. Seasonal variation in primary production of a large high altitude tropical lake (Lake Tana, Ethiopia): effects of nutrient availability and water transparency. *Aquat Ecol* 41:195-207.



## 5 CAPÍTULO 2

### ESTABILIDADE VERTICAL DA PRODUÇÃO PRIMÁRIA E DA ESTRUTURA DA COMUNIDADE FITOPLANCTÔNICA EM UMA LAGOA COSTEIRA SUBTROPICAL

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Vertical stability of primary production and phytoplankton community structure in a subtropical coastal lagoon

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Abstract

In order to assess the vertical structure of phytoplankton community and pelagic metabolism in a subtropical coastal lagoon, the pelagic primary production and respiration rates and phytoplankton community were investigated vertically, by incubating light and dark bottles, as well as the relationship of these rates with biotic and abiotic variables. We hypothesized that the pelagic primary production rates have vertical variation in a subtropical lagoon coupled with phytoplankton density and that the pelagic respiration will be higher than primary production rates in an environment with low nutrients concentration and dominated for Cyanobacteria. The incubation of the light and dark bottles was placed within four different depths in the central part of the lagoon, bimonthly from June/2009 to December/2010 and biotic and abiotic variables were collected those four depths. The water column of the Peri lagoon did not show vertical variation in relation to biotic, abiotic variables and metabolic rates. The average gross primary production was  $70.9 \text{ mg C m}^{-3} \text{ h}^{-1}$ , average net primary production was  $38.0 \text{ mg C m}^{-3} \text{ h}^{-1}$  and respiration was  $24.0 \text{ mg C m}^{-3} \text{ h}^{-1}$ , which resembles other Brazilian aquatic environments, but was lower than other tropical lakes. We propose that nutrients and light limitation and dominance by Cyanobacteria restrict the primary production in this environment and exposure wind promotes the water column homogeneously. The phytoplankton community was dominated by filamentous cyanobacteria, especially *Cylindrospermopsis raciborskii* during the period of study. However Chlorophyta was more correlated with production rates than Cyanobacteria.

Keywords Subtropical Coastal Lagoon. Primary Production. Respiration. Phytoplankton. *Cylindrospermopsis raciborskii*.

## Introduction

Lakes are sites of intensive carbon cycling, especially those with high nutrients concentrations, which demonstrate high productivity. Despite this, they are often disregarded in models of the global carbon cycle due to their small percentage on the Earth's surface area (Downing et al. 2006; Cole et al. 2007).

In the tropics and subtropics high temperatures and light availability favor the process of planktonic primary production and respiration (Berman et al. 1995; Amarasinghe and Vijverberg 2002; Esteves 2011). Primary production plays an essential role in element cycling and food production for heterotrophs, forming the basis of the ecological pyramid. It is an important biological process with an influence on many chemical reactions throughout a lake and on all trophic levels. Respiration is regulated by phosphorus and dissolved organic matter and it is responsible for organic matter oxidation (Del Giorgio and Peters 1994; Hanson et al. 2003).

Primary producers of aquatic environments, especially phytoplankton, show vertical and temporal distribution directly influenced by light and nutrients (Phlips et al. 1995; Diehl et al. 2002; Arst et al. 2008). These organisms have fundamental importance in the dynamics of aquatic communities, where its structure and diversity is responsible for variations in production rates (Jouenne et al. 2007; Ryabov et al. 2010; Mellard et al. 2011; Gaard et al. 2011; Nöges et al. 2011).

Phytoplankton is directly related with photosynthetic active radiation, where photoinhibition occurs generally in surface, followed by a depth of maximum density and primary production, decreasing toward the bottom, where decomposition process are more intense (Erikson et al. 1998; Wondie et al. 2007; Arst et al. 2008; Tilahun and Ahlgren 2010).

The Peri lagoon is a subtropical coastal lagoon, which has been observed spatial homogeneity of nutrients and chlorophyll *a*, low nutrients concentration and elevated densities of the cyanobacteria *Cylindrospermopsis raciborskii* (Woloszinska) Seenayya et Subba-Raju (Komárková et al 1999; Laudares-Silva 1999; Hennemann and Petrucio 2011). Their morphological characteristics make it an important site for studying in subtropics, because it presents a large area compared to other lakes in the world and deeper than other coastal lakes (Downing et

al. 2006). Furthermore, the subtropical and tropical lakes remain underrepresented (Marotta et al. 2009). We hypothesized that the pelagic primary production rates has vertical variation in a subtropical coastal lagoon coupled with phytoplankton density and that the pelagic respiration will be higher than primary production rates in an environment with low nutrients concentration and dominated for Cyanobacteria.

## Materials and methods

### Study area

The Peri lagoon (27°44'S and 48°31'W) is located in the southeast of Santa Catarina Island, Brazil, within an area of the Peri Lagoon Municipal Park that is protected by environment legislation. The lagoon has a surface area of 5.7 km<sup>2</sup> and average and maximum depths of 4.2 m and 11.0 m respectively. Spatial homogeneity of nutrients and chlorophyll *a* and elevated densities of the cyanobacteria *Cylindrospermopsis raciborskii* have been observed in the lagoon (Laudares-Silva 1999; Grellmann 2006). The lagoon was classified as oligotrophic for nutrients concentrations and meso-eutrophic for transparency and chlorophyll *a* (Hennemann and Petrucio 2011). The lagoon's main tributaries are the Cachoeira Grande and Ribeirão Grande Streams. The environment does not exchange water with the ocean because it is at 3 m above sea level, which means it is a freshwater lagoon. It is the largest source of drinking water to human supply in Santa Catarina Island. The only anthropogenic activities permitted in the lagoon are recreational (Figure 1).

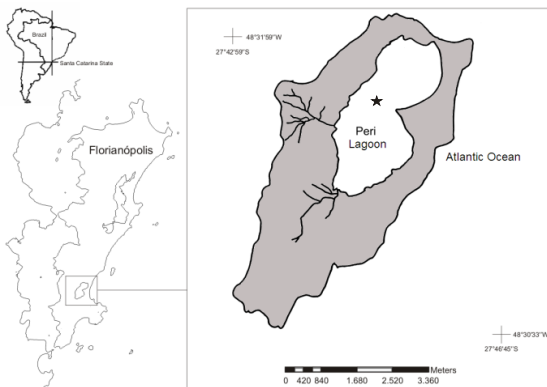


Figure 1: Map and location of the Peri lagoon, Santa Catarina Island, Brazil, showing the incubation station. Adapted from Hennemann and Petrucio (2011).

### Sampling and data collection

The environment was sampled bimonthly from June/2009 to December/2010. Abiotic variables, bottles incubation and water samples were taken from the central part of the Peri lagoon (27°43'47''S and 48°31'26''W), where the average maximum depth was 8.4 m. Samples were collected with a Van Dorn sampler at four depths according to the light penetration, calculated by a Secchi disk, and the euphotic zone was estimated by multiplying the Secchi disk depth by a factor of three (Cole 1994): depth 1: 100% of incident radiation (surface), depth 2: 10% of incident radiation (~ 1.0 m), depth 3: 1% of incident radiation (~ 3.0 m) and depth 4: aphotic zone (~ 6.0 m).

### Abiotic variables

The following climatological variables were measured *in situ*: photosynthetic active radiation (PAR) on the subsurface of the water column using a radiometer with a spherical sensor (Li-cor 250A), wind speed with portable anemometer (Instrutherm TAD 500) and air temperature with a mercury thermometer. The precipitation values were obtained from EPAGRI/CIRAM (Information Center for Environmental Resources and Hydrometeorology of Santa Catarina), where was estimated the mean precipitation for seven days prior to the sampling day.

The following limnological variables were measured *in situ*, in four depths: water temperature, conductivity, pH and dissolved oxygen using multiparameter probe (YSI-85). Immediately after collection, total alkalinity was determined by Gran's titration method (Mackereth et al. 1978). Unfiltered water samples were frozen at -20°C for determination of total nitrogen (TN) and total phosphorus (TP) (Valderrama 1981), and filtered samples for nitrite (Golterman et al. 1978), ammoniacal nitrogen (Koroleff 1976), soluble reactive phosphorus (Strickland and Parsons 1960) and dissolved organic carbon (Shimadzu TOC-5000A).

### Phytoplankton analyses

The biomass of the phytoplankton community was estimated by analyzing chlorophyll *a*, corrected for phaeophytin. 500 mL of water was filtrated using a Millipore AP40 glass fiber (0.7 µm pore size and 47 mm in diameter) and kept frozen at -20°C, followed by its extraction using 90% acetone (Lorenzen 1967).

Total phytoplankton samples from the four depths were preserved with formalin (final concentration 1.6%). Subsamples (5 mL) were sedimented for 24 h, in Utermöhl chambers with Lugol solution, where

400 individuals of the dominant species were counted, using an inverted microscope following the Utermöhl technique (Hasle 1978). Every cell, filament or colony was considered one individual. Dominant and abundant species (Lobo and Leighton 1986), as well as the percentage of phytoplankton groups were determined from density (ind. mL<sup>-1</sup>).

Pelagic Gross Primary Production (GPP), Net Primary Production (NPP) and Respiration (R)

Phytoplankton primary production was estimated by light and dark bottles incubations, where the amount of dissolved oxygen was determined by the Winkler method (Wetzel and Likens 2000). Two light and two dark bottles were incubated at each depth for three to five hours, starting at 9:00 am. The dissolved oxygen variation was used to determine respiration rates (R) in dark bottles (initial concentration minus final concentration) and net primary production (NPP) in light bottles (final concentration minus initial concentration). The gross primary production (GPP) was calculated as the sum of the dissolved oxygen variation in the light and dark bottles. The results, in mg O<sub>2</sub> L<sup>-1</sup> h<sup>-1</sup>, were then converted to carbon consumption using the respiratory quotient (RQ = 1.0) and carbon productivity using the photosynthetic quotients (PQ = 1.2) (Wetzel and Likens 2000), thereby obtaining values for R, NPP and GPP in mg C m<sup>-3</sup> h<sup>-1</sup>. The estimated NPP rates were normalized for chlorophyll *a* concentration, thereby obtaining the assimilation number – mg C (mg Chl *a* h)<sup>-1</sup> – as described by Ryther and Yentsch (1957), which determines the photosynthetic efficiency and nutrient conditions in aquatic environments (Curl and Small 1965).

#### Statistical analyses

Descriptive statistics were used to evaluate the abiotic data obtained during sampling using the mean, minimum, maximum and standard deviation. A parametric analysis of variance (one-way ANOVA) was used to evaluate differences in GPP, NPP, R and phytoplankton community densities at different depths. Months were grouped by climatic season for verify seasonal variation in metabolic rates. A nonparametric analysis of variance (Kruskal-Wallis) was used to evaluate the existence of differences between depths for the limnological variables, considering significant differences when  $p < 0.05$ . To check correlations between phytoplankton community and abiotic variables with GPP, NPP and R rates, Spearman correlation was calculated. To estimate relationships between phytoplankton community and metabolic rates, linear regressions were performed with data

$\log(x+1)$  transformed. All analyses were completed using *software* Statistica 7 (StatSoft®).

## Results

### Abiotic variables

Over the 10 sampling dates, climatological variables showed oscillations in air temperature, measured *in situ* (17.5°C to 27°C) and mean precipitation for the seven days previously the sampling (0.0 to 8.8 mm day<sup>-1</sup>). PAR oscillations, measured *in situ*, were recorded on the subsurface (85 to 685  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and the average depth of the euphotic zone was three meters (Figure 2). The wind speed during the sampling reached values of 9.1 m s<sup>-1</sup>, being briefly absent in June/09 and August/09.

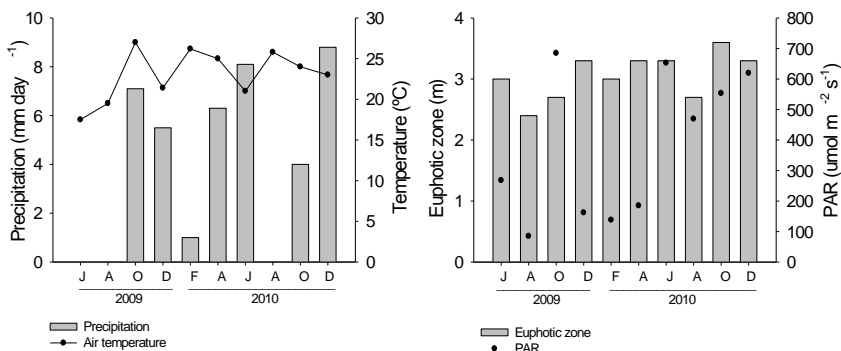


Figure 2: Mean values of precipitation in the seven days prior and air temperature during sampling, euphotic zone and PAR on the subsurface of the water column, sampled from June/09 to December/10 in the Peri lagoon.

The limnological variables at four depths demonstrated that the water column of the Peri lagoon is homogeneous without significant vertical variation and thermal stratification ( $p > 0.05$ ). The minimum and maximum values of the variables record the variation amplitude over the sampling months (Table 1). The mixing zone ( $\sim 6.0$  m) was higher than euphotic zone ( $\sim 3.0$  m) demonstrating that Peri lagoon is limited by light.

Table 1: Mean, standard deviation (SD), minimum (min) and maximum (max) values for limnological variables sampled in four depths, from June/09 to December/10 in the pelagic region of Peri lagoon.

Variables	Depth 1 Mean±SD (min-max)	Depth 2 Mean±SD (min-max)	Depth 3 Mean±SD (min-max)	Depth 4 Mean±SD (min-max)
Water temperature (°C)	22.0±4.07 (17.6-28.7)	21.6±3.64 (17.5-28.7)	21.5±3.68 (17.4-28.8)	21.5±3.67 (17.5-28.7)
Conductivity ( $\mu\text{s cm}^{-1}$ )	68.9±5.94 (60.2-75.0)	70.2±13.09 (57.1-104.4)	71.4±12.15 (61.4-104.1)	75.5±18.21 (61.2-119.1)
pH	7.1±0.30 (6.6-7.5)	7.1±0.34 (6.5-7.6)	7.1±0.34 (6.5-7.7)	7.0±0.40 (6.3-7.5)
Alkalinity(mEq l <sup>-1</sup> )	0.1±0.07 (0.0-0.2)	0.1±0.06 (0.0-0.2)	0.1±0.06 (0.0-0.1)	0.1±0.07 (0.0-0.2)
Dissolved oxygen (mg L <sup>-1</sup> )	8.4±1.21 (6.4-10.1)	8.3±1.14 (5.7-9.7)	8.2±1.23 (5.3-9.5)	8.3±1.14 (5.8-9.3)
Chlorophyll <i>a</i> ( $\mu\text{g L}^{-1}$ )	19.7±2.96 (13.6-22.6)	20.0±3.70 (12.8-24.0)	18.8±3.34 (13.1-23.1)	19.0±2.87 (15.1-23.5)
Nitrite ( $\mu\text{g L}^{-1}$ )	0.4±0.18 (0.2-0.7)	0.4±0.18 (0.2-0.7)	0.4±0.18 (0.2-0.7)	0.4±0.18 (0.2-0.7)
Ammoniacal nitrogen ( $\mu\text{g L}^{-1}$ )	14.7±5.22 (8.7-22.2)	13.2±5.19 (6.0-22.2)	14.5±5.95 (7.8-25.8)	13.4±5.16 (6.9-20.4)
Dissolved organic carbon (mg L <sup>-1</sup> )	3.2±0.42 (2.7-4.1)	3.3±0.45 (2.7-4.3)	3.2±0.33 (2.7-3.8)	3.3±0.50 (2.6-4.5)
Soluble reactive phosphorus ( $\mu\text{g L}^{-1}$ )	2.4±3.01 (0.4-10.2)	2.1±1.36 (1.0-5.5)	2.2±1.82 (1.0-6.2)	2.6±2.30 (0.6-7.1)
Total nitrogen ( $\mu\text{g L}^{-1}$ )	497.7±289.45 (162.8-969.3)	508.6±267.83 (138.7-927.6)	520.9±299.12 (174.3-992.4)	511.9±289.79 (158.1-965.1)
Total phosphorus ( $\mu\text{g L}^{-1}$ )	11.0±2.48 (7.8-14.7)	11.1±2.65 (7.3-15.2)	12.6±6.87 (7.5-31.2)	14.0±9.09 (8.7-39.1)



## Pelagic Gross Primary Production (GPP), Net Primary Production (NPP) and Respiration (R)

The GPP rates showed significant vertical variation ( $p < 0.05$ ), with the highest rates occurring at depths 1 and 2 (Figure 3, black bars). The average GPP in depth 1 was  $82.8 \text{ mg C m}^{-3} \text{ h}^{-1}$  and in depth 2 was  $83.8 \text{ mg C m}^{-3} \text{ h}^{-1}$ . In depth 3 the average GPP was  $60.4 \text{ mg C m}^{-3} \text{ h}^{-1}$  and in depth 4 it was  $56.4 \text{ mg C m}^{-3} \text{ h}^{-1}$ . Mean values of four depths showed that October/09 was the month with highest GPP ( $119.0 \text{ mg C m}^{-3} \text{ h}^{-1}$ ) and October/10 had the lowest rate ( $34.2 \text{ mg C m}^{-3} \text{ h}^{-1}$ ). The mean GPP of the sampling period was  $70.9 \text{ mg C m}^{-3} \text{ h}^{-1}$ .

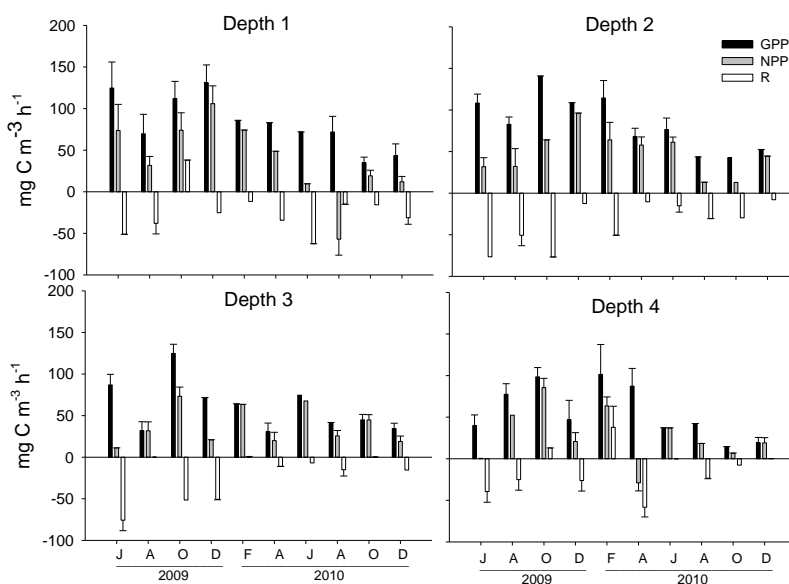


Figure 3: Mean values and standard error of gross primary production (GPP), net primary production (NPP) and Respiration (R) expressed in  $\text{mg C m}^{-3} \text{ h}^{-1}$ , in sampling depths, from June/09 to December/10 in pelagic region of the Peri lagoon.

The NPP rates (Figure 3, grey bars) were higher in depth 2, with an average of  $47.8 \text{ mg C m}^{-3} \text{ h}^{-1}$ , but did not show significant vertical variation ( $p > 0.05$ ). The average NPP in depth 1 was of  $39.1 \text{ mg C m}^{-3} \text{ h}^{-1}$ , in depth 3 it was  $37.7 \text{ mg C m}^{-3} \text{ h}^{-1}$  and in depth 4 it was  $27.5 \text{ mg C m}^{-3} \text{ h}^{-1}$ . Higher NPP was in October/09 ( $74.2 \text{ mg C m}^{-3} \text{ h}^{-1}$ ) and the lowest rates in August/10 ( $0.1 \text{ mg C m}^{-3} \text{ h}^{-1}$ ). The mean NPP of the sampling period was  $38.0 \text{ mg C m}^{-3} \text{ h}^{-1}$ .

R rates (Figure 3, white bars) did not show significant vertical difference ( $p>0.05$ ). In depth 1 the average R rate was  $24.6 \text{ mg C m}^{-3} \text{ h}^{-1}$ , in depth 2 it was  $36.0 \text{ mg C m}^{-3} \text{ h}^{-1}$ , in depth 3 it was  $22.5 \text{ mg C m}^{-3} \text{ h}^{-1}$  and the depth 4 it was  $12.9 \text{ mg C m}^{-3} \text{ h}^{-1}$ . June/09 had a higher R rate ( $60.7 \text{ mg C m}^{-3} \text{ h}^{-1}$ ) and February/10 had the lowest rate ( $5.9 \text{ mg C m}^{-3} \text{ h}^{-1}$ ). The mean R rate of the sampling period was  $24.0 \text{ mg C m}^{-3} \text{ h}^{-1}$ .

Assimilation number did not show significant differences between depths ( $p>0.05$ ). For depth 1 the average was  $2.1 \text{ mg C (mg Chla h)}^{-1}$ , for depth 2 it was  $2.4 \text{ mg C (mg Chla h)}^{-1}$ , for depth 3 it was  $2.1 \text{ mg C (mg Chla h)}^{-1}$  and for depth 4 it was  $1.5 \text{ mg C (mg Chla h)}^{-1}$ .

Grouping by climate season, the primary production and respiration rates did not show significant variation ( $p>0.05$ ), due the large variation observed between the months in the same season. However, NPP was higher in spring and summer coupled with higher PAR incidence, water temperature and phytoplankton density. Respiration rates were higher in autumn, while GPP was similar between seasons (Figure 4).

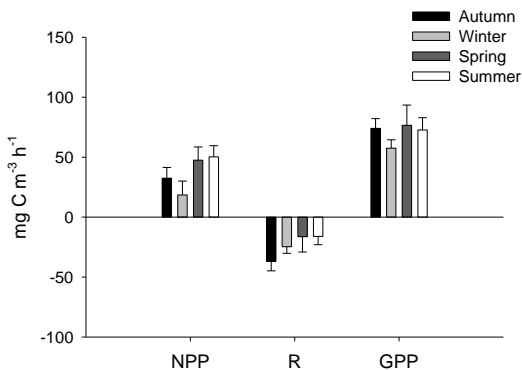


Figure 4: Seasonal variation in NPP, R and GPP expressed in  $\text{mg C m}^{-3} \text{ h}^{-1}$ , in sampling months, from June/09 to December/10, in pelagic region of the Peri lagoon. Values were grouped by climate season.

### Phytoplankton community

Phytoplankton community was composed of five groups, with 28 taxa of freshwater: Cyanobacteria (7 taxa), Chlorophyta (16 taxa), Bacillariophyta (3 taxa), Dinophyta (1 taxa) e Euglenophyta (1 taxa). Cyanobacteria were the most important group with an average density of 90.0% and Chlorophyta was second with an average density of 9.6%. Dinophyta, Bacillariophyta and Euglenophyta have, together, an average

density of 0.4%. Taxa identified in counting chambers during sampling months and depths are shown in Table 2.

Table 2: Taxa found in the Peri lagoon, identified in counting chambers from June/09 to December/10.

Taxa
Cyanobacteria
<i>Microcystis cf. lameliformis</i> Holsinger
<i>Pseudanabaena cf. galeata</i> Bocher
<i>Aphanocapsa</i> spp.
<i>Planktolyngbya</i> spp.
<i>Chroococcus turgidus</i> (Kützing) Nägeli
<i>Cylindrospermopsis raciborskii</i> (Woloszinska) Seenayya et Subba-Raju
<i>Limnothrix planctonica</i> (Woloszynska) Meffert
Chlorophyta
<i>Actinastrum aciculare</i> Playfair var. <i>aciculare f. minimum</i> (Huber-Pestalozzi)
<i>Chlorella homosphaera</i> Skuja
<i>Tetraedrum caudatum</i> (Corda) Hansgirg
<i>Monoraphidium irregulare</i> (G.M Smith) Komárková-Legnerová
<i>Monoraphidium arcuatum</i> (Korsikov) Hindák
<i>Scenedesmus cf. oahuensis</i> (Lemmermann) G.M Smith
<i>Cosmarium bioculatum</i> Brébisson var. <i>depressum</i> (Schaar.) Schmidle
<i>Cosmarium</i> sp. 1
<i>Cosmarium</i> sp. 2
<i>Botryococcus</i> sp.
<i>Closterium</i> sp.
<i>Coelastrum polychordum</i> (Korsikov) Hindák
<i>Staurastrum tetracerum</i> Ralfs var. <i>evolutum</i> West e West
<i>Staurastrum pseudotetracerum</i> (Nordstedt) West e West
<i>Spyrogira</i> sp.
<i>Chlamydomonas</i> sp.
Dinophyta

*Peridinium* spp.

Euglenophyta

*Euglena* sp.

Bacillariophyta

*Aulacoseira ambigua* (Grunow) Simonsen

*Fragillaria* spp.

*Encyonema* spp.

The phytoplankton total density did not show significant vertical variation ( $p > 0.05$ ). For depth 1 the average was  $122 \times 10^3$  ind.  $\text{mL}^{-1}$ , for depth 2 it was  $126 \times 10^3$  ind.  $\text{mL}^{-1}$ , for depth 3 it was  $124 \times 10^3$  ind.  $\text{mL}^{-1}$  and depth 4 it was  $119 \times 10^3$  ind.  $\text{mL}^{-1}$ . The total density varied of  $61 \times 10^3$  ind.  $\text{mL}^{-1}$  in August/10 to  $230 \times 10^3$  ind.  $\text{mL}^{-1}$  in October/09.

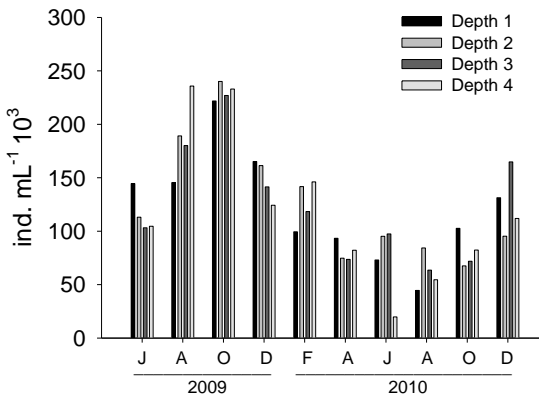


Figure 5: Phytoplankton total density of the four depths sampled from June/09 to December/10 in pelagic region of the Peri lagoon.

The composition and density of phytoplankton groups did not show differences between sampling depths ( $p > 0.05$ ). The filamentous Cyanobacteria *Cylindrospermopsis raciborskii* was the most important specie in the Peri lagoon, its density ranged from  $44 \times 10^3$  ind.  $\text{mL}^{-1}$  in April/10 to  $197 \times 10^3$  ind.  $\text{mL}^{-1}$  in October/09. In all the sampling months and depths *C. raciborskii* was dominant, except December/09, in depth 2, where *C. raciborskii* and *Limnothrix planctonica* were abundant, both filamentous. In the depths 3 and 4 of the same month *L. planctonica* was

dominant. In depth 4 of April/10 *C. raciborskii*, *L. planctonica* and *Monoraphidium irregulare* (Chorophyta) were abundant.

The Spearman correlation analysis of GPP, NPP and R with the abiotic and biotic variables (Table 3) showed significant positive correlation of NPP with dissolved organic carbon, ammoniacal nitrogen, Cyanobacteria and Chlorophyta. Respiration showed significant positive correlation only with nitrite. The strongest positive correlation of GPP was with dissolved organic carbon, Chlorophyta and Cyanobacteria.

The simple linear regression coefficient models show the relationship of NPP and GPP with phytoplankton groups more representative in Peri lagoon. Relationship of Chlorophyta with NPP and GPP were higher than Cyanobacteria with those rates (Figure 6).

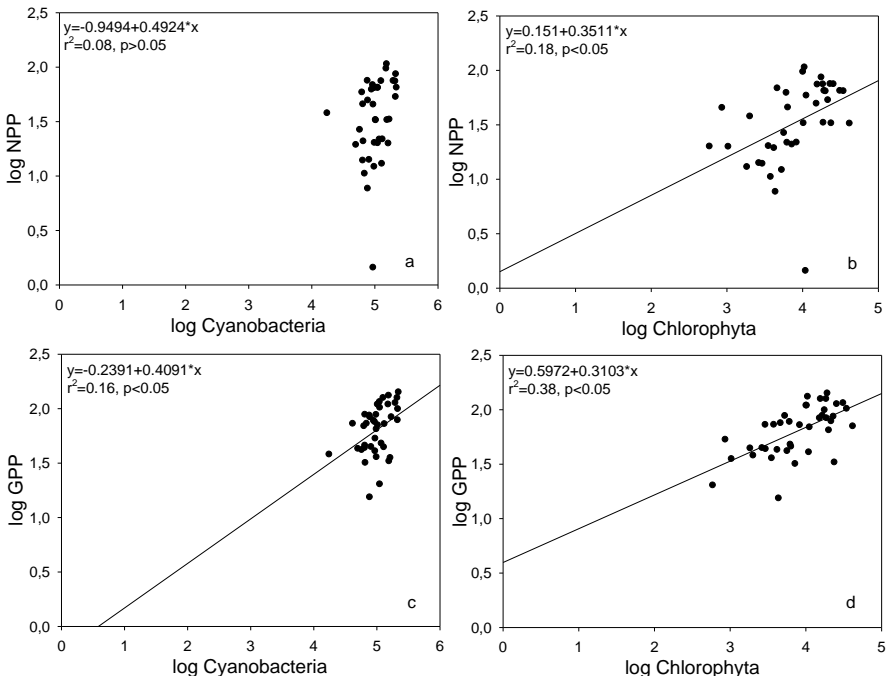


Figure 6: Relationship between variables log (x+1) transformed obtained from data of all sampling months and depths (n=40, p<0.05), in Peri lagoon. The line corresponds to linear regression model.

Table 3: Spearman correlation coefficient for relationship between GPP, NPP, R and abiotic and biotic variables, sampled from June/09 to December/10 in the Peri lagoon. All the values shown are significant ( $p < 0.05$ ,  $n = 40$ ). - represent not significant. Abbreviations: NO<sub>2</sub> – nitrite; NH<sub>4</sub> – ammoniacal nitrogen; SRP – soluble reactive phosphorus; WT – water temperature; Cond. – conductivity; Alk – alkalinity; DO – dissolved oxygen; Chla – chlorophyll *a*; Prec – precipitation; PAR – photosynthetic active radiation; k – light attenuation; DOC – dissolved organic carbon; Cyano – Cyanobacteria; Bacilla – Bacillariophyta; Dino – Dinophyta; Eugleno – Euglenophyta; Chloro – Chlorophyta.

	NPP	R	GPP	NO <sub>2</sub>	NH <sub>4</sub>	SRP	WT	Cond	pH	Alcal	DO	Chla	Wind	Prec	PAR	K	DOC	Cyano	Bacilla	Dino	Eugleno	
NPP	1.0																					
R	-	1.0																				
GPP	0.64	-	1.0																			
NO <sub>2</sub>	-	0.41	-	1.0																		
NH <sub>4</sub>	0.34	-	-	0.54	1.0																	
SRP	-	-	-	-	-	1.0																
WT	-	-	-	-0.47	-	-	1.0															
Cond	-	-	-	-	-	-	-	1.0														
pH	-	-	-	-	-	-	-	-	1.0													
Alcal	-0.47	-	-0.52	-0.70	-0.55	-	-	-	-	1.0												
DO	-0.47	-	-0.37	-	-	-0.36	-0.79	-	-	-	1.0											
Chla	-	-	-	-0.51	-	-	0.46	-	-	0.41	-0.41	1.0										
Wind	-	-	-0.40	-0.59	-	-	-	-	0.51	0.62	-	-	1.0									
Prec	-	-	-	-0.37	-	-	0.44	-	0.79	-	-0.38	-	0.63	1.0								
PAR	-	-	-	-	-	-0.36	-	-	-	-	-	-	0.54	0.63	1.0							
k	-	-	-	-	-	-	-	-	-	-0.42	-	-	-0.78	-0.45	-0.78	1.0						
DOC	0.62	-	0.60	-	-	0.37	0.41	-	-	-0.66	-0.65	-	-0.44	-	-	0.44	1.0					
Cyano	0.45	-	0.43	0.46	0.57	-	-	-	-	-0.54	-	-	-	-	-	-	0.41	1.0				
Bacilla	-	-	-	-	-	-0.45	-	-	-	-	-	-	-	-	-	-0.41	-	-	1.0			
Dino	-	-	-	0.37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0		
Eugleno	-	-	-	-	-	-	-	-	0.38	-	-	-	-	0.49	-	-	-	-	-	-	1.0	
Chloro	0.56	-	0.58	0.45	-	0.38	-	-	-	-0.64	-	-	-0.82	-0.37	-0.53	0.71	0.64	0.42	-	-	-	-

## Discussion

The Peri lagoon did not show vertical variation for the abiotic variables sampled, making this water column homogeneous and without thermal stratification. We attribute this feature to wind, that in general, has a principal importance in coastal environments (Amarasinghe and Vijverberg 2002; Cardoso and Motta Marques 2004; Crossetti et al. 2007; Wondie et al. 2007; Hennemann and Petrucio 2011; Montero et al. 2011).

A strong driving force for phytoplankton productivity is the ratio between euphotic zone and the mixing zone (Lewis 1987). This ratio indicated that Peri lagoon is limited by light. Thus the highest gross primary production rates in depths 1 and 2 were associated with higher PAR in these depths than depths 3 and 4. GPP in depth 1 was lower than depth 2, suggesting photoinhibition in the surface. This is especially true to phytoplankton species with low light requirements, such as Cyanobacteria, which is dominant in Peri lagoon (Padisák 1997; Komárková et al. 1999; Laudares-Silva, 1999; Grellmann, 2006).

Since the environment is limited by light and the phytoplankton individuals remain for longer time in the dark, would be expected that respiration rates were higher. Contrary to expectations, we did not find respiration higher than primary production rates. This may be the effect of the incubation and sampling time (Carignan et al. 2000; Robinson et al. 2002), bacterial activity or other sources of oxygen that not biological, contributing for oxygen production in Peri lagoon (Fontes et al. 2011; Sadro et al. 2011).

Vertical variation of net primary production, although not significant, was highest in depth of highest assimilation number and phytoplankton density, which had the highest light incidence. The same was registered by Tilahun and Ahlgren (2010) and Arst et al. (2008), which the maximum production layer are related with maximum phytoplankton density and photosynthetic capacity, showing occurrence of photoinhibition in the surface.

The lack of significant vertical variation in net production may result from the capability of some Cyanobacteria tolerance high and low light conditions and some species can to keep their photosynthetic rates below 1% underwater radiation (Padisák 1997; Reynolds et al. 1983; Briand et al. 2004; Mihaljevic and Stevic 2011). Furthermore, the water column is homogeneous and these organisms are in constant motion within the water column, especially *Cylindrospermopsis raciborskii* that

had good floating ability in water column, through of the presence of gas vacuoles.

Peri lagoon showed production rates lower than some tropical lakes (Erikson et al. 1998; Stenuite et al. 2007; Arst et al. 2008; Tilahun and Ahlgren 2010), but similar to Itapeva Lake (Cardoso and Motta Marques 2009) and seven lakes in the middle Rio Doce basin (Petrucio et al. 2006). Production rates of the Peri lagoon are within the range of data derived from Bassoli (2006), where phytoplanktonic production in Brazilian lakes, reservoirs and flood lakes did not exceed  $300 \text{ mg C m}^{-2} \text{ day}^{-1}$ . The production rates founded to Peri lagoon are result of the nutrients concentration that limit phytoplankton growth (Reynolds 1999; Reynolds 2006) and the dominance by Cyanobacteria that have lower photosynthetic potential than other phytoplankton groups (Maguire and Neill 1971; Hodoki et al. 2011).

Respiration rates, little studied in lakes, were relationship with nitrite in Peri lagoon, indicating occurrence of decomposition process. The R rates in Peri lagoon were lower than Itapeva Lake, which varied from  $49.9 \text{ mg C m}^{-3} \text{ h}^{-1}$  to  $131.1 \text{ mg C m}^{-3} \text{ h}^{-1}$  (Cardoso and Motta Marques 2009).

The highest NPP rates in spring and summer were related with water temperature, PAR and phytoplankton density. Despite nutrients are essential for production and act in different ways within different lakes, especially nitrogen, which favors production rates (Cole et al. 2000; Dodds and Cole 2007), the availability reduced of total nitrogen in summer did not affect the NPP, since Peri lagoon is dominated by nitrogen-fixing Cyanobacteria (*Cylindrospermopsis raciborskii*). The lack of significant variation between seasons is due the large variation observed between the months in the same season. Interannual variability in the phytoplankton abundance and production rates is common, changing only the hierarchy of causal agents (Teubner 2003; Hillmer et al. 2008; Cardoso and Motta Marques 2009; Liu et al. 2010).

Cyanobacteria were the major contributor to phytoplanktonic density in the Peri lagoon, especially *C. raciborskii*, a species recorded in different regions of the world (Bouvy et al. 2000; Saker et al. 2003; Bormans et al. 2005; Wiedner et al. 2008; Mihaljevic e Stevic 2011), specially in Brazilian lakes of different trophic status (Huszar et al. 2000; Crossetti et al. 2007; Crossetti and Bicudo 2008; Dantas et al. 2008; Dantas et al. 2011).

The occurrence of filamentous Cyanobacteria, including *C. raciborskii*, is typical of mixed and turbid environments with considerably light deficient (Nixdorf et al. 2003). *C. raciborskii* has



slow growth, high adaptive capacity, which gives them an ecological advantage under particular situations (Padisák 1997), which includes preventing the development of the other species, high capacity to fix atmospheric nitrogen, store phosphate and is not easily grazed upon (Gragnani et al. 1999). Its physiological flexibility has a competitive edge in ecosystems that fluctuate between trophic conditions (Moisander et al. 2012).

The strong relationship of dissolved organic carbon with production rates and phytoplankton total density observed in the Peri lagoon was most likely because of cyanobacterial cell lysis, a mechanism for dissolved organic carbon release (Ye et al. 2011). Chlorophyta had more diversity and have higher photosynthetic potential than Cyanobacteria, this demonstrated the strong relationship of Chlorophyta with NPP and GPP. We found that the increased of soluble reactive phosphorus favored the filamentous Cyanobacteria *Limnothrix planctonica* in December/09 and April/10, however this fact seems did not have reflect in production rates.

In summary, our hypotheses were not confirmed, because net primary production and respiration rates and phytoplankton community did not vary at different depths, reflecting the stability of the water column. We propose that nutrients and light limitation and dominance by Cyanobacteria restrict the primary production in this environment. Furthermore respiration was not higher than primary production rates, possibly because other sources of oxygen contribute for oxygen production in Peri lagoon.

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#### References

- Amarasinghe PB, Vijverberg J (2002) Primary production in a tropical reservoir in Sri Lanka. *Hydrobiologia* 487:85-93
- Arst H, Nõges T, Nõges P, Paavel B (2008) Relations of phytoplankton *in situ* primary production, chlorophyll concentration and underwater irradiance in turbid lakes. *Hydrobiologia* 599:169-176

Bassoli F (2006) Produção fitoplanctônica em ecossistemas límnicos brasileiros: Síntese e cenário atual. Dissertação, Universidade Federal do Rio de Janeiro

Berman T, Stone L, Yacobi YZ, Kaplan B, Schlichter M, Nishri A, Pollinger U (1995) Primary production and phytoplankton in Lake Kinneret: A long-term record (1972-1993). *Limnol Oceanogr* 40:1064-1076

Bormans M, Ford PW, Fabbro L (2005) Spatial and temporal variability in Cyanobacterial populations controlled by physical processes. *Journal of Plankton Research* 27:61-70

Bouvy M, Falcão D, Marinho M, Pagano M, Moura A (2000) Occurrence of *Cylindrospermopsis* (Cyanobacteria) in 39 Brazilian tropical reservoirs during the 1998 drought. *Aquat Microb Ecol* 23:13-27

Briand JF, Leboulanger C, Humbert JF, Bernard C, Dufour P (2004) *Cylindrospermopsis raciborskii* (Cyanobacteria) invasion at mid-latitudes: selection, wide physiological tolerance, or global warming? *J phycol* 40:231-238

Cardoso LS, Motta Marques D (2004) Seasonal composition of the phytoplankton community in Itapeva Lake (north coast of Rio Grande do Sul – Brazil) in function of hydrodynamic aspects. *Acta Limnol Brasil* 16:401-416

Cardoso LS, Motta Marques D (2009) Hydrodynamics-driven plankton community in a shallow lake. *Aquat Ecol* 43:73-84

Carignan R, Planas D, Vis C (2000) Planktonic production and respiration in oligotrophic Shield lakes. *Limnol Oceanogr* 45:189-199

Cole GA (1994) Textbook of Limnology. Publisher: Waveland. 412p

Cole JJ, Pace ML, Carpenter SR, Kitchell JF (2000) Persistence of net heterotrophy lakes during nutrient addition and food web manipulations. *Limnol Oceanogr* 45:1718-1730

Cole JJ, Prairie YT, Caraco NF, McDowell WH, Tranvik LJ, Striegl RG, Duarte CM, Kortelainen P, Downing JA (2007) Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. *Ecosystems* 10:171-184

Crosseti LO, Cardoso LS, Callegaro VLM, Alves-Da-Silva SM, Werner VR, Rosa ZM, Motta Marques D (2007) Influence of the hydrological changes on the structure and dynamics in a subtropical wetland-lake system, *Acta Limnol Brasil* 19:315-329

Crosseti LO, Bicudo CEM (2008) Adaptations in phytoplankton life strategies to imposed change in a shallow urban tropical eutrophic reservoir, Garças Reservoir, over 8 years. *Hydrobiologia* 614:91-105

Curl H, Small LF (1965) Variations in photosynthetic assimilation ratios in natural, marine phytoplankton communities. *Limnol Oceanogr Suppl* 10:67-73

Dantas ÊW, Moura AN, Bittencourt-Oliveira MC, Neto JDT, Cavalcanti AD (2008) Temporal variation of the phytoplankton community at short sampling intervals in the Mundaú reservoir, Northeastern Brazil. *Acta Bot Brasil* 22:970-982

Dantas ÊW, Bittencourt-Oliveira MC, Moura AN (2011) Dynamics of phytoplankton associations in three reservoirs in northeastern Brazil assessed using Reynolds' theory. *Limnologica* doi:10.1016/j.limno.2011.09.002

Del Giorgio PA, Peters RH (1994) Patterns in planktonic P:R ratios in lakes: influence of lake trophic and dissolved organic carbon. *Limnol Oceanogr* 39:772-787

Diehl S, Berger S, Ptacnik R, Wild A (2002) Phytoplankton, light, and nutrients in a gradient of mixing depths: field experiments. *Ecology* 83:399-411

Dodds WK, Cole JJ (2007) Expanding the concept of trophic state in aquatic ecosystems: It's not just the autotrophs. *Aquatic Sciences* 69:427-439

Downing JA et al. (2006) The global abundance and size distribution of lakes, ponds, and impoundments. *Limnol Oceanogr* 51:2388-2397

Erikson R, Hooker E, Mejia M, Zelaya A, Vammen K (1998) Optimal conditions for primary production in a polymictic tropical lake (Lake Xolotlán, Nicaragua). *Hydrobiologia* 382:1-16

Esteves FA (2011) *Fundamentos em Limnologia*. Rio de Janeiro: Interciência 826p.

Fontes ML, Suzuki MT, Cottrell MT, Abreu PC (2011) Primary production in a subtropical stratified coastal lagoon – Contribution of anoxygenic phototrophic bacteria. *Microb Ecol* 61:223-237

Gaard E, Nordi GA, Simonsen K (2011) Environmental effects on phytoplankton production in a Northeast Atlantic fjord, Faroe Islands. *Journal of Plankton Research* 33:947-959

Greellmann C (2006) Aspectos da morfologia e da ecologia de *Cylindrospermopsis raciborskii* (Woloszinska) Seenayya et Subba-Raju e da produção de cianotoxinas na lagoa do Peri, Florianópolis, SC, Brasil. Dissertação. Universidade de Santa Catarina

Golterman HL, Clymo RS, Ohnsta DMAM (1978) *Methods for chemical analysis of freshwater*. Oxford: Blackwell Scientific Publications. 213 p

Graghani A, Scheffer M, Rinaldi S (1999) Top-down control of cyanobacteria: a theoretical analysis. *Am Nat* 153:59-72

Hanson PC, Bade DL, Carpenter SR (2003) Lake metabolism: Relationships with dissolved organic carbon and phosphorus. *Limnol Oceanogr* 48:1112-1119

Hasle G (1978) The invert-microscope method. In Sournia, A. (ed.) *Phytoplankton Manual*. Monographs on Oceanographic Methodology. Unesco Publishers, Paris: 88-96

Hennemann MC, Petrucio MM (2011) Spatial and temporal dynamic of trophic relevant parameters in a subtropical coastal lagoon in Brazil. *Environ Monit Assess* doi: 10.1007/s10661-010-1833-5

Hillmer I, Reenen P, Imberger J, Zohary T (2008) Phytoplankton patchiness and their role in the modeled productivity of a large, seasonally stratified lake. *Ecological modeling* 218:49-59

Hodoki Y, Ohbayashi K, Kobayashi Y, Okuda N, Nakano S (2011) Temporal variation in cyanobacteria species composition and photosynthetic activity in experimentally induced blooms. *Journal of Plankton Research* 33:1410-1416

Huszar VLM, Silva LHS, Marinho M, Domingos P, Sant'Anna CL (2000) Cyanoprokaryote assemblages in eight productive tropical Brazilian Waters. *Hydrobiologia* 424:67-77

Jouenne F, Lefebvre S, Véron B, Lagadeuc Y (2007) Phytoplankton community structure and primary production in small intertidal estuarine-bay ecosystem (eastern English Channel, France). *Mar Biol* 151:805-825

Komárková J, Laudares-Silva R, Senna PAC (1999) Extreme morphology of *Cylindrospermopsis raciborskii* (Nostocales, Cyanobacteria) in the Lagoa do Peri, a freshwater coastal lagoon, Santa Catarina, Brazil. *Algological Studies* 94:207-222.

Koroleff F (1976) Determination of nutrients. In: Grasshoff K. (Ed) *Methods of sea water analysis*. Verlag Chemie Weinheim 117 181

Laudares-Silva R (1999) Aspectos limnológicos, variabilidade especial e temporal na estrutura da comunidade fitoplanctônica da Lagoa do Peri, Santa Catarina, Brasil. 216f. Tese (Doutorado) Universidade Federal de São Carlos

Lewis WM (1987) Tropical limnology. *Ann Rev Ecol Syst* 18:158-184

Liu C, Liu L, Shen H (2010) Seasonal variations of phytoplankton community structure in relation to physico-chemical factors in Lake Baiyangdian, China. *Procedia Environmental Sciences* 2:1622-1631

Lobo EA, Leighton G (1986) Estruturas comunitarias de las fitocenoses planctônicas de los sistemas de desembocaduras de rios e esteros de La zona central do Chile. *Revista de Biología Marinha* 22:1-9

Lorenzen CJ (1967) Determination of chlorophyll and pheopigments: Spectrophotometric equations. *Limnol Oceanogr* 12:343-346

Mackereth FJH, Heron JE, Talling JF (1978) *Water Analysis: some revised methods for limnologists*. Freshwater Biological Association, Scientific Publication 36

Maguire B, Neill WE (1971) Species and individual productivity in phytoplankton communities. *Ecology* 52:903-907

Marotta H, Duarte CM, Sobek S, Enrich-Prast A (2009) Large CO<sub>2</sub> disequilibria in tropical lakes. *Global Biogeochemical Cycles* 23 GB4022 doi:10.1029/2008GB003434

Mellard JP, Yoshiyama K, Litchman E, Klausmeier CA (2011) The vertical distribution of phytoplankton in stratified water columns. *Journal of Theoretical Biology* 269:16-30

Mihaljevic M, Stevic F (2011) Cyanobacterial blooms in a temperate river-floodplain ecosystem: the importance of hydrological extremes. *Aquat Ecol* 45:335-349

Moisander PH, Cheshire LA, Braddy J, Calandrino ES, Hoffman M, Piehler MF, Paerl HW (2012) Facultative diazotrophy increases *Cylindrospermopsis raciborskii* competitiveness under fluctuating nitrogen availability. *FEMS Microbiol Ecol* 79:800-811

Montero P, Daneri G, González H, Iriarte JL, Tapia FJ, Lizárraga L, Sanchez N, Pizarro O (2011) Seasonal variability of primary production in a fjord ecosystem of the Chilean Patagonia: Implications for the transfer of carbon within pelagic food webs. *Continental Shelf Research* 31:202-215

Nixdorf B, Mischke U, Rucker J (2003) Phytoplankton assemblages and steady state in deep and shallow eutrophic lakes – an approach to differentiate the habitat properties of Oscillatoriales. *Hydrobiologia* 502:111-121

Nöges T, Arst H, Laas A, Kauer T, Nöges P, Töming K (2011) Reconstructed long-term time series of phytoplankton primary

production of a large shallow temperate lake: the basis to assess the carbon balance and its climate sensitivity. *Hydrobiologia* 667:205-222

Padisák J (1997) *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba-Raju, and expanding, highly adaptive cyanobacteria: Worldwide distribution and review of its ecology. *Archiv für Hydrobiologie* 107:563-593

Petrucio MM, Barbosa FAR, Furtado ALS (2006) Bacterioplankton and phytoplankton production in seven lakes in the Middle Rio Doce basin, south-east Brazil. *Limnologia* 36:192-203

Phlips EJ, Aldridge FJ, Hanlon C (1995) Potential limiting factors for phytoplankton biomass in a shallow subtropical lake (Lake Okeechobee, Florida, USA). *Arch Hydrobiol* 45:137-155

Reynolds CS, Tundisi IG, Hino K (1983) Observation on a metalimnetic *lyngbya* population in a stably stratified Tropical Lake (Lagoa Carioca Eastern, Brazil). *Arch Hydrbiol* 97:1-17

Reynolds CS. 1999. Non-determinism to probability, or N:P in the community ecology of phytoplankton. *Archiv fur Hydrobiologie* 146:23-35.

Reynolds CS. 2006. *The ecology of phytoplankton*. Cambridge University Press, Cambridge, 535p.

Robinson C, Serret P, Tilstone G, Teira E, Zubkov MV, Rees AP, Woodward EMS (2002) Plankton respiration in the Eastern Atlantic Ocean. *Deep-Sea Research I* 49:787-813

Ryabov AB, Rudolf L, Blasius B (2010) Vertical distribution and composition of phytoplankton under the influence of an upper mixed layer. *Journal of Theoretical Biology* 263:120-133

Ryther JH, Yentsch CS (1957) The Estimation of Phytoplankton Production in the Ocean from Chlorophyll and Light Data. *Limnol Oceanogr* 2:281-286

Sadro S, Nelson CE, Melack JM (2011) Linking diel patterns in community respiration to bacterioplankton in an oligotrophic high-elevation lake. *Limnol Oceanogr* 56:540-550

Saker ML, Nogueira CG, Vasconcelos VM, Neilan BA, Eaglesham GK, Pereira P (2003) First report and toxicological assessment of the cyanobacterium *Cylindrospermopsis raciborskii* from Portuguese freshwaters. *Ecotoxicology and Environmental Safety* 55:243-250

Stenuite S, Pirlot S, Hardy M, Sarmiento H, Tarbe A, Leporcq B, Descy J (2007) Phytoplankton production and growth rate in Lake Tanganyika: evidence of a decline in primary productivity in recent decades. *Freshwater Biology* 52:2226-2239

Strickland JDH, Parsons TR (1960) A manual of seawater analysis. *Bull Fish Res Board Can* 125:1 18

Teubner K (2003) Phytoplankton, pelagic community and nutrients in a deep oligotrophic alpine lake: ratios as sensitive indicators of the use of P-resources (DRP:DOP:PP and TN:TP:SRSi). *Water Research* 37:1583-1592

Tilahun G, Ahlgren G (2010) Seasonal variations in phytoplankton biomass and primary production in the Ethiopian Rift Valley lakes Ziway, Awassa and Chamo – The basis for fish production. *Limnologica* 40:330-342

Valderrama JC (1981) The simultaneous analysis of total nitrogen and phosphorus in natural waters. *Marine Chemistry* 10:1109-1122

Wetzel RG, Likens GE (2000) *Limnological Analyses*. Springer-Verlag New York. 150p

Wiedner C, Rucker J, Fastner J, Chorus I, Nixdorf B (2008) Seasonal dynamics of cylindrospermopsin and cyanobacteria in two German lakes. *Toxicon* 52:677-686

Wondie A, Mengistu S, Vijverberg J, Dejen E (2007) Seasonal variation in primary production of a large high altitude tropical lake (Lake Tana, Ethiopia): effects of nutrient availability and water transparency. *Aquat Ecol* 41:195-207



Ye L, Shi Z, Wu X, Zhang M, Yu Y, Li D, Kong F (2011) Dynamics of dissolved organic carbon after a cyanobacterial bloom in hypereutrophic Lake Taihu (China). *Limnologica* 41:382-388

## 6 CONSIDERAÇÕES FINAIS

As variações ambientais encontradas na região de clima subtropical, apesar de apresentarem menor amplitude quando comparadas a região de clima temperado, permitiram variações significativas nas taxas de produção primária e respiração pelágica, direcionadas pelas características bióticas e abióticas. As taxas encontradas para a lagoa do Peri são menores quando comparadas com alguns ambientes tropicais e subtropicais, mas semelhantes a outros ambientes brasileiros. Limitação por luz e nutrientes na lagoa do Peri e a dominância por cianobactérias possivelmente são os fatores responsáveis por esses baixos valores.

A partir da incubação em garrafas claras e escuras, durante 24 horas, foi possível verificar que as maiores taxas de produção primária, ocorreram com três horas de incubação no outono e na primavera, e com seis horas de incubação no inverno e no verão.

A estimativa de autotrofia e heterotrofia a partir do oxigênio dissolvido, em incubações em garrafa, recebe críticas, principalmente porque impede a ocorrência dos processos espontâneos na coluna d'água, devido ao elevado tempo de incubação. Assim, não seria esperado que os resultados obtidos em garrafas incubadas e por método de vida livre fossem iguais, uma vez que a primeira metodologia nos dá resultados relativos ao metabolismo planctônico, enquanto a segunda metodologia nos dá resultado do metabolismo do ecossistema.

Apesar disso, ambas as metodologias forneceram resultados semelhantes, não confirmando a nossa hipótese de que a lagoa do Peri seria permanentemente heterotrófica, com observado em outros ambientes tropicais e subtropicais. Na lagoa do Peri períodos autotróficos e heterotróficos foram registrados ao longo de um ano. Sendo que no outono e inverno ocorreu heterotrofia, com maiores taxas de respiração do que produção primária, enquanto a primavera e verão foram autotróficos, com taxas de produção maiores que as taxas de respiração.

Os períodos autotróficos estiveram relacionados com maiores temperaturas e luz, favorecendo a atividade fotossintética, enquanto a heterotrofia foi influenciada pelas concentrações de fósforo e, possivelmente, pela entrada de matéria orgânica alóctone, decorrente das chuvas, suportando assim as elevadas taxas de respiração, e diminuindo a transparência d'água, sendo um fator limitante a fotossíntese.

A lagoa do Peri, apesar de mais profunda que outras lagoas costeiras, não apresentou variação vertical nas condições limnológicas,

como já registrado em trabalhos anteriores no mesmo ambiente e em outras lagoas costeiras brasileiras. Tal fato vem sendo relacionado à constante homogeneização da coluna d'água promovida pelos ventos e pela capacidade de movimentação de algumas espécies de fitoplâncton.

Também verificamos limitação por luz e nutrientes na lagoa do Peri, que aliada à baixa eficiência fotossintética de Cyanobacteria corrobora com as taxas de produção primária encontradas neste trabalho, menores que alguns lagos tropicais e semelhantes a outros ambientes brasileiros.

Na profundidade média de 1 m foi encontrada maior densidade fitoplanctônica, além de maior capacidade fotossintética, refletindo em maiores taxas de produção que diminuíram em direção às camadas mais profundas. Este padrão é característico de ambientes tropicais e subtropicais, sugerindo a ocorrência de fotoinibição na superfície, uma vez que as taxas de produção primária na superfície foram menores que em 1 m de profundidade.

A densidade fitoplanctônica exerceu efeito direto sobre as taxas de produção primária, sendo que a comunidade fitoplanctônica apresentou predominância de Cyanobacteria em todas as profundidades e meses amostrados, com destaque para *Cylindrospermopsis raciborskii* e *Limnothrix planctonica* que foram as únicas espécies que apresentaram períodos de dominância na lagoa do Peri. Chlorophyta foi o segundo grupo mais importante em densidade, mas com maior diversidade de táxons que Cyanobacteria, com destaque para *Monoraphidium irregulare*, uma espécie oportunista, que apresentou períodos de abundância.

A presença constante de *C. raciborskii* desde seu primeiro registro em 1996, e seu crescente aumento de densidade, demonstra que a lagoa do Peri não apresenta limitações aparentes para o desenvolvimento dessa espécie e de outras cianobactérias filamentosas, que toleram bem ambientes túrbidos, bem misturados e limitados por luz.

Intensificar as estimativas de autotrofia e heterotrofia, por métodos de vida livre, e as taxas de produção primária poderá ser útil na estimativa mais precisa sobre a importância da lagoa do Peri, bem como outros ambientes subtropicais, na ciclagem do carbono, visto que observa-se uma tendência dos lagos tropicais a heterotrofia. Medidas do metabolismo das outras comunidades de um lago e também dos ciclos biogeoquímicos podem ajudar a entender como um lago insere-se na escala global de emissão de gases e na ciclagem dos elementos.

Sabendo que as variáveis ambientais induzem rápida resposta da comunidade fitoplanctônica, a escala de amostragem em menores intervalos de tempo poderá ajudar a demonstrar de forma mais clara, a dinâmica temporal dessa comunidade e a atividade metabólica da lagoa do Peri, permitindo um melhor ajuste entre os eventos ambientais e a resposta da comunidade biológica, além de um entendimento da ocorrência ou não de padrões temporais.

Por fim, essa pesquisa contribuiu para o melhor entendimento de como os lagos subtropicais comportam-se e contribuem para o metabolismo global dos ecossistemas aquáticos.

## REFERÊNCIAS

- Álvarez-Góngora C, Herrera-Silveira JA. 2006. Variations of phytoplankton community structure related to water quality trends in a tropical karstic coastal zone. *Marine Pollution Bulletin* 52:48-60.
- Arst H, Nõges T, Nõges P, Paavel B. 2008. Relations of phytoplankton *in situ* primary production, chlorophyll concentration and underwater irradiance in turbid lakes. *Hydrobiologia* 599:169-176.
- Barnes, RSK. 1980. Coastal lagoons. Cambridge: Cambridge University Press. 106p.
- Bassoli F. 2006. Produção fitoplanctônica em ecossistemas límnicos brasileiros: Síntese e cenário atual. Dissertação, Universidade Federal do Rio de Janeiro.
- Becker V, Caputo L, Ordóñez J, Marcé R, Armengol J, Crosseti L, Huszar V. 2010. Driving factors of the phytoplankton functional groups in a deep Mediterranean reservoir. *Water Research* 44:3345-3354.
- Caraco NF, Cole JJ. 2002. Contrasting impacts of a native and alien macrophyte on dissolved oxygen in a large river. *Ecol Appl* 12:1496-1509.
- Cardoso LS, Motta Marques D. 2003. Rate of change of the phytoplankton community in Itapeva Lake (North Coast of Rio Grande do Sul, Brazil), based on the wind driven hydrodynamic regime. *Hydrobiologia* 497:1-12.
- Cardoso LS, Motta Marques D. 2004. Seasonal composition of the phytoplankton community in Itapeva Lake (north coast of Rio Grande do Sul – Brazil) in function of hydrodynamic aspects. *Acta Limnol Brasil* 16:401-416.
- CECCA – Centro de Estudos, Cultura e Cidadania. 1997. Unidades de Conservação e áreas protegidas da Ilha de Santa Catarina: caracterização e legislação. Florianópolis: Insular.
- Crosseti LO, Cardoso LS, Callegaro VLM, Alves-Da-Silva SM, Werner VR, Rosa ZM, Motta Marques D. 2007. Influence of the hydrological

changes on the structure and dynamics in a subtropical wetland-lake system, *Acta Limnol Brasil* 19:315-329.

Cole BE, Cloern JE. 1987. An empirical model for estimating phytoplankton productivity in estuaries. *Mar Ecol Prog Ser* 36:299-305.

Cole GA. 1994. *Textbook of Limnology*. Publisher: Waveland. 412p.

Cole JJ, Caraco NF, Kling GW, Kratz TK. 1994. Carbon dioxide supersaturation in the surface waters of lakes. *Science* 265:1568-1570.

Cole JJ, Caraco NF. 1998. Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF<sub>6</sub>. *Limnol Oceanogr* 43:647-656.

Cole JJ, Pace ML, Carpenter SR, Kitchell JF. 2000. Persistence of net heterotrophy lakes during nutrient addition and food web manipulations. *Limnol Oceanogr* 45:1718-1730.

Cole JJ, et al. 2007. Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. *Ecosystems* 10:171-184.

Coloso JJ, Cole JJ, Pace ML. 2011. Short-term variation in thermal stratification complicates estimation of lake metabolism. *Aquatic Sciences* 73:305-315.

Dantas ÊW, Moura AN, Bittencourt-Oliveira MC, Neto JDT, Cavalcanti AD. 2008. Temporal variation of the phytoplankton community at short sampling intervals in the Mundaú reservoir, Northeastern Brazil. *Acta Bot Brasil* 22:970-982.

Del Giorgio PA, Peters RH. 1994. Patterns in planktonic P:R ratios in lakes: influence of lake trophic state and dissolved organic carbon. *Limnol Oceanogr* 39:772-787.

Del Giorgio PA, Duarte CM. 2002. Respiration in the open ocean. *Nature* 420:379-384.

Dodds WK, Cole JJ. 2007. Expanding the concept of trophic state in aquatic ecosystems: It's not just the autotrophs. *Aquatic Sciences* 69:427-439.

Downing JA, et al. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. *Limnol Oceanogr* 51:2388-2397.

Duarte CM, Prairie YT. 2005. Prevalence of heterotrophy and atmospheric CO<sub>2</sub> emissions from aquatic ecosystems. *Ecosystems* 8:862-870.

Ducklow H. 2008. Microbial services: Challenges for microbial ecologists in a changing world. *Aquat MicrobEcol* 53:13-19.

Esteves FA, Ishii IH, Camargo AFM. 1984. Pesquisas limnológicas em 14 lagoas do litoral do Estado do Rio de Janeiro. In: Lacerda LD, Araújo DSD, Cerqueira R, Turc S (Eds.) *Restingas: origem, estrutura e processos* 443-454. Niterói: CEUFF.

Esteves FA. 1998. Lagoas costeiras: origem, funcionamento e possibilidades de manejo. In: Esteves FA (Ed.) *Ecologia das lagoas costeiras do Parque Nacional da Restinga de Jurubatiba e do Município de Macaé (RJ)* 63-87. Rio de Janeiro: NUPEM/UFRJ.

Esteves FA. 2011. *Fundamentos de Limnologia*. Rio de Janeiro: Interciência. 826p.

Falkowski PG. 1994. The role of phytoplankton photosynthesis in global biogeochemical cycles. *Photosynth Res* 39:235-258.

Falkowski PG, Fenchel T, Delong EF. 2008. The microbial engines that drive Earth's biogeochemical cycles. *Science* 320:1034-1039.

Fonseca BM, Bicudo CEM. 2008. Phytoplankton seasonal variation in a shallow stratified eutrophic reservoir (Garças Pond, Brazil). *Hydrobiologia* 600:267-282.

Goldman CR. 1988. Primary productivity, nutrient, and transparency during the onset of eutrophication in ultra-oligotrophic lake Tahoe, California-Nevada. *Limnol Oceanogr* 33:1321-1333.

Golterman HL, Clymo RS, Ohnstad MAM. 1978. *Methods for physical and chemical analysis of freshwater*. Blackwell Sci. Publisher, Oxford. 213p.

Grellmann C. 2006. Aspectos da morfologia e da ecologia de *Cylindrospermopsis raciborskii* (Woloszinska) Seenayya et Subba-Raju e da produção de cianotoxinas na lagoa do Peri, Florianópolis, SC, Brasil. Dissertação. Universidade de Santa Catarina.

Hanson PC, Bade DL, Carpenter SR. 2003. Lake metabolism: Relationships with dissolved organic carbon and phosphorus. *Limnol Oceanogr* 48:1112-1119.

Hasle GR. 1978. The invert-microscope method. In Sournia, A. (ed.) *Phytoplankton Manual. Monographs on Oceanographic Methodology*. Unesco Publishers, Paris: 88-96.

Hennemann MC, Petrucio MM. 2011. Spatial and temporal dynamic of trophic relevant parameters in a subtropical coastal lagoon in Brazil. *Environ Monit Assess* doi: 10.1007/s10661-010-1833-5.

Hillmer I, Reenen P, Imberger J, Zohary T. 2008. Phytoplankton patchiness and their role in the modeled productivity of a large, seasonally stratified lake. *Ecological modeling* 218:49-59.

Howarth RW, Schneider R, Swaney D. 1996. Metabolism and organic carbon fluxes in the tidal freshwater Hudson River. *Estuaries* 19:848-865.

Huszar VLM, Esteves FA. 1988. Considerações sobre o fitoplâncton de rede de 14 lagoas costeiras do estado do Rio de Janeiro, Brasil. *Acta Limnol Brasil* 11:323-345.

Huszar VLM, Sampaio LHS, Esteves FA. 1990. Estrutura das comunidades fitoplanctônicas de 18 lagoas da região do Baixo Rio Doce, Linhares, Espírito Santo, Brasil. *Revista Brasileira de Biologia* 50:585-598.

IPCC. 2007. *Climate change 2007: Synthesis report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Geneva, Switzerland.



Jassby AD, Powel TM, Goldman CR. 1990. Interannual fluctuations in primary production: Direct physical effects and the trophic cascade at Castle Lake, California. *Limnol Oceanogr* 35:1021-1038.

Kjerve B. 1994. Coastal lagoons processes. Amsterdam: Elsevier. 577p.

Kennish MJ, Paerl HW. 2010. Coastal lagoon. Critical habitats of environmental change. CRC Press. 539p.

Komárková J, Laudares-Silva R, Senna PAC. 1999. Extreme morphology of *Cylindrospermopsis raciborskii* (Nostocales, Cyanobacteria) in the Lagoa do Peri, a freshwater coastal lagoon, Santa Catarina, Brazil. *Algological Studies* 94:207-222.

Koroleff F. 1976. Determination of nutrients. In: Grasshoff K. (Ed) *Methods of sea water analysis*. Verlag Chemie Weinheim 117 181.

Kosten S, Roland F, Motta Marques DML, Van Nes EH, Mazzeo N, Sternberg LSL, Scheffer M, Cole JJ. 2010. Climate-dependent CO<sub>2</sub> emissions from lakes, *Global Biogeochem. Cycles* 24 GB2007, doi:10.1029/2009GB003618.

Krebs CJ. 1994. *Ecology: The Experimental Analysis of Distribution and Abundance*, fourth ed. Harper Collins College Publishers, New York, 801p.

Laudares-Silva R. 1999. Aspectos limnológicos, variabilidade espacial e temporal na estrutura da comunidade fitoplanctônica da Lagoa do Peri, Santa Catarina, Brasil. Dissertação, Universidade de São Carlos.

Lennon JT. 2004. Experimental evidence that terrestrial carbon subsidies increase CO<sub>2</sub> flux from lake ecosystems. *Oecologia* 138:584-591.

Lewis WM Jr. 1996. "Tropical lakes: how latitude makes a difference" 43-64. In: Schiemer F, Boland KT (Eds.) *Perspectives in Tropical Limnology*, Amsterdam, SBP Academic Publishing bv.

Lewis WM Jr. 2011. Global primary production of lakes: 19<sup>th</sup> Baldi Memorial Lecture. *Inland Waters* 1:1-28.

Liu C, Liu L, Shen H. 2010. Seasonal variations of phytoplankton community structure in relation to physico-chemical factors in Lake Baiyangdian, China. *Procedia Environmental Sciences* 2:1622-1631.

Lloret J, Marín A, and Marín-Guirao L. 2008. Is coastal lagoon eutrophication likely to be aggravated by global climate change? *Estuar Coastal Shelf Sci* 78:403-412.

Lobo EA, Leighton G. 1986. Estruturas comunitarias de las fitocenoses planctónicas de los sistemas de desembocaduras de rios e esteros de La zona central do Chile. *Revista de Biologia Marinha* 22:1-9.

Lorenzen CJ. 1976. Determination of chlorophyll and pheopigments: Spectrophotometric equations. *Limnol Oceanogr* 12:343-346.

Mackereth FJH, Heron JE, Talling JF. 1978. *Water Analysis: some revised methods for limnologists*. Freshwater Biological Association, Scientific Publication 36. 120p.

Marotta H, Paiva LT, Petrucio MM. 2009. Changes in thermal and oxygen stratification pattern coupled to CO<sub>2</sub> outgassing persistence in two oligotrophic shallow lakes of the Atlantic Tropical Forest, Southeast Brazil. *Limnology* 10:195-202.

Marotta H, Duarte CM, Pinho L, Enrich-Prast A. 2010. Rainfall leads to increased pCO<sub>2</sub> in Brazilian coastal lakes. *Biogeosciences* 7:1607-1614.

Medina-Gómez I, Herrera-Silveira JA. 2006. Primary production dynamics in a pristine groundwater influenced coastal lagoon of the Yucatan Peninsula. *Continental Shelf Research* 26:971-986.

Melack JM. 1979. Temporal variability of phytoplankton in tropical lakes. *Oecologia (Berl.)* 44:1-7.

Melo S, Huszar VLM. 2000. Phytoplankton in an Amazonian flood-plain lake (Lago Batata, Brasil): Diel variation and species strategies. *Journal of Plankton Research* 22:63-76.

Moura AN, Dantas EW, Oliveira HSB, Bittencourt-Oliveira MC. 2011. Vertical and temporal dynamics of cyanobacteria in the Carpina potable water reservoir in northeastern Brazil. *Braz J Biol* 71:1-9.

- Odum EP. 1956. Primary production in flowing waters. *Limnol. Oceanogr.* 1:102-117.
- Oliveira JS. 2002. Análise sedimentar em zonas costeiras: subsídio ao diagnóstico ambiental da Lagoa do Peri - Ilha de Santa Catarina - SC, Brasil. Florianópolis. Dissertação (Mestrado). Universidade Federal de Santa Catarina.
- O'Sullivan PE, Reynolds CS. 2004. *The lakes Handbook*. Blackwell Publishing. 699p.
- Reynolds CS. 1980. Phytoplankton assemblages and their periodicity in stratifying lake systems. *Holarct Ecol* 3:141-159.
- Reynolds CS. 2006. *The ecology of phytoplankton*. Cambridge University Press, Cambridge, 535p.
- Roland F, Vidal LO, Pacheco FS, Barros NO, Assireu A, Ometto JPHB, Cimleris ACP, Cole JJ. 2010. Variability of carbon dioxide flux from tropical (Cerrado) hydroelectric reservoirs. *Aquatic Sciences* 72:283-293.
- Staehr PA, Sand-Jensen K. 2007. Temporal dynamics and regulation of lake metabolism. *Limnol Oceanogr* 52:108-120.
- Staehr PA, Bade D, Van de Bogert MC, Koch GR, Williamson C, Hanson P, Cole JJ, Kratz T. 2010. Lake metabolism and the diel oxygen technique: State of the science. *Limnol Oceanogr Methods* 8:628-644.
- Strickland JDH, Parsons TR. 1960. A manual of seawater analysis. *Bull Fish Res Board Can* 125:1 18.
- Stumm W, Morgan JJ. 1996. *Aquatic chemistry: chemical equilibria and rates in natural waters*. Wiley-Interscience, New York. 1022p.
- Tadonlélé RD. 2010. Evidence of warming effects on phytoplankton productivity rates and their dependence on eutrophication status. *Limnol Oceanogr* 55:973-982.
- Teubner K. 2003. Phytoplankton, pelagic community and nutrients in a deep oligotrophic alpine lake: ratios as sensitive indicators of the use of

P-resources (DRP:DOP:PP and TN:TP:SRSi). *Water Research* 37:1583-1592.

Valderrama JC. 1981. The simultaneous analysis of total nitrogen and phosphorus in natural waters. *Marine Chemistry* 10:1109-1122.

Wanninkhof R, Knox M. 1996. Chemical enhancement of CO<sub>2</sub> exchange in natural waters. *Limnol Oceanogr* 41:689-697.

Wetzel RG, Likens GE. 1991. *Limnological Analyses*. Springer-Verlag New York. 105p.

Wondie A, Mengistu S, Vijverberg J, Dejen E. 2007. Seasonal variation in primary production of a large high altitude tropical lake (Lake Tana, Ethiopia): effects of nutrient availability and water transparency. *Aquat Ecol* 41:195-207.