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TESE DE DOUTORADO

FATORES CONTROLADORES DO METABOLISMO AQUÁTICO EM LAGOS DE MATA ATLÂNTICA

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

Denise Tonetta

Tese julgada e aprovada em sua forma final pelos membros titulares da Banca Examinadora (15/PPGECO/2016) do Programa de Pós-Graduação em Ecologia - UFSC.

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Vista aérea da Lagoa do Peri, julho de 2012
Foto: acervo pessoal

A lake is the landscape’s most beautiful and expressive feature. It is earth’s eye; looking into which the beholder measures the depth of his own nature. The fluviatile trees next the shore are the slender eyelashes which fringe it, and the wooded hills and cliffs around are its overhanging brows (Henry David Thoreau).

Science is built up of facts, as a house is built of stones; but an accumulation of facts is no more science than a heap of stones is a house (Henri Poincaré).

RESUMO

Os lagos inseridos no bioma Mata Atlântica são importantes ecossistemas para a ciclagem do carbono podendo atuar como fontes ou sumidouros de carbono. Nesta tese foi abordado o metabolismo aquático ecossistêmico de dois lagos brasileiros, utilizando as taxas de produção primária e respiração, bem como o fluxo de CO_2 entre a água e a atmosfera, para entender como as variáveis limnológicas e meteorológicas direcionam a dinâmica espaço-temporal do metabolismo ecossistêmico. Nossos resultados mostraram que a Lagoa do Peri foi predominantemente heterotrófica, com períodos de autotrofia em condições de alta temperatura e luminosidade. Analisando a dinâmica espacial das taxas metabólicas, a região litorânea apresentou maior variabilidade que a região pelágica, bem como maiores taxas de respiração, em função da baixa profundidade da coluna d'água, influência do sedimento e do ecossistema terrestre. Verticalmente maiores taxas de produção primária foram registradas na superfície, diminuindo em direção ao fundo, e as taxas de respiração mostraram padrão inverso. Ao longo de oito anos consecutivos observamos que a diminuição do nível d'água ao longo dos anos de 2012 e 2014 foi reflexo da baixa precipitação. Essa mudança física promoveu aumento na concentração de clorofila-a, nutrientes, carbono e o fluxo de CO_2 para a atmosfera. A Lagoa Carioca também se mostrou heterotrófica e o fluxo de CO_2 foi intensificado quando adições experimentais de matéria orgânica foram conduzidas em mesocosmos. Por outro lado, a adição de nutrientes inorgânicos resultou no aumento do O_2, com diminuição do CO_2 e alta variabilidade diária. Esta tese mostrou que o metabolismo ecossistêmico de lagos de Mata Atlântica é altamente dinâmico e predominantemente heterotrófico com diferentes variáveis sendo importantes nas diversas escalas espacial e temporal. Entretanto, sugerimos que em um lago polimítico as variáveis físicas como disponibilidade de luz, estabilidade térmica e profundidade da coluna d'água determinam a variação espaço-temporal das taxas metabólicas. Além disso, mudanças climáticas afetando a região tropical pode alterar as características limnológicas dos lagos, que por sua vez podem intensificar ou alterar a função dos ecossistemas na ciclagem do carbono.

Palavras-chave: Produção primária. Respiração. Ecossistemas aquáticos. Variação temporal. Dinâmica espacial. Alta frequência. Heterotrofia. Oxigênio dissolvido. Fluxo de CO_2.

ABSTRACT

Lakes in the Atlantic Forest are important ecosystems for the carbon cycling and they can be sources or carbon sinks. This thesis addressed the aquatic ecosystem metabolism of two Brazilian lakes, using the primary production and respiration rates, as well as the air-water CO_2 flux to understand how limnological and meteorological variables affect the spatio-temporal dynamics of ecosystem metabolism. Our results showed that the Peri Lake was predominantly heterotrophic due to bacterioplankton. However, during high temperature and light conditions the lake was net autotrophic. Regarding to the spatial dynamics of metabolic rates, the coastal area showed higher variability than the pelagic area, as well as higher respiration rates, which was related to the low water column depth, influence of sediment and terrestrial ecosystem. Vertically we recorded higher primary production rates at surface, decreasing toward the bottom, and respiration rates showed the opposite pattern. Over eight consecutive years Peri Lake featured decrease in water level over the years 2012 and 2014 due to low rainfall. This physical change increased the chlorophyll-a, nutrients, carbon and CO_2 flux to the atmosphere. Carioca Lake was also heterotrophic and experimental additions of organic matter promoted the increase in CO_2, while the addition of inorganic nutrients resulted in an O_2 increase concomitant with CO_2 decrease and high daily variability in both gases. This thesis showed that the ecosystem metabolism from Atlantic Forest lakes is highly dynamic and predominantly heterotrophic with many variables being important in the different spatio-temporal scales. However, we suggest that in a polymictic lake the physical variables, such as light availability, thermal stability and water column depth, determine the spatial and temporal variation in the metabolic rates. In addition, climate change affecting tropical areas can change the limnological conditions in the lakes, intensifying or changing the ecosystems function in the carbon cycling.

Keywords: Primary production. Respiration. Aquatic ecosystems. Temporal variation. Spatial dynamics. High frequency. Heterotrophy. Dissolved oxygen. CO_2 flux.

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1 INTRODUÇÃO

A ecologia de ecossistemas busca entender a relação entre os organismos e o ambiente onde vivem, considerando a troca de matéria e energia entre eles (Townsend et al., 2010). O termo ecossistema foi proposto por Arthur Tansley, em 1935, embora os estudos ecossistêmicos remontem de datas anteriores. Inserido nessa abordagem, o metabolismo ecossistêmico, de ambientes terrestres e/ou aquáticos, envolve todos os processos de produção e degradação da matéria orgânica, sendo que a produção primária e a respiração são etapas do metabolismo ecossistêmico (Odum, 2013; Weathers et al., 2013).

A Mata Atlântica é um dos biomas brasileiros e se extende de norte à sul do país, pela região litorânea, planaltos e serras do interior do Rio Grande do Norte ao Rio Grande do Sul. A Mata Atlântica está associada à mangues, enseadas, foz de grandes rios, baías, lagos e lagunas de clima tropical e subtropical. No entanto, a Mata Atlântica encontra-se altamente reduzida, no qual 88% da sua área original foi perdida para processos de urbanização, cultivo e extração de madeira. Os fragmentos remanescentes, em sua maioria são menores que 50 hectares, e apenas 9% da mata remanescente está protegida pela legislação ambiental (Ribeiro et al., 2009). Importantes rios cortam a Mata Atlântica, como por exemplo: São Francisco, Doce, Paraíba do Sul, Grande, Tietê, Paraná, Iguaçu e Uruguai (Galindo-Leal e Câmara, 2003), e sua interface com diferentes ecossistemas fazem da Mata Atlântica um local de elevada biodiversidade e endemismo que é foco dos programas de conservação.

Os lagos são formados a partir de depressões naturais do solo que apresentam forma, profundidade e extensão variáveis. Podem ser costeiros, apresentando ou não influência marinha, ou interiores, de água doce (Esteves, 2011). Lagoas são geralmente corpos d’água mais rasos que os lagos, embora não há um limite para a classificação dos ambientes. Uma estimativa aponta que em todo o mundo existem aproximadamente 304 milhões de lagos naturais, correspondendo a aproximadamente 3% da superfície terrestre (Downing et al., 2006). Mesmo tendo pouca representatividade em extensão, os lagos são considerados *hot spots* para a produção, degradação, estocagem e transporte do carbono (Cole e Caraco, 2001; Tranvik et al., 2009), principalmente os lagos inseridos na Mata Atlântica, uma vez que recebem elevado aporte de matéria orgânica terrestre. A importância dos ambientes aquáticos de água doce na ciclagem do carbono foi estudada por Bauer et al. (2013), no qual estimaram que o gás carbônico (CO_2) emitido por lagos e rios é similar ao CO_2 absorvido pelos oceanos.

Os estudos sobre metabolismo aquático iniciaram com Odum (1956) estimando as taxas de produção primária e respiração ecossistêmicas em rios, através das variações diárias do oxigênio dissolvido (O_2). A produção primária bruta (GPP; do inglês gross primary production) é a conversão autotrófica do carbono inorgânico em orgânico, e a respiração do ecossistema (R) é a oxidação do carbono orgânico em inorgânico por organismos autotróficos e heterotróficos (Staehr et al., 2012a). O balanço entre o que foi produzido e o que foi consumido (GPP – R) determina o metabolismo líquido do ecossistema aquático (NEP; do inglês net ecossystem production; Dodds e Cole, 2007). Quando as taxas de produção primária são maiores que as taxas de respiração o ecossistema é classificado como autotrófico (NEP>0) e quando a produção primária é menor que a respiração o ecossistema é classificado como heterotrófico (NEP<0). Neste sentido, a estimativa da produção líquida do ecossistema, é útil para compreender a importância dos ecossistemas aquáticos na ciclagem do carbono e para definir o seu papel como fonte ou sumidouro de carbono (Lovett et al., 2006; Cole et al., 2007).

Outra maneira de determinar se um ecossistema é fonte ou sumidouro de carbono é através da concentração de CO_2 na água e o fluxo desse gás entre a água e a atmosfera (Cole et al., 1994). Quando a pressão parcial do CO_2 (pCO_2) na água é maior do que a observada na atmosfera, em torno de 387 µatm (valor médio anual dos últimos 10 anos obtidos do NOAA, Dlugokencky e Tans, 2016), o ambiente está supersaturado e em geral o fluxo de CO_2 é positivo para a atmosfera. Por outro lado, quando a concentração é menor na água que na atmosfera, o fluxo assume direção inversa e o CO_2 é absorvido da atmosfera. Os estudos usando CO_2 podem ser feitos através de medidas diretas desse gás ou de estimativas do CO_2 a partir dos valores de pH e alcalinidade (Trolle et al., 2012; Pinho et al., 2016).

O metabolismo ecossistêmico e seus processos de produção primária e respiração são dependentes de variáveis limnológicas, como clorofila, nutrientes e carbono orgânico, que interagem entre si e são influenciadas pelas condições meteorológicas, como a temperatura, o vento e a precipitação (Hall et al., 2015). Os nutrientes são um importante recurso aos organismos autotróficos, portanto, o aumento na concentração de nitrogênio e fósforo leva ao aumento da clorofila que na presença de luz e com temperatura adequada favorece a produção primária (Balmer et al., 2011; Pacheco et al., 2013). Ademais, os nutrientes também favorecem o aumento da atividade microbiana heterotrófica, gerando competição entre os organismos autotrótricos e heterotróficos (Azam, 1998). A maior disponibilidade de carbono orgânico dissolvido na água impulsiona a respiração (Hanson et al., 2003; Couture et al., 2015), bem como a temperatura e a precipitação, a primeira por acelerar a atividade metabólica e a segunda por conduzir matéria orgânica de origem terrestre para dentro dos ecossistemas aquáticos (Brown et al., 2004; Marotta et al., 2010). Elevada temperatura também promove maior estabilidade térmica da coluna d’água, limitando a disponibilidade de nutrientes e matéria orgânica, que pode resultar em maiores taxas metabólicas durante o período de circulação da água, uma vez que nesse período ocorre a ressuspensão de matéria orgânica e nutrientes das águas mais profundas (Brighenti et al., 2015). Entretanto, durante o período de circulação pode também ocorrer limitação da produção primária através da diminuição da disponibilidade de luz na coluna d’água (Staehr et al., 2012b).

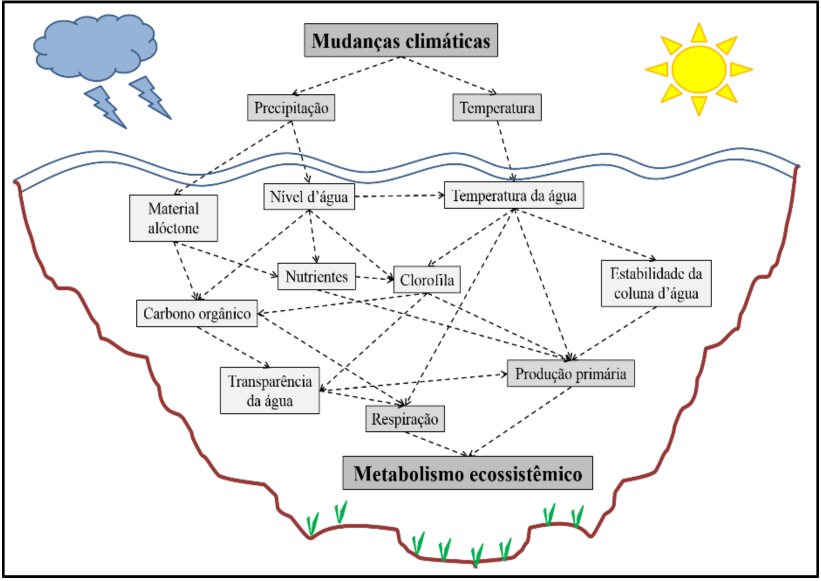
A variação espaço-temporal dos processos metabólicos também é dependente de diversos fatores. A variabilidade vertical além de responder diretamente à disponibilidade de matéria orgânica e nutrientes é altamente dependente da disponibilidade de luz nos diferentes estratos da coluna d’água (Palmer et al., 2013; Obrador et al., 2014). Lagos com menor disponibilidade de luz tendem a ter reduzidas taxas de produção primária e com isso a respiração pode ser predominante. Por outro lado, luz em excesso pode causar fotoinibição nas camadas superficiais da coluna d’água (Staehr et al., *in press*). A heterogeneidade intralagunar, especialmente entre as zonas litorâneas e pelágicas promove diferentes taxas de produção primária e respiração em função da profundidade da coluna de água, da descarga de riachos e da presença de macrófitas (Lauster et al., 2006; Staehr et al., 2012c; Van de Borget et al., 2012; They et al., 2013). Nas áreas mais rasas, maior contribuição dos processos metabólicos que ocorrem no sedimento é esperada, aumentando a concentração de CO_2 e O_2 na coluna d’água (Van de Bogert et al., 2007). Na escala latitudinal, a temperatura exerce forte influência na respiração, em geral com maiores concentrações de CO_2 nos ambientes mais quentes (Kosten et al., 2010; Pinho et al., 2016).

A variação diária da temperatura e luminosidade afeta diretamente a atividade metabólica dos organismos autotróficos que dependem da luz para a produção primária e indiretamente os organismos heterotróficos (Nimick et al., 2011; Marotta et al., 2012a; Jiang et al., 2013). Com isso, maiores taxas de respiração geralmente ocorrem durante o início da noite, onde a disponibilidade de matéria orgânica autóctone é maior (Sadro et al., 2011). A temperatura e o vento por sua vez podem acelerar a troca gasosa entre a água e a atmosfera por influenciarem no aquecimento e resfriamento da coluna d’água ao longo do ciclo diário (MacIntyre et al., 2010). Variações sazonais e interanuais também são importantes para direcionar os padrões anuais da ciclagem do carbono dentro dos ecossistemas e são influenciados principalmente pelos padrões meteorológicos de precipitação, vento, luz e temperatura, que influenciam as condições de nutrientes e estabilidade térmica da coluna d’água (Tsai et al., 2008; Laas et al., 2012; Tsai et al., 2016).

Eventos climáticos como tempestades, tornados e secas estão cada vez mais frequentes e promovem distúrbios nos ambientes aquáticos (Kerr, 2007). No sul do Brasil o impacto dos eventos El Niño e La Niña Oscilação Sul alteram o padrão de precipitação, causando grande variabilidade interanual das condições meteorológicas (Grimm et al., 1998). Em anos de El Niño geralmente ocorre maior precipitação e períodos de seca são registrados nos anos de La Niña. O aumento da precipitação promove a entrada de matéria orgânica para dentro dos sistemas aquáticos que altera a estrutura da comunidade aquática e seus processos metabólicos (Figura 1). A ausência de precipitação também afeta as condições limnológicas por reduzir o nível d’água e com isso aumentar a concentração de nutrientes e clorofila, bem como alterara estabilidade térmica dos ambientes aquáticos (Tsai et al., 2016). A intensidade e a frequência com que essas condições meteorológicas incidem sobre os ambientes aquáticos determinam como esses ecossistemas irão responder biológica e metabolicamente. Essa resposta pode ser acessada através da resistência e a resiliência dos processos metabólicos ecossistêmicos (Pimm, 1984, Carpenter et al., 2001). A intensidade em que determinada variável muda após a perturbação determina a resistência do ecossistema, enquanto que a velocidade com que a mesma variável retorna para a condição pré-distúrbio, ou alcança um novo estado de equilíbrio, determina a resiliência do ambiente (Pimm, 1984). Determinar a resistência e a resiliência é importante para entender quão adaptativo é o sistema para manter suas funções metabólicas (Carpenter et al., 2001). Essa abordagem é uma nova proposta para o uso dos termos resiliência e resistência considerando os gases CO_2 e O_2 envolvidos na produção primária e respiração dos ecossistemas aquáticos.

Nos últimos dez anos, determinar as variações do oxigênio dissolvido em tempo real e alta frequência vem mostrando maior precisão e confiabilidade nas taxas metabólicas estimadas (Staehr et al., 2010). Ademais, através da alta resolução dos dados obtidos é possível acessar a variabilidade diária do ambiente em resposta à eventos climáticos que anteriormente não eram identificados nas estratégias de monitoramento em baixa frequência (Jennings et al., 2012; Klug et al., 2012). Apesar do número crescente de estudos sobre o metabolismo aquático, lagos tropicais e subtropicais, especialmente os brasileiros, permanecem pouco estudados (Marotta et al., 2009a; Kosten et al., 2010; Brighenti et al., 2015; Cavalcanti et al., 2016; Pinho et al., 2016), embora sejam considerados importantes fontes de CO_2 para a atmosfera. Raymond et al. (2013) estimaram que os lagos tropicais, compreendendo cerca de 2,4% da área global dos lagos, contribuem para 34% da emissão total de carbono.

Figura 1: Principais relações da precipitação e temperatura do ar com as variáveis aquáticas associadas ao metabolismo ecossistêmico.



Fonte: O autor.

Uma revisão feita por Hoellein et al. (2013) mostra que os resultados obtidos sobre o metabolismo aquático podem ser valorosos para o gerenciamento e a restauração dos ambientes e do seu entorno. Portanto, em escalas regionais, é essencial determinar a importância dos lagos na ciclagem do carbono, bem como entender como as alterações do clima, da paisagem e das condições limnológicas podem afetar o metabolismo aquático ecossistêmico. Portanto, esta tese está estruturada de maneira a elucidar os potenciais fatores controladores dos processos de respiração e produção primária ecossistêmica em diferentes escalas espaço-temporal, em ecossistemas aquáticos inseridos no bioma Mata Atlântica. A Lagoa do Peri, na região subtropical, e a Lagoa Carioca na região tropical do Brasil, são lagos oligo-mesotróficos de água doce, inseridos em áreas de proteção ambiental. Em geral, os lagos de Mata Atlântica são supersaturados em CO_2 e apresentam relação direta com a matéria orgânica de origem terrestre, no qual a degradação dessa matéria orgânica é dependente da temperatura (Marotta et al., 2009b; Marotta et al., 2012b; Pinho et al., 2016).

No primeiro capítulo será abordada a variação diária e sazonal na concentração de CO_2 e sua relação com as variáveis meteorológicas e limnológicas, com o objetivo de determinar a influência da biomassa bacteriana, luz, temperatura e disponibilidade de carbono no fluxo de CO_2 entre a água e a atmosfera. No segundo capítulo será abordada a importância das variáveis físicas, relacionadas à temperatura, luz, vento e profundidade da coluna d’água, na variação espacial das taxas de produção primária e respiração, através das medições de oxigênio, luz e temperatura em alta frequência. No terceiro capítulo, a abordagem envolve oito anos consecutivos de amostragens mensais, avaliando a dinâmica do CO_2 quando alterações meteorológicas promovem mudanças físicas e limnológicas no ecossistema aquático. Finalmente, no quarto capítulo, através de um experimento em mesocosmo, será abordado como adições de matéria orgânica e nutrientes afetam a dinâmica diária do CO_2 e do O_2 e como essas adições podem afetar a resistência e a resiliência dos gases nestas diferentes condições aquáticas.

Cada capítulo desta tese contém hipóteses e metodologias específicas. No entanto, esta tese é guiada pelas seguintes perguntas:

- Como o fluxo de CO_2 varia em um ciclo diário, em diferentes estações meteorológicas, e quais os possíveis fatores relacionados à essas mudanças na Lagoa do Peri?
- Que fatores físicos relacionados ao vento, temperatura, luz e profundidade da coluna d’água tem maior influência sobre a variabilidade da produção primária e da respiração em duas áreas distintas da Lagoa do Peri?
- Como o CO_2 responde à redução da precipitação que afeta o nível d’água e a concentração de nutrientes e clorofila na Lagoa do Peri?
- De que maneira adições de matéria orgânica e nutrientes afetam a dinâmica diária do CO_2 e O_2 no ambiente pelágico da Lagoa Carioca?

1.1 Objetivos

1.1.1 Objetivo geral

Analisar a dinâmica espaço-temporal do metabolismo aquático de dois lagos inseridos no bioma Mata Atlântica, relacionando com potenciais fatores limnológicos e meteorológicos direcionadores da respiração e produção primária ecossistêmica.

1.1.2 Objetivos específicos

- Determinar a variação diária das condições limnológicas, assim como as concentrações de CO_2 na água e o fluxo com a atmosfera sob diferentes condições meteorológicas;
- Verificar se as taxas de produção primária e respiração na região pelágica e litorânea diferem e quais variáveis físicas relacionadas à temperatura, luz, vento e profundidade da coluna d’água, explicam essas variações espaciais;
- Analisar a dinâmica do CO_2 em um cenário de mudanças climáticas, no qual a diminuição da precipitação afeta o nível d’água do ecossistema e as concentrações de nutrientes e clorofila-a;
- Descrever a dinâmica diária do CO_2 e O_2, sua resistência e resiliência frente às adições de matéria orgânica e nutrientes.

2 ÁREA DE ESTUDO

Este estudo foi desenvolvido em dois lagos inseridos no bioma Mata Atlântica, a Lagoa do Peri e a Lagoa Carioca. A Lagoa do Peri (27°44’S 48°31’W) está situada em Santa Catarina e inserida na área de proteção ambiental do Parque Municipal da Lagoa do Peri. Esse parque foi criado em 1981 para preservar o maior manancial de água doce e um importante remanescente de Mata Atlântica Subtropical da ilha de Santa Catarina. A Lagoa Carioca (19°75’S 42°6’W) em Minas Gerais, está inserida no Parque Estadual do Rio Doce, criado 1939. Este parque é o maior remanescente da Mata Atlântica Tropical no Estado de Minas Gerais, com aproximadamente 36 mil hectares de florestas e aproximadamente 40 lagoas estão inseridas nessa área, correspondendo à aproximadamente 9,8% da área protegida.

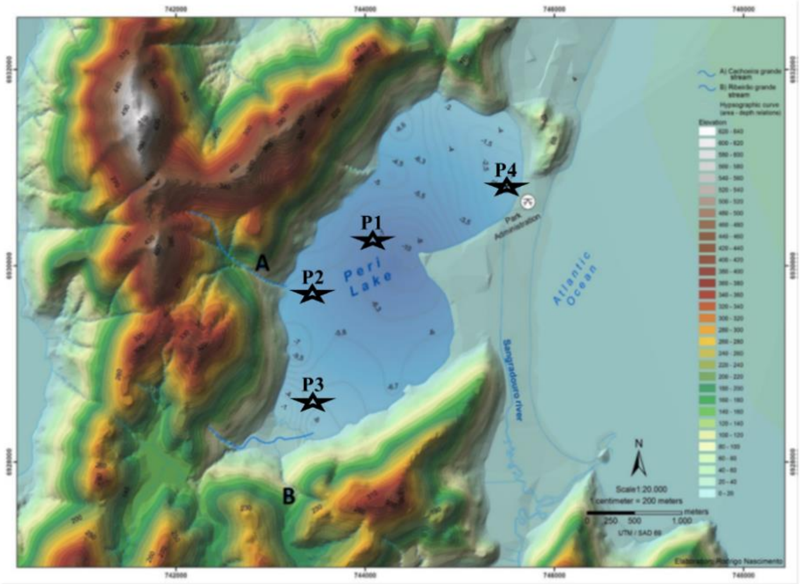
2.1 Lagoa do Peri

A Lagoa do Peri é uma lagoa costeira subtropical de água doce, situada 3 metros acima do nível do mar, com o qual se conecta através de um canal de sentido único lagoa→mar. A lagoa apresenta área superficial de 5,07 km^2, comprimento máximo de 4 km, largura média de 1,7 km, profundidade média de 4,2 m e profundidade máxima de 11 m e é usada para abastecimento público de aproximadamente 17% da população residente na ilha de Santa Catarina (Companhia Catarinense de Águas e Saneamento – CASAN, comunicação pessoal). A bacia hidrográfica da Lagoa do Peri tem aproximadamente 20,3 km^2, e os rios Cachoeira Grande (Figura 2, letra A) e Ribeirão Grande (Figura 2, letra B) são os principais tributários da lagoa, a qual teve seu volume calculado em 21,2 milhões de metros cúbicos (Laudares-Silva, 1999).

Nas porções norte, oeste e sul a lagoa é margeada por encostas com alturas médias de 300 metros, encoberta por vegetação de Mata Atlântica em estado avançado de regeneração, e a leste é separada do Oceano Atlântico por vegetação típica de restinga. Chuvas ocorrem ao longo de todo o ano e a precipitação média acumulada entre 1992 e 2011 foi de 1.629 mm por ano. Neste mesmo período a temperatura variou entre 12,0 e 27,3ºC (dados obtidos da estação meteorológica localizada no Aeroporto de Florianópolis, através do Instituto de Controle do Espaço Aéreo – ICEA). De acordo com o Instituto Nacional de Meteorologia, a normal climatológica de 1961-1990 foi 1.518 mm de precipitação média anual e a temperatura média anual foi 20,4ºC.

Estudos prévios têm mostrado que a lagoa é polimítica e apresenta homogeneidade espacial para clorofila-a e nutrientes e característica oligo-mesotrófica (Hennemann e Petrucio, 2011; Tonetta et al., 2013), mas que vem apresentando indícios de eutrofização incipiente, de acordo com análises do sedimento (Hennemann et al., 2015). Apresenta elevadas densidades de cianobactérias filamentosas, principalmente *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya e Subba-Raju, (Laudares-Silva, 1999; Silveira, 2013; Tonetta et al., 2013) e a comunidade de zooplâncton é composta predominantemente de rotíferos e cladóceros de pequeno tamanho (Gerzson, 2013). As taxas de produção primária planctônicas são menores que as taxas de respiração, em parte relacionadas à baixa capacidade fotossintética das cianobactérias e a limitação por luz e nutrientes (Tonetta et al., 2015).

Figura 2: Mapa batimétrico da Lagoa do Peri e a curva hipsográfica com a elevação da área do Parque Municipal da Lagoa do Peri. A letra A representa o riacho Cachoeira Grande e B representa o riacho Ribeirao Grande. P1, P2, P3 e P4 representam as estações de amostragem entre 2007 e 2015.

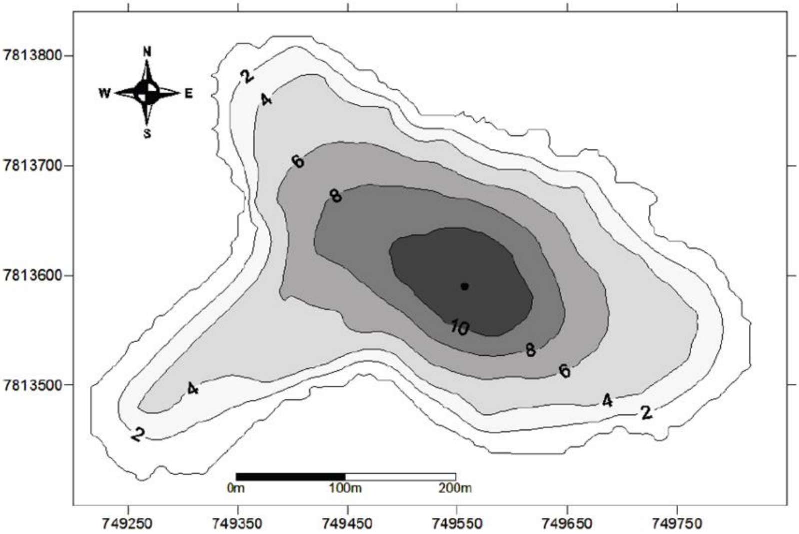


Fonte: Modificado de Fontes et al. (2015).

2.2 Lagoa Carioca

A Lagoa Carioca é uma lagoa oligo-mesotrófica tropical com área superficial de 0,14 km^2, volume de 671 mil metros cúbicos e profundidade máxima e média de 11,8 e 4,8 m, respectivamente (Figura 3; Bezerra-Neto et al., 2010). É uma lagoa considerada fechada, sem efluentes ou afluentes e protegida do vento pela vegetação, apresentando assim elevada estabilidade térmica. A lagoa é classificada como monomítica quente com curto período de circulação (junho a agosto) durante o inverno e apresenta-se estratificada no restante do ano (Henry e Barbosa, 1989; Petrucio et al., 2006). Durante o verão a concentração de clorofila é em média 5,5 µg/L (3,6 – 9,0 µg/L, mínima e máxima respectivamente), o fósforo total é de 5,9 µg/L (5,6 – 6,1 µg/L), o nitrogênio total é 259,0 µg/L (246,0 – 265,0 µg/L) e o carbono orgânico dissolvido é em média 6,1 mg/L, variando de 5,4 a 7,1 mg/L (Brighenti et al., 2015).

Figura 3: Mapa batimétrico com o ponto central indicando a profundidade máxima da Lagoa Carioca.



Fonte: Bezerra-Neto et al. (2010).

O clima da região é definido como tropical semi-úmido com duas estações bem definidas: seca e chuvosa. A estação seca (maio a setembro) apresenta baixas temperaturas (15ºC) e reduzida pluviosidade. A estação chuvosa (setembro a abril) apresenta altas temperaturas (30ºC) e alta pluviosidade, com 80% da precipitação ocorrendo geralmente no mês de janeiro. A pluviosidade média anual da região é de 1.480 mm e a temperatura média anual é de 21,9°C.

3 MATERIAL E MÉTODOS

3.1 Desenho amostral

Para cada capítulo desta tese foram desenvolvidos e executados desenhos amostrais específicos, para atender aos respectivos objetivos e hipóteses. Os desenhos amostrais envolveram medidas discretas em escala horária no primeiro capítulo, medidas de alta frequência, a cada 15 minutos no segundo capítulo, medidas mensais no terceiro capítulo e medidas diárias no quarto capítulo. A descrição detalhada de cada metodologia de coleta e análise está descrita em cada capítulo. Aqui estão apresentadas, em linhas gerais, as metodologias usadas nessa tese.

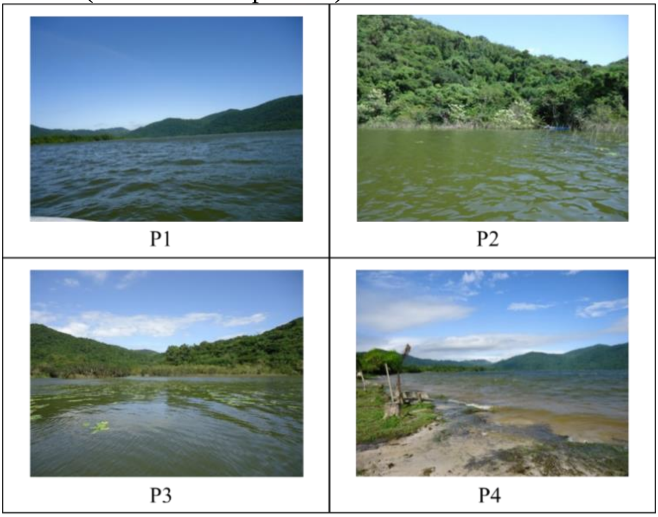
3.2 Monitoramento mensal dos parâmetros físico-químicos

Coletas mensais foram efetuadas ao longo de oito anos (2007 – 2015) na Lagoa do Peri, nas estações destacadas na Figura 2, e apresentadas na Figura 4. A estação P1 foi amostrada em quatro profundidades de acordo com a extinção da luz: 100% de luminosidade incidente (superfície), 10% de luminosidade (profundidade do desaparecimento visual do disco de Secchi), 1% de luminosidade (três vezes a profundidade do desaparecimento visual do disco de Secchi) e zona afótica. Nas estações P2, P3 e P4 as amostragens foram conduzidas na profundidade de 10% de luminosidade incidente.

Amostras de água foram usadas para determinação da alcalinidade, em que 50 mL da água do ambiente foi acidificada com ácido sulfúrico (0,01N), seguido por medições do pH com pHmetro com precisão de 0,01 unidades (Digimed DM-22), até o ponto final de 3,75 (Mackereth et al., 1978). Outras alíquotas foram coletadas para a determinação de fósforo e nitrogênio total (Valderrama, 1981). Volumes conhecidos de amostra foram filtrados a vácuo e os filtros (0.7 µm, Whatman GF/F) analizados para a determinação de clorofila-a de acordo com Lorenzen (1967). O filtrado foi usado para a determinação de nitrito (Golterman et al., 1978), nitrato (Mackereth et al., 1978), amônia (Koroleff, 1976), fósforo reativo solúvel (Strickland e Parsons, 1960) através de espectrofotometria; e o carbono orgânico dissolvido foi analisado através da combustão em alta temperatura da amostra acidificada (TOC-5000 Shimadzu analyzer).

Medidas de transparência da água, temperatura, oxigênio dissolvido, condutividade e pH foram feitas *in situ*, com sonda multiparâmetros. Os valores de precipitação, velocidade do vento e temperatura do ar foram fornecidos pelo ICEA e os dados de nível da água da Lagoa do Peri foram fornecidos pela CASAN.

Figura 4: Estações de amostragem: P1: área central com 7 m de profundidade; P2: desembocadura do riacho Cachoeira Grande com aproximadamente 3 m de profundidade; P3: desembocadura do riacho Ribeirão Grande com aproximadamente 2 m de profundidade; P4: região próxima à área de lazer com aproximadamente 1,5 m de profundidade. (Fotos: acervo pessoal).



Fonte: Acervo pessoal.

3.3 Estimativa da pressão parcial e do fluxo de CO_2

A concentração de CO_2 na água da Lagoa do Peri foi estimada a partir dos valores de pH e alcalinidade, de acordo com Stumm e Morgan (1996). Constantes de equilíbrio e especiação para o carbono inorgânico foram corrigidas para temperatura e a força iônica foi estimada a partir da condutividade elétrica (Snoeyink e Jenkins, 1980). O fluxo de CO_2 na interface água-ar foi estimado com base na equação 1 (Stumm e Morgan, 1996), que usa o coeficiente de transferência de gás (k), baseado na velocidade do vento (K); difusão química (β); e a diferença entre a concentração de CO_2 na superfície da água a na atmosfera (em µmol L^{-1}; Cole e Caraco, 1998). A pressão parcial do CO_2 (pCO_2) foi calculada a partir da constante da lei de Henry (K_H), com correções para temperatura e salinidade (Weiss, 1974):

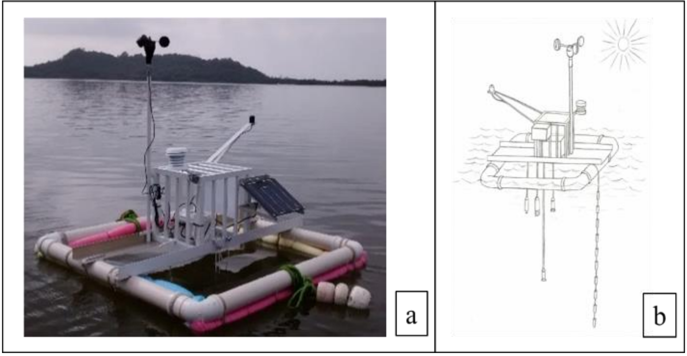
$$\mathbf{JCO_2(mol\ cm^{-2}h^{-1}) = K\,.\,\beta\,.\,([CO_{2(aq)}] - K_H\,.\,pCO_{2(air)})}\ \mathit{(1)}$$

Para os valores de equilíbrio do CO_2 com a atmosfera foram usados os dados obtidos do observatório de Mauna Loa, Hawaii (Dlugokencky e Tans, 2016), uma vez que para águas doces os fluxos calculados a partir do pH e alcalinidade são menos sensíveis às variações da pressão atmosférica do CO_2.

3.4 Monitoramento em alta frequência

Para as medidas de alta frequência, uma estação de monitoramento foi montada no ponto central da Lagoa do Peri, com profundidade total de 7 metros (Figura 5a).

Figura 5: Estação de monitoramento utilizada na amostragem de alta frequência das variáveis limnológicas e meteorológicas (a). Em b o desenho esquemático da disposição dos sensores no ar e na água.



Fonte: Foto: acervo pessoal e desenho: Mari e Clisten Staffen.

Sensores de temperatura da água e radiação ativa fotossinteticamente – PAR (UA-002 HOBO® ± 0.53°C) foram dispostos na subsuperfície, 0,5 m, 1,0 m, 1,5 m, 2,0 m, 3,0 m, 4,0 m, 5,0 m e 6,0 m de profundidade. Um sensor de oxigênio dissolvido (MiniDO$_2$T®), com precisão de ± 5% para o oxigênio dissolvido e ± 0,1ºC para a temperatura, foi colocado na subsuperfície da coluna d'água e outro a 1,0 m de profundidade (zona eufótica), juntamente com um sensor de pressão barométrica (U20-001 HOBO® ±0,3%). Outro sensor de oxigênio dissolvido foi colocado a 5,0 m (zona afótica; Figura 5b). No ar, foram instalados sensores para velocidade do vento (S-WSB-M003 HOBO® ±1,1m/s), PAR (S-LIA-M003 HOBO® ±5 $\mu mol/m^2/s$) e temperatura do ar (HOBO® ±0,2°C). Todos os sensores foram programados para fazer as medições a cada 15 minutos, durante 24 horas e sete dias por semana. Mensalmente os sensores foram limpos e os dados foram coletados. O intervalo sem medições, entre as coletas, e erros nas medições foram corrigidos através de verificação visual e gráfica, seguida por interpolação dos dados faltantes.

3.5 Estimativas da produção primária e respiração do ecossistema

As taxas de produção primária bruta (GPP), respiração (R) e produção líquida do ecossistema (NEP) foram calculadas de acordo com Obrador et al. (2014), a partir das medições de oxigênio dissolvido a cada 30 minutos, nas diferentes profundidades e expressas em mmol $O_2/m^3/h$. Este modelo inclui os processos biológicos de produção e consumo do oxigênio, trocas físicas entre a água e a atmosfera e entre as diferentes profundidades (equação 2), de acordo com a profundidade da camada de mistura e difusividade (Staehr et al., 2012b):

$$\frac{\mathbf{\Delta O_{2(i)}}}{\mathbf{\Delta t}} = \mathbf{NEP_{(i)}} + \mathbf{D_{z(i)}} - \mathbf{D_{v(i)}} - \mathbf{D_{s(i)}} \quad \textit{(2)}$$

As taxas do $NEP_{(i)}$ foram determinadas como a diferença entre $GPP_{(i)}$ e $R_{(i)}$ em cada profundidade amostrada (i), de acordo com a equação 3. Foi adotado o procedimento de modelagem inversa (Hanson et al., 2008), que calcula a NEP_i a partir da radiação fotossinteticamente ativa (PAR_i) e temperatura da água (T) em cada profundidade específica (i). O modelo inclui a resposta de saturação à PAR (primeiro termo da equação 3; Jassby e Platt, 1976), e a dependência da respiração em relação à temperatura (segundo termo da equação 3). PAR_i foi obtida de medidas contínuas na subsuperfície e do coeficiente de atenuação da luz na coluna d’água (K_d/m). P_{max} é a taxa fotossintética máxima (mmol $O_2/m^3/h$) na saturação luminosa, α é a eficiência fotossintética (mmol $O_2/m^3/h/[\mu mol\ photons/m^2/s]$). R$x$ é a taxa de respiração a xºC (mmol $O_2/m^3/h$), e θ é o coeficiente da dependência térmica da respiração, determinado como 1,07:

$$\mathbf{NEP_{(i)}} = \mathbf{P_{max}tanh}\left(\frac{\boldsymbol{\alpha}\mathbf{PAR_i}}{\mathbf{P_{max}}}\right) - \mathbf{R}_{\boldsymbol{x}}\boldsymbol{\theta}^{(\mathbf{T_i}-\boldsymbol{x})} \quad \textit{(3)}$$

O fluxo difusivo entre as camadas d’água (equação 4) influenciada pela profundidade da camada de mistura $D_{z(i)}$ foi calculada de acordo com Bell et al. (2006). A variação da profundidade da camada de mistura foi considerada em função do tempo ($\Delta Z_{mix}/\Delta t$) e a diferença na concentração de O_2 entre as profundidades em função da profundidade da camada da água (h):

$$\mathbf{D_z} = \frac{\mathbf{\Delta Z_{mix}}}{\mathbf{\Delta t}} \times \frac{(\mathbf{O_{2(i)}} - \mathbf{O_{2(i+1)}})}{\mathbf{h}} \quad (4)$$

O fluxo entre as camadas camadas d'água direcionada pela difusividade ($D_{v(i)}$; equação 5) foi estimada do coeficiente vertical de eddy difusividade (K_v; m^2/h; equação 6) descrito por Hondzo e Stefan (1993). Para esse cálculo foi considerado o volume e a área do lago ($V_{(i)}$; $A_{(i)}$), e o índice de Brunt-Väisälä ($N^2_{(i)}$):

$$\mathbf{D_{v(i)}} = [\frac{(\mathbf{K_{v(i)}} \times (\mathbf{O_{2(i)}} - \mathbf{O_{2(i-1)}}) + \mathbf{K_{v(i+1)}} \times (\mathbf{O_{2(i)}} - \mathbf{O_{2(i+1)}}))}{\mathbf{h}}] \times \frac{\mathbf{A_{(i)}}}{\mathbf{V_{(i)}}} \quad (5)$$

$$\mathbf{K_{v(i)}} = \mathbf{2.941 \times 10^{-3} (A_{(i)} \times 10^{-6})^{0.56} (N^2_{(i)})^{-0.43}} \quad (6)$$

A troca de gases entre a água e a atmosfera ($D_{s(i)}$; equação 7), foi calculada de acordo com Staehr et al. (2010). $O_{2(i)}$ é o oxigênio medido na água e $O_{2sat(i)}$ é a concentração em equilíbrio com a atmosfera. Ks é o coeficiente de troca gasosa para o O_2 e Z_{mix} na profundidade da camada de mistura (m), calculado em função da velocidade do vento e normalizado para o número de Schmidt (Sc600), de acordo com equações de aquecimento e resfriamento de MacIntyre et al. (2010).

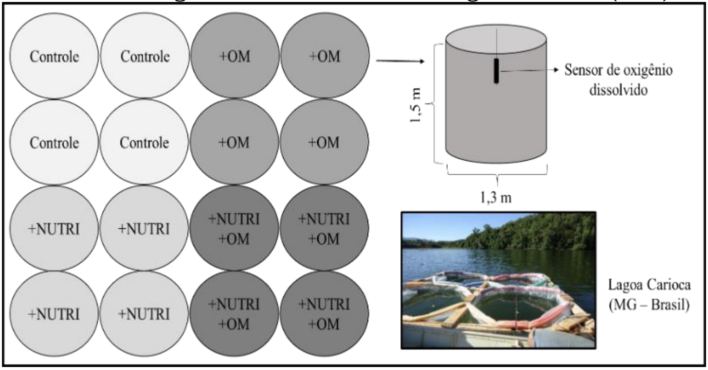
$$\mathbf{D_{s(i)}} = \frac{\mathbf{Ks(O_{2(i)} - O_{2sat(i)})}}{\mathbf{Z_{mix}}} \quad (7)$$

3.6 Experimento em mesocosmo

O experimento em mesocosmo foi desenvolvido na região pelágica da Lagoa Carioca (Figura 6). Os mesocosmos consistiram em sacos de polietileno de baixa densidade, transparentes, com ~ 1,5 m de profundidade, 1,30 m de diâmetro e cerca de 2000 litros de volume, fechados na parte inferior, e sem sedimento, e abertos na superfície para permitir as trocas gasosas entre a água e a atmosfera.

O controle consistiu de quatro mesocosmos com as concentrações de nutrientes e carbono orgânico naturais da lagoa, como segue: 0,06 ± 0,02 mg/L de nitrogênio inorgânico dissolvido (DIN = nitrato + nitrito + amônia); 6,70 ± 3,48 µg/L de fósforo reativo solúvel e 8,14 ± 0,37 mg/L de DOC. Para o tratamento +NUTRI quatro mesocosmos tiveram a adição de nutrientes inorgânicos ($NaNO_3$, K_2HPO_4 and NH_4Cl), resultando nas seguintes concentrações: 2,62 ± 0,17 mg/L de DIN; 156,38 ± 25,76 µg/L de fósforo reativo solúvel e 7,81 ± 0,20 mg/L de carbon orgânico dissolvido (DOC). Quatro mesocosmos tiveram adição de matéria orgânica extraída das folhas da mata próxima à lagoa (+OM) resultando em 0,06 ± 0,01 mg/L de DIN; 12,22 ± 0,92 µg/L de fósforo reativo solúvel e 8,59 ± 0,10 mg/L de DOC. Finalmente, quatro mesocosmos tiveram a adição de nutrientes e matéria orgânica (+NUTRI +OM) com o intuito de verificar o efeito combinado dessas adições, que resultaram em 2,57 ± 0,12 mg/L de DIN; 149,79 ± 36,90 µg/L de fósforo reativo solúvel e 8,60 ± 0,09 mg/L de DOC. No total foram 16 mesocosmos conduzidos durante nove dias, com início em 20 de janeiro de 2015.

Figura 6: Desenho esquemático das combinações testadas no experimento e a imagem do mesocosmo na Lagoa Carioca (MG).



Fonte: O autor.

Foram feitas medições diárias de CO_2 e O_2 em cada mesocosmo. Para os dados de oxigênio foram utilizados sensores MiniDO_2T® e para a $p$$CO_2$ foram feitas medidas diretas usando um analisador de gás infravermelho (IRGA – monitor de gás ambiental EDS EGM4), no qual as amostras foram coletadas através da técnica de headspace (Cole e Caraco, 1998). Amostras de água foram coletadas a cada três dias para análise de nutrientes dissolvidos através de cromatografia iônica (Metrohm 883 Basic IC), clorofila-a (Lorenzen, 1967) e carbono orgânico dissolvido (TOC analyzer Shimadzu 5000A). Medidas diárias de temperatura da água, turbidez, pH e condutividade foram feitas *in situ* com o uso de sonda multiparâmetros (Hydrolab DS5 Hach Inc.).

4 REFERÊNCIAS

Azam F. 1998. Microbial control of oceanic carbon flux: The plot thickens. Science 280:694-696.

Balmer MB, Downing JA. 2011. Carbon dioxide concentrations in eutrophic lakes: undersaturation implies atmospheric uptake. Inland Waters 1:125-132.

Bauer JE, Cai W-J, Raymond PA, Bianchi TS, Hopkinson CS, Regnier PAG. 2013. The changing carbon cycle of the coastal ocean. Nature 504:61-70.

Bell VA, George DG, Moore RJ, Parker J. 2006. Using a 1-D mixing model to simulate the vertical flux of heat and oxygen in a lake subject to mixing. Ecological Modelling 190:41-54.

Bezerra-Neto JF, Brighenti LS, Pinto-Coelho RM. 2010. A new morphometric study of Carioca Lake, Parque Estadual do Rio Doce (PERD), Minas Gerais State, Brazil. Acta Scientarum. Biological Sciences 32:49-54.

Brighenti LS, Staehr PA, Gagliardi LM, Brandão LPM, Elias EC, Mello NAST, Barbosa FAR, Bezerra-Neto JF. 2015. Seasonal changes in metabolic rates of two tropical lakes in the Atlantic Forest of Brazil. Ecosystems 18:589-604.

Brown JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. Ecology 85:1771-1789.

Cavalcanti JR, Motta-Marques D, Fragoso Jr CR. 2016. Process-based modeling of shallow lake metabolism: Spatio-temporal variability and relative importance of individual processes. Ecological Modelling 323:28-40.

Carpenter SR, Walker B, Anderies JM, Abel N. 2001. From metaphor to measurement: resilience of what to what? Ecosystems 4:765-781.

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 SF6. Limnology and Oceanography 43:647-656.

Cole JJ, Caraco NF. 2001. Carbon in catchments: connecting terrestrial carbon losses with aquatic metabolis. Marine and Freshwater Research 52:101-110.

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.

Couture R-M, Wit HA, Tominaga K, Kiuru P, Markelov I. 2015. Oxygen dynamics in a boreal lake responds to long-term changes in climate, ice phenology, and DOC inputs. Journal of Geophysical Research: Biogeosciences 120:2441-2456.

Dlugokencky E, Tans P. 2016. National Oceanic and Atmospheric Administration – NOAA/ESRL. <URL:http://www.esrl.noaa.gov/gmd/ccgg/trends/>.

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, Prairie YT, Cole JJ, Duarte CM, Tranvik LJ, Striegl RG, McDowell WH, Kortelainen P, Caraco NF, Melack JM. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnology and Oceanography 51:2388-2397.

Esteves FA. 2011. Fundamentos de Limnologia – 3ª Ed. Interciência.

Fontes MLS, Marotta H, MacIntyre S, Petrucio MM. 2015. Inter- and intra-annual variations of $p\mathrm{CO}_2$ and $p\mathrm{O}_2$ in a freshwater subtropical coastal lake. Inland waters 5:107-116.

Galindo-Leal C, Câmara IG. 2003. The Atlantic Forest of South America: Biodiversity status, threats, and outlook. Washington, Island Press.

Gerzson ND. 2013. Estrutura da comunidade zooplanctônica em uma lagoa costeira subtropical dominada por cianobactérias. Dissertação (mestrado) – Universidade Federal de Santa Catarina. 64p.

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

Grimm A, Ferraz SET, Gomes J. 1998. Precipitation anomalies in southern Brazil associated with El Niño and La Niña events. Journal of Climate 11:2863-2880.

Hall EK, Schoolmaster DR, Amado AM, Stets EG, Lennon JT, Domine LM, Cotner JB. 2015. Scaling relationships among drivers of aquatic respiration in temperate lakes: from the smallest to the largest freshwater ecosystems. Inland Waters 6:1-10.

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

Hanson PC, Carpenter SR, Kimura N, Wu C, Cornelius SP, Kratz TK. 2008. Evaluation of metabolism models for free-water dissolved oxygen methods in lakes. Limnology and Oceanography Methods 6:454-465.

Hennemann MC, Petrucio MM. 2011. Spatial and temporal dynamic of trophic relevant parameters in a subtropical coastal lagoon in Brazil. Environmental Monitoring and Assessment 181:347-361.

Hennemann MC, Simonassi JC, Petrucio MM. 2015. Paleolimnological record as an indication of incipient eutrophication in an oligotrophic subtropical coastal lake in Southern Brazil. Environmental Monitoring and Assessment 187:513.

Henry R, Barbosa FAR. 1989. Thermal structure, heat content and stability of two lakes in the National Park of Rio Doce Valley (Minas Gerais, Brazil). Hydrobiologia 171:189-199

Hoellein TJ, Bruesewitz DA, Richardson DC. 2013. Revisiting Odum (1956): A synthesis of aquatic ecosystem metabolism. Limnology and Oceanography 58:2089-2100.

Hondzo M, Stefan HG. 1993. Lake water temperature simulation model. Journal of Hydraulic Engineering 119:1251-1273.

Jassby AD, Platt T. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnology and Oceanography 21:540-547.

Jennings E, Jones S, Arvola L, Staehr PA, Gaiser E, Jones ID, Weathers KC, Weyhenmeyer GA, Chiu CY, Eyto E. 2012. Effects of weather-related episodic events in lakes: an analysis based on high-frequency data. Freshwater Biology 57:589-601.

Jiang Y, Hu Y, Schirmer M. 2013. Biogeochemical controls on daily cycling of hydrochemistry and $\delta^{13}C$ of dissolved inorganic carbon in a karst spring-fed pool. Journal of Hydrology 478:157-168.

Kerr RA. 2007. Global warming is changing the world. Science 316:188-190.

Klug, JL, Richardson DC, Ewing HA, Hargreaves BR, Samal NR, Vachon D, Pierson DC, Lindsey AM, O’Donnel DM, Effler SW, Weathers KC. 2012. Ecosystem effects of a tropical cyclone on a network of lakes in northeastern North America. Environ. Sci. Technol. 46:11693-11701.

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

Kosten S, Roland F, Motta Marques DML, Van Nes EH, Mazzeo N, Sternberg LSL, Scheffer M, Cole JJ. 2010. Climate-dependent CO_2 emissions from lakes. Global Biogeochemical Cycles 24:GB2007.

Laas A, Nõges P, Kõiv T, Nõges T. 2012. High-frequency metabolism study in a large and shallow temperate lake reveals seasonal switching between net autotrophy and net heterotrophy. Hydrobiologia 694:57-74.

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.

Lauster G, Hanson P, Kratz T. 2006. Gross primary production and respiration differences among littoral and pelagic habitats in northern Wisconsin lakes. Canadian Journal Fisheries Aquatic Sciences 63:1130-1141.

Lorenzen CJ. 1976. Determination of chlorophyll and pheopigments: Spectrophotometric equations. Limnology and Oceanography 12:343-346.

Lovett GM, Cole JJ, Pace M. 2006. Is net ecosystem production equal to ecosystem carbon accumulation? Ecosystems 9:1-4.

MacIntyre S, Jonsson A, Jansson M, Aberg J, Turney DE, Miller SD. 2010. Buoyancy flux, turbulence, and the gas transfer coefficient in a stratified lake. Geophysical Research Letters 37:L24604.

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

Marotta H, Duarte CM, Sobek S, Enrich-Prast A. 2009a. Large CO_2 disequilibria in tropical lakes. Global Biogeochemical Cycles 23 GB4022.

Marotta H, Paiva LP, Petrucio MM. 2009b. Changes in thermal and oxygen stratification pattern coupled to CO_2 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 $p\mathrm{CO}_2$ in Brazilian coastal lakes. Biogeosciences 7:1607-1614.

Marotta H, Ricci RMP, Sampaio PL, Melo PP, Enrich-Prast A. 2012a. Variações de curto prazo do metabolismo e da $p\mathrm{CO}_2$ na lagoa Rodrigo de Freitas: elevado dinamismo em um ecossistema tropical urbano. Oecologia Australis 16:391-407.

Marotta H, Fontes MLS, Petrucio MM. 2012b. Natural events of anoxia and low respiration index in oligotrophic lakes of the Atlantic Tropical Forest. Biogeosciences Discussion 9:4225-4244

Nimick DA, Gammons CH, Parker SR. 2011. Diel biogeochemical processes and their effect on the aqueous chemistry of streams: A review. Chemical Geology 283:3-17.

Obrador B, Staehr PA, Christensen JPC. 2014. Vertical patterns of metabolism in three contrasting stratified lakes. Limnology and Oceanography 59:1228-1240.

Odum HT. 1956. Primary production in flowing waters. Limnology and Oceanography 1:102-117.

Odum EP. 2013. Ecologia. Rio de Janeiro: Guanabara Koogan, 460p.

Pacheco FS, Roland F, Downing JA. 2013. Eutrophication reverses whole-lake carbon budgets. Inland Waters 4:41-48.

Palmer MA, van Dijken GL, Mitchell BG, Seegers BJ, Lowry KE, Mills MM, Arrigo KR. 2013. Light and nutrient control of photosynthesis in natural phytoplankton populations from the Chukchi and Beaufort seas, Artic Ocean. Limnology and Oceanography 58:2185-2205.

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

Pimm SL. 1984. The complexity and stability of ecosystems. Nature 5949:321-326.

Pinho L, Duarte CM, Marotta H, Enrich-Prast A. 2016. Temperature-dependence of the relationship between *p*CO_2 and dissolved organic carbono in lakes. Biogeosciences 13:865-871.

Raymond PA, Hartmann J, Lauerwald R, Sobek S, McDonald C, Hoover M, Butman D, Striegl R, Mayorga E, Humborg C, Kortelainen P, Durr H, Meybeck M, Ciais P, Guth P. 2013. Global carbon dioxide emissions from inland waters. Nature 503:355-359.

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142:1141-1153.

Sadro S, Nelson CE, Melack JM. 2011. Linking diel patterns in community respiration to bacterioplankton in an oligotrophic high-elevation lake. Limnology and Oceanography 56:540-550.

Silveira MH. 2013. Estrutura e dinâmica do fitoplâncton e fatores direcionadores da dominância anual de cianobactérias em uma lagoa rasa subtropical (lagoa do Peri, SC). Dissertação (mestrado) – Universidade Federal de Santa Catarina. 79p.

Snoeyink VL, Jenkins D. 1980. Water chemistry. Wiley, New York.

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. Limnology and Oceanography-Methods 8:628-644.

Staehr PA, Testa JM, Kemp WM, Cole JJ, Sand-Jensen K, Smith SV. 2012a. The metabolism of aquatic ecosystems: history, applications, and future challenges. Aquatic Sciences 74:15-29.

Staehr PA, Christensen JPA, Batt R, Read J. 2012b. Ecosystem metabolism in a stratified lake. Limnology and Oceanography 57:1317-1330.

Staehr PA, Baastrup-Spohr L, Sand-Jensen K, Stedmon C. 2012c. Lake metabolism scales with lake morphometry and catchment conditions. Aquatic Sciences 74:155-169.

Staehr PA, Brighenti LS, Honti M, Christensen J, Rose KC. Global patterns of light saturation and photo-inhibition of lake primary production. Inland waters. *In press*.

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.

They NH, Motta-Marques D, Souza RS. 2013. Lower respiration in the littoral zone of a subtropical shallow lake. Frontiers in Microbiology doi: 10.3389/fmicb.2012.00434.

Tonetta D, Petrucio MM, Laudares-Silva R. 2013. Temporal variation in phytoplankton community in a freshwater coastal lake of southern Brazil. Acta Limnologica Brasiliensia 25:99-110.

Tonetta D, Laudares-Silva R, Petrucio MM. 2015. Planktonic production and respiration in a subtropical lake dominated by cyanobacteria. Brazilian Journal of Biology 75:460-470.

Townsend CR, Begon M, Harper J. 2010. Fundamentos em Ecologia. 3ª edição. Artmed, Porto Alegre.

Tranvik LJ, et al. 2009. Lakes and reservoirs as regulators of carbon cycling and climate. Limnology and Oceanography 54:2298-2314.

Trolle D, Staehr PA, Davidson TA, Bjerring R, Lauridsen TL, Søndergaard M, Jeppesen E. 2012. Seasonal dynamics of CO_2 flux across the surface of shallow temperate lakes. Ecosystems 15:336-347.

Tsai JW, Kratz TK, Hanson PC, Wu JT, Chang WYB, Arzberger PW, Lin BS, Lin FP, Chou HM, Chiu CY. 2008. Seasonal dynamics, typhoons and the regulation of lake metabolism in a subtropical humic lake. Freshwater Biology 53:1929-1941.

Tsai JW, Kratz TK, Rusak JA, Shih WY, Liu WC, Tang SL, Chiu CY. 2016. Absence of winter and spring monsoon changes water level and rapidly shifts metabolism in a subtropical lake. Inland Waters 6:436-448.

Valderrama JC. 1981. The simultaneous analysis of total nitrogen and phosphorous in natural waters. Marine Chemistry 10:109-122.

Van de Bogert MC, Carpenter SR, Cole JJ, Pace ML. 2007. Assessing pelagic and benthic metabolism using free water measurements. Limnology and Oceanography-Methods 5:145-155.

Van de Bogert MC, Bade DL, Carpenter SR, Cole JJ, Pace ML, Hanson PC, Langman OC. 2012. Spatial heterogeneity strongly affects estimates of ecosystem metabolism in two north temperate lakes. Limnology and Oceanography 57:1689-1700.

Weathers KC, Strayer D, Likens GE. 2013. Fundamentals of Ecosystem Science. Elsevier.

Weiss RF. 1974. Carbon dioxide in water and seawater: The solubility of a non-ideal gas. Marine Chemistry 2:203-215.

5 CAPÍTULO 1

Linking summer conditions to CO_2 undersaturation and CO_2 influx in a subtropical coastal lake

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Lagoa do Peri após um período de chuvas intensas, em maio de 2010
Foto: acervo pessoal

5.1 Abstract

In this study, we tested the hypothesis that pCO_2 and air-water CO_2 fluxes in the surface waters of a subtropical lake vary on two time scales (diel and seasonally) and that CO_2 concentrations would decrease during the day and in summer. We estimated the variability of pCO_2 and the air-water CO_2 flux from pH-alkalinity in four 48-hour periods that were representative of each subtropical season. There was high variability in pCO_2 and the air-water gas flux over 48 hours, but there was no clear pattern between day and night. CO_2 concentrations showed a strong positive correlation with heterotrophic bacterial biomass and a negative correlation with dissolved organic carbon concentrations and water temperature. The lake was predominantly diel and seasonally CO_2 supersaturated; the highest CO_2 efflux was observed in the spring and a CO_2 influx was observed in summer. Our hypothesis was confirmed; pCO_2 was lowest in summer and during the daytime in spring and summer due to physical and biological conditions that favoured photosynthetic activities. These findings suggest that temporal shifts in the microbial community and meteorological variables, which are indirectly related to temperature, may be important drivers of CO_2 concentrations in Peri Lake. In conclusion, pCO_2 and the air-water CO_2 flux vary temporally (diel and seasonally) in the littoral zone of this subtropical coastal lake, with shifts between CO_2 influx and efflux throughout the sampling periods.

Keywords: bacterioplankton, gaseous exchanges, metabolism, heterotrophy.

5.2 Introduction

Inland waters are highly active sites of transport, transformation, and storage of considerable amounts of carbon from watersheds, making them important systems for carbon budget studies (Tranvik et al. 2009). Lakes are, in general, supersaturated with CO_2 in terms of equilibrium with the atmosphere (Cole et al. 1994; Sobek et al. 2005; Duarte and Prairie 2005). In recent years, tropical lakes have been considered major CO_2 sources to the atmosphere among global lakes (Kosten et al. 2010), with higher variability compared to non-tropical lakes (Marotta et al. 2009a). Myriad chemical and physical variables appear to drive this latitudinal CO_2 concentration and flux variability, except for temperature. These variables include the availability of dissolved organic carbon (DOC) to bacterial respiration (Del Giorgio et al. 1997; Cole et al. 2007), lateral transport of CO_2 (Marotta et al. 2010; Maberly et al. 2012), wind speed, and heat loss (Read et al. 2012). In addition, atmospheric circulation and rainfall patterns at a lake's geographic location (Fontes et al. 2015), lake size (Raymond et al. 2013), and nutrients (Pacheco et al. 2013) are related to increases in the concentration of CO_2 in ecosystems.

Because $p\mathrm{CO}_2$ values vary more in tropical lakes (Sobek et al. 2005; Marotta et al. 2009a), we would also expect a higher variability in subtropical lakes (i.e., lakes distributed between 23.4 and 30 degrees north and south) (Corlett 2013) compared to temperate and polar systems. Because the majority of time series studies are carried out in temperate lakes, studies in subtropical lakes are necessary to improve the global CO_2 efflux models. Seasonality in $p\mathrm{CO}_2$ and air-water CO_2 fluxes, for example, has been reported in temperate lakes, in which CO_2 influx often occurs in the summer (Pinardi et al. 2014; Sejr et al. 2014) and higher CO_2 emissions occur in winter (Trolle et al. 2012). Fontes et al. (2013) reported the highest CO_2 concentrations in the spring and the lowest levels in summer in Peri Lake, but no CO_2 flux was estimated. In their 6-year study, Fontes et al. (2015) estimated the CO_2 concentrations and fluxes to be related to rainfall events and wind mixing.

Metabolic processes in lakes are also known to vary over the course of the day; however, few studies have dealt with this variable. In general, the diel cycle of light and temperature affect biological activity and act on the regulation of metabolic processes, biogeochemical cycles and gas dynamics (Petrucio and Barbosa 2004; Nimick et al. 2011; Jiang et al. 2013). For example, community respiration is highest during the day through the first hours of the night and represents the response of bacterioplankton to labile dissolved organic carbon (Coffin et al. 1993, Petrucio and Barbosa 2004; Sadro et al. 2011). Biological-independent processes such as night-time cooling can also reflect higher air-water gas fluxes to the atmosphere at night (MacIntyre et al. 2010). However, a diel study carried out in Peri Lake in 2009-2010 reported no significant variations in CO_2, DOC concentrations, or bacterial abundance when comparing morning, afternoon and night hours (Fontes et al. 2013), but light and dark cycles were not explored by the authors. Although changes in temporal patterns have been studied for several decades, much less is known about the diel changes in aquatic metabolism in subtropical lakes (Marotta et al. 2012a), and recent approaches have estimated aquatic metabolism from continuous measurements of dissolved oxygen (Staehr and Sand-Jensen 2007).

In this regard, the present study relies on a combination of efforts: diel and seasonal distributions of $p\mathrm{CO}_2$ and air-water CO_2 fluxes in the water-atmosphere interface of Peri Lake, a subtropical lake, during the four climatic seasons of one year, with simultaneous measurements of meteorological and limnological variables. Our main hypothesis was that high pCO_2 and air-water CO_2 flux variability would be observed on two time scales (diel and seasonal) in Peri Lake and that pCO_2 and the efflux of CO_2 to the atmosphere would be lower during daylight on the diel time scale and lower during summer on the seasonal time scale.

5.3 Materials and methods

Study area

The study was conducted in Peri Lake, a subtropical coastal lake situated in the southern region of Florianópolis Island, Santa Catarina, Brazil (Figure 1). Peri Lake has a surface area of 507 ha, a maximum depth of 11 m and mean depth of 4 m; it is weakly stratified (Tonetta *in prep*.) and spatially homogeneous in terms of chlorophyll *a* and nutrients (Hennemann and Petrucio 2011; Tonetta et al. 2013). It is oligotrophic in nutrients (total phosphorous, 10 to 27 $\mu g\ L^{-1}$ and total nitrogen, 400 to 1000 $\mu g\ L^{-1}$) and meso-eutrophic in chlorophyll *a* (between 4 and 32 $\mu g\ L^{-1}$; Henneman and Petrucio 2011). Additionally, a cyanobacterial dominance of *Cylindrospermopsis raciborskii* has been recorded since 2009 (Tonetta et al. 2013).

Peri Lake has two main tributaries, Cachoeira Grande and Ribeirão Grande Streams; its watershed is within a conservation area for the Subtropical Atlantic Forest, and its water is used as a drinking water supply, providing water to approximately 17.2% of the population of Florianópolis Island. The weather in the area is characteristically subtropical, and summer months (January-March) are a slightly rainier than winter months (June-August) due to the influence of the South American Monsoon (Vera et al. 2006).

Sampling design

The sampling site was located at the littoral zone of Peri Lake at 27º43’S and 48º30’W (~1.0 m deep) and was free of aquatic vegetation. Subsurface water (~0.2 m deep) was sampled at 3-h intervals during the day and at 6-h intervals at night for a consecutive 48 hours, which resulted in 13 samples per season. This same design was repeated during the four annual climatic seasons (austral spring, summer, autumn and winter) as follows: 24-Oct-2009 (spring), 11-Mar-2010 (summer), 22-May-2010 (autumn) and 31-Jul-2010 (winter) (total n=52).

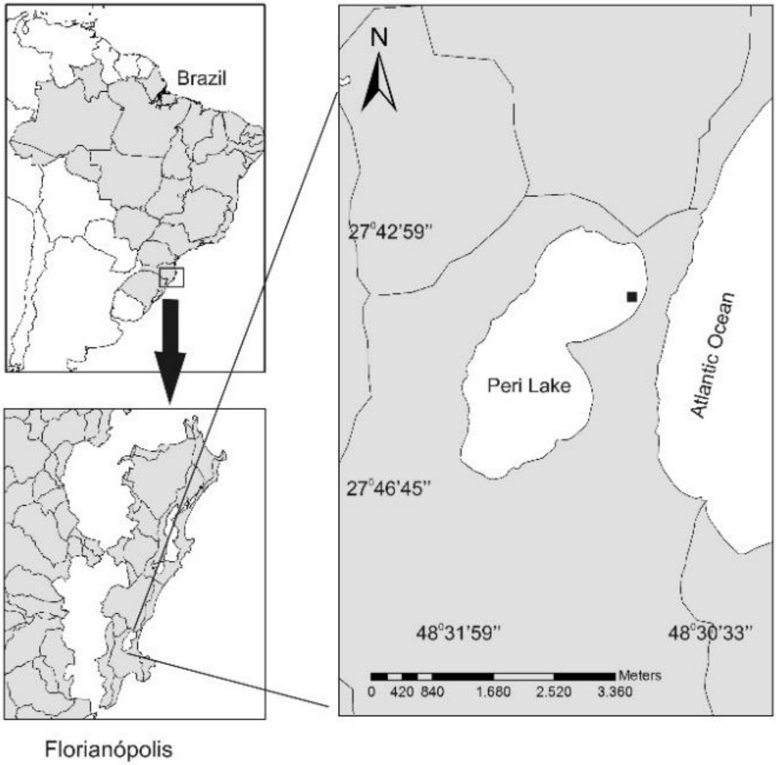

Figure 1: Peri Lake (Florianópolis City, Brazil) and the site sampled at the littoral zone.

Estimates of pCO_2 and air-water CO_2 flux

We estimated CO_2 concentration in water from pH and alkalinity measurements (Stumm and Morgan 1996). Equilibrium constant for inorganic carbon dissolution and speciation were corrected for temperature (Table 4.3 in Stumm and Morgan 1996), and ionic strength was estimated from conductivity, using the conversion factor from Russell (1976) in Snoeyink and Jenkins (1980), where ionic strength is ~1.6×10^{-5} specific conductivity (µS cm^{-1}). CO_2 flux across air-water interface was estimated based on the diffusive model of Stumm and Morgan (1996):

J_{CO2}(mol cm^{-2} h^{-1}) = $k \cdot \beta \cdot ([CO_{2(aq)}] - K_H \cdot pCO_{2(air)})$, that uses the gas transfer coefficient (k) based on wind speed (k=2.07+(0.215x$U^{1.7}$)), the chemical enhancement of diffusion (β), and the difference between the equilibrium and ambient CO_2 concentrations in surface water in µmol L^{-1} (Cole and Caraco 1998), which occurs at high pH and low wind speeds (Wanninkhof and Knox 1996). pCO_2 was calculated from the Henry's law constant (K_H) with appropriate adjustments for temperature and salinity (Weiss 1974), considering equilibrium with an atmosphere of 384 µatm in October/2009, 391 µatm in March/2010, 393 µatm in May/2010 and 390 µatm in July/2010 (Data from Mauna Loa Observatory, NOAA webpage – Tans, 2013). The model selection to estimate gas exchange can create uncertainty about interpretation of the results because the gas exchange across the air-water interface is largely independent of both wind speed and system size (Cole and Caraco 1998; Vachon and Prairie 2013).

Limnological variables recorded *in situ* included water temperature, salinity, conductivity and dissolved oxygen using a calibrated multiparameter probe (model YSI-85). Meteorological variables obtained *in situ* were air temperature (estimated using a mercury thermometer), wind speed (estimated using an anemometer – Instrutherm TAD 500), and photosynthetically active radiation (PAR, measured with a Li-Cor 250A radiometer with a spherical sensor). Rainfall was obtained from the REDEMET/Florianópolis (Rede de Meteorologia do Comando da Aeronáutica – Aeroporto de Florianópolis/ Hercílio Luz, SC), which is located near Peri Lake, and we calculated the accumulated rainfall back to seven days prior to sampling.

pH and alkalinity were analysed immediately after sampling in the laboratory located at Peri Lake. pH was measured with a pH meter (model Digimed DM-22) with a precision of 0.01, and alkalinity was determined by Gran titration. Filtration was also carried out in the laboratory, and samples were frozen at -20°C for posterior nutrient analyses. Dissolved organic carbon (DOC) was measured in filtered (Whatman GF/F) and acidified water samples using a high-temperature catalytic oxidation method on a Shimadzu TOC-5000 analyser (Shimadzu Scientific Instruments, Kyoto, Japan). The remaining filtered water was then used to determine soluble reactive phosphorus (SRP; Strickland and Parsons, 1960), nitrite (Golterman et al. 1978), nitrate (Mackereth et al. 1978) and ammonia (Koroleff 1976), which were summed and considered as dissolved inorganic nitrogen (DIN).

Filters (Whatman GF/F) were used to analyse chlorophyll *a* concentrations by extraction with 90% acetone (Lorenzen 1967). For the determination of heterotrophic bacterial biomass (HB), samples were fixed with para-formaldehyde and filtered onto 0.2 µm polycarbonate membrane filters. Bacterial cells were counted under epifluorescence microscopy following the Porter and Feig (1980) method. The heterotrophic bacterial density was converted into heterotrophic bacterial biomass by first calculating the individual cells' biovolume according to Massana et al. (1997) and then applying the algorithm proposed by Norland (1993) that estimates the total amount of carbon per μm^3 and consequently by cell (fg C $cell^{-1}$).

Statistical methods

We tested all variables (meteorological and limnological) for differences among the four seasons of the year (spring, summer, autumn and winter) using the analysis of variance (ANOVA) test. When $p<0.05$, Tukey's post-hoc test was used to determine which period differed. A t-test was used to verify differences between day (from 6:00 to 18:00 h) and night (from 18:00 to 6:00 h). Correlations between pCO_2 and meteorological and limnological variables, as well as between the air-water CO_2 flux and all variables, were assessed by Pearson correlation analysis. Because pCO_2 and CO_2 flux are estimated from pH and alkalinity, these variables were omitted from the analysis. Empirical models for the variation in pCO_2 were analysed by multiple regression analysis, in which the most influential variables were sought via a forward stepwise multiple linear regression with a variable retention criterion of $p=0.05$. All data were log(x+1)-transformed, and all analyses were performed in SPSS Statistics 19.0 (IBM Corp., NY).

5.4 Results

Meteorological and limnological variables

The highest air temperature was observed in summer, 29ºC, while in spring and autumn, it was approximately 21ºC; in winter, it decreased to 12ºC (Figure 2a). We observed a similar pattern of water temperature, in which the maximum and minimum temperatures were 28ºC in summer and 15ºC in winter, respectively (Figure 2b). Additionally, there was diel variability in water temperature, with night-time cooling of the surface waters (Figure 2b). All detailed results regarding the meteorological and limnological variables can be assessed in Table 1 of the electronic supplementary material.

The subsurface PAR exhibited strong variation among the sampling periods, which can be explained by the meteorological variables – the 7-day accumulated rainfall and wind speed prior to sampling (Table 1). Maximum PAR was measured in summer (970 $\mu mol\ m^{-2}\ s^{-1}$) and winter (900 $\mu mol\ m^{-2}\ s^{-1}$), both at midday (Figure 2c).

However, daytime averages were 297 µmol m^{-2} s^{-1} in summer, 192 µmol m^{-2} s^{-1} in spring, 174 µmol m^{-2} s^{-1} in winter, and 125 µmol m^{-2} s^{-1} in autumn.

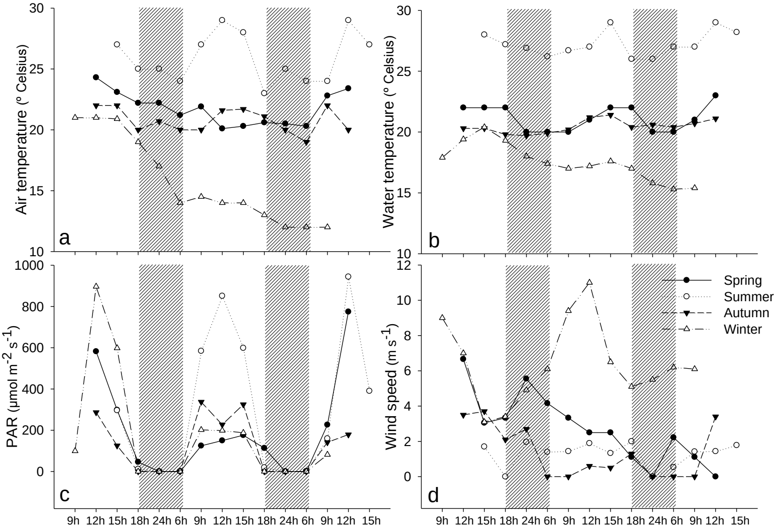

Figure 2: Air and water temperatures (a, b), photosynthetic active radiation (PAR) at subsurface (c), and wind speed (d) measured during two consecutive days (48 hours) in spring, summer, autumn and winter in Peri Lake. Striped areas represent nighttime sampling.

Wind speed also varied strongly throughout the 48 h period, especially in winter when it oscillated between 3 and 11.5 m s^{-1}, averaging 6.4 m s^{-1}. In summer, wind speed was lower, with a maximum of 2.0 m s^{-1} (Figure 2d). Accumulated rainfall showed that summer (170 mm) and autumn (182 mm) were the wetter periods compared to spring (0.7 mm) and winter (0.4 mm) (Table 1).

Dissolved oxygen was higher in winter and spring (Figure 3f), whereas pH was lower in those same periods (Table 1). Soluble reactive phosphorus (SRP) was low in all periods, typical of oligotrophic lakes, while chlorophyll *a* (Figure 3e) was consistent with that of meso-eutrophic lakes. The highest nutrient concentrations occurred in autumn (5 µg L^{-1} of SRP and 45.4 µg L^{-1} of DIN; Figures 3a and b), whereas the highest DOC concentration was registered in the summer (9.0 mg L^{-1}; Figure 3c). All variables (meteorological and limnological) except for PAR varied significantly among the seasons (spring, summer, autumn, winter; $p<0.05$), but no significant difference was observed on the diel scale ($p>0.05$), except for air temperature ($p<0.05$) (PAR was not included in the diel tests).

Table 1: Accumulated rainfall and limnological variables recorded in Peri Lake during four seasons (spring, summer, autumn, winter).

	Spring (min-max)	Summer (min-max)	Autumn (min-max)	Winter (min-max)
Accum. rainfall (mm)*	0.7	170.0	182.1	0.4
pH	6.4 ± 0.11^{a}	7.6 ± 0.24^{c}	7.1 ± 0.12^{b}	7.1 ± 0.07^{b}
	(6.3-6.6)	(7.2-7.9)	(7.0-7.3)	(7.0-7.3)
Alkalinity (mEq L^{-1})	0.04 ± 0.004^{a}	0.13 ± 0.012^{b}	0.11 ± 0.003^{b}	0.13 ± 0.021^{b}
	(0.029-0.044)	(0.112-0.147)	(0.105-0.115)	(0.113-0.193)
Conductivity (µS cm^{-1})	62.7 ± 1.65^{b}	76.6 ± 1.75^{d}	67.9 ± 0.76^{c}	59.5 ± 3.95^{a}
	(60.3-65.9)	(72.5-78.7)	(66.6-69.8)	(55.9-69.7)

* Absolute values for seven-days of accumulated rainfall prior the sampling. Other variables are average ± standard deviation, minimum and maximum values. Similar lowercase letters represent the homogeneous groups after Tukey's post-hoc test for seasons ($p<0.05$).

The heterotrophic bacterial biomass (Figure 3d) was lower in the summer (average: 51.5 µg C L^{-1}), and higher in winter and spring, where averages were 189.4 µg C L^{-1} and 185.4 µg C L^{-1}, respectively ($p<0.05$). The chlorophyll *a* concentration oscillated between 2 and 11.5 µg L^{-1} and was lower in spring/autumn than in summer/winter (Figure 3e; $p<0.05$).

pCO$_2$ and air-water CO$_2$ flux

pCO$_2$ varied significantly among the four seasons ($p<0.05$), with values below atmospheric equilibrium only in summer (269 ± 120.3 µatm; Figure 4a). In the other seasons, pCO$_2$ was above the atmospheric values, with the highest average in spring (889 ± 203.4 µatm). Autumn and winter were similar, with values oscillating between 473 ± 118.8 µatm in autumn, and 476 ± 106.4 µatm in winter.

Regarding the diel cycle, pCO$_2$ averaged 867.0 µatm in the daytime versus 979.3 µatm at night in spring; 250.7 and 309.1 µatm, respectively, in summer; 474.4 and 471.6 µatm in autumn; and 494.5 and 453.8 µatm in winter. Although spring and summer had slightly more pCO$_2$ at night compared to during the day, no significant difference between day and night was observed ($p>0.05$). The overall air-water CO$_2$ flux was predominantly positive, and the highest efflux occurred in spring (0.67 ± 0.317 mmol m^{-2} h^{-1}), followed by winter (0.36 ± 0.479 mmol m^{-2} h^{-1}) and autumn (0.11 ± 0.133 mmol m^{-2} h^{-1}; Figure

4b; $p<0.05$). Summer measurements suggested a CO_2 sink because a negative flux was recorded (-0.16 ± 0.191 mmol m^{-2} h^{-1}) coupled with high chlorophyll *a* (Figure 3e), higher light availability (Figure 2c) and lower biomass of heterotrophic bacterioplankton (Figure 3d). Detailed results are in Table 1 of the electronic supplementary material.

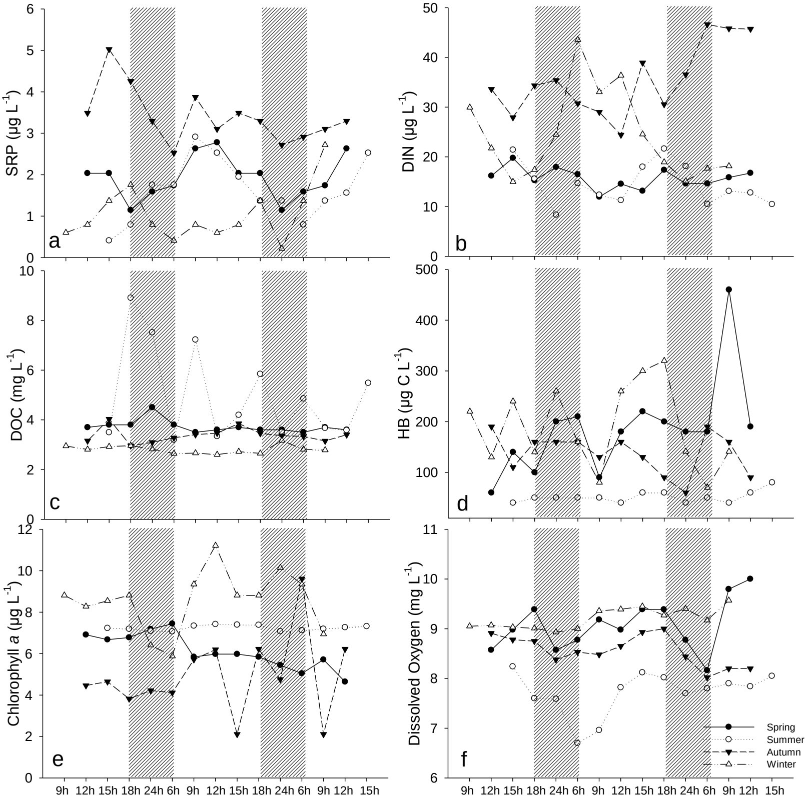

Figure 3: Diel variation of (a) soluble reactive phosphorus (SRP), (b) dissolved inorganic nitrogen (DIN), (c) dissolved organic carbon (DOC), (d) heterotrophic bacterial biomass (HB), (e) chlorophyll *a*, and (f) dissolved oxygen; during 48 hours in spring, summer, autumn and winter. Striped areas represent nighttime sampling.

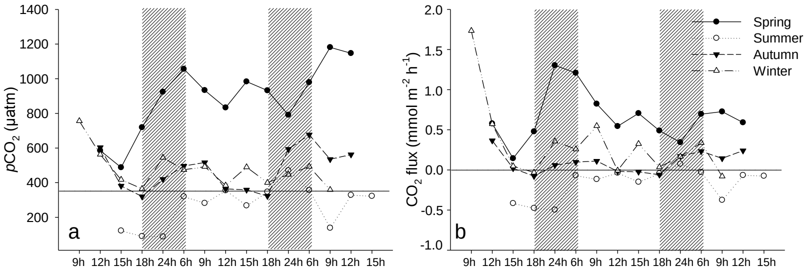

Figure 4: Diel variation of pCO$_2$ (a) and CO$_2$ fluxes across air–water interface (b) during 48 hours in spring, summer, autumn and winter in Peri Lake. Striped areas represent nighttime sampling.

During the 48-hour samplings, air-water CO$_2$ fluxes were higher at night in the spring (0.89 mmol m^{-2} h^{-1} at night versus 0.56 mmol m^{-2} h^{-1} during the day) coupled to a high biomass of heterotrophic bacterioplankton (Figure 3d). In summer, CO$_2$ fluxes were negative (-0.20 mmol m^{-2} h^{-1} during the day and -0.13 mmol m^{-2} h^{-1} at night). In other seasons, CO$_2$ fluxes were slightly smaller at night (autumn: 0.12 mmol m^{-2} h^{-1} during the day and 0.07 mmol m^{-2} h^{-1} at night; winter: 0.45 mmol m^{-2} h^{-1} during the day and 0.19 mmol m^{-2} h^{-1} at night). However, due to the high diel variability, no significant difference was observed for CO$_2$ fluxes between day and night ($p>0.05$).

Table 2: Pearson correlation performed with pCO$_2$ and CO$_2$ flux as dependent variables, and meteorological and limnological as independent variables.

	WT	PAR	Cond	Wind	DO	DIN	SRP	DOC	Chla	HB
pCO$_2$	-0.46*	-0.00	-0.55*	0.11	0.54*	0.14	0.13	-0.44*	-0.15	0.62*
CO$_2$ flux	-0.50*	0.00	-0.53*	0.34*	0.52*	0.12	-0.04	-0.41*	-0.00	0.57*

Abbreviations: WT: water temperature; PAR: photosynthetically active radiation; Cond: conductivity; Wind: wind mean speed; DO: dissolved oxygen; DIN: dissolved inorganic nitrogen; SRP: soluble reactive phosphorus; DOC: dissolved organic carbon; Chla: chlorophyll *a*; HB: heterotrophic bacterial biomass. * represents significant correlations ($p<0.05$, $n=52$). Analysis was performed on log(x+1)-transformed data.

pCO$_2$ and air-water gas flux were positively correlated with dissolved oxygen and bacterioplankton biomass (Table 2), whereas water temperature, conductivity and DOC were negatively correlated with pCO$_2$ and the CO$_2$ flux. Wind was positively correlated with the CO$_2$ flux because it is used to estimate the flux, but it can also be related to the cooling of surface waters, which indirectly affects the gas exchange at the air/water interface (Table 2). The relationship between heterotrophic bacterial biomass and DOC with pCO$_2$ was confirmed by the stepwise multiple regression analysis (Table 3), with both variables explaining 42% of the model of pCO$_2$ variability.

Table 3: Stepwise multiple linear regression analysis for pCO$_2$. $F_{(4,47)}=10.337$ $p<0.001$. Standard error of estimate: 0.18920 (n= 52). Adjusted $r^2=0.42$.

Dependent variable	Explaining variable	Coefficient	*t* value	*P*
pCO$_2$	Intercept	2.439112	5.17970	<0.001
	HB	0.502716	4.54992	<0.001
	DOC	-0.821785	-2.29545	<0.05

HB: heterotrophic bacterial biomass; DOC: dissolved organic carbon. Analysis was performed on log(x+1)-transformed data. Only parameters that fulfilled the required significance of $p<0.05$ are shown.

5.5 Discussion

The main finding of this study was that, in general, CO$_2$ concentrations in Peri Lake tended to increase at night and decrease in the summer due to its limnological and meteorological characteristics, resulting in undersaturated pCO$_2$ and CO$_2$ influx in this season. Our results also highlighted the importance of the inverse relationship between heterotrophic bacterioplankton and organic carbon, which contribute to the CO$_2$ variability in Peri Lake. Therefore, the high variability recorded in both pCO$_2$ and air-water CO$_2$ flux over 48 hours cannot be ignored, as it can create misunderstandings or an underestimation of metabolic rates in lakes.

The diel variability in bacterial production dependent on primary production is well known, with increasing values during the day until the first hours of the night when they start to decrease to minimum values (Petrucio and Barbosa 2004; Panzenbock 2007). This dependence is due to the labile DOC releases by photoautotrophs during the day, resulting in decreased respiration at night and a minimum at dusk when DOC becomes limiting to heterotrophic bacteria (Sadro et al. 2011). In

Peri Lake, we observed a distinctive diel pattern in spring/summer compared to winter/autumn, in which $p\mathrm{CO}_2$ was clearly lower during the day in spring and summer. Prokaryotes dominate phytoplankton in Peri Lake, with filamentous cyanobacteria (primarily *Cylindrospermopsis raciborskii*) comprising more than 90% of the total phytoplankton abundance in the lake year round, even at 6 m depth (Tonetta et al. 2013). The optimal growth of *C. raciborskii* is 25-30°C (Briand et al. 2004; Chonudomkul et al. 2004), and one would therefore expect higher CO_2 fixation at this temperature, which is often in summer.

Peri Lake is predominantly CO_2 supersaturated (Tonetta et al. *in press*; Fontes et al. 2015; and this study) with at least one period of influx (summer). The $p\mathrm{CO}_2$ concentrations and CO_2 flux can also be regulated by meteorological factors such as turbulence in the water column caused by advection or wind shear (MacIntyre et al. 2010; Read et al. 2012). The complex interactions among all of the possible driving factors are better explained when long time series studies are maintained. In a 6-year study, Fontes et al. (2015) observed that peaks in $p\mathrm{CO}_2$ were related to rainfall events and that the highest values were observed in the transition periods of spring/summer to autumn/winter, and vice-versa. However, the periods of higher rainfall investigated in this study were not enough to explain peaks in $p\mathrm{CO}_2$.

Concentrations of CO_2 in the surface waters of Peri Lake may have increased from a deepening of the mixed layer or from sediments via physical processes (such as wind and convection), without changing the rates of respiration in the water column (Marotta et al. 2009b; Marotta et al. 2012b; Marotta et al. 2014). Thus, turbulence is important to potentially increasing $p\mathrm{CO}_2$ in surface waters and consequently fluxes to the atmosphere. Horizontal transfer of CO_2 from western streams to the east side of the lake by the larger wind fetch can be another source to the littoral zone. The opposite, undersaturation of surface $p\mathrm{CO}_2$, can be related to higher stabilization of the water column and decreased fluxes (MacIntyre et al. 2010) that are caused by surface heating, which is more common in summer and retards the intrusions of CO_2 from the bottom waters or sediments to the surface. In this way, temperature can also have an indirect relationship with CO_2 by influencing the water stratification dynamics, as shown by Fontes et al. (2015), who observed a weak stratification in the summer. In other seasons, CO_2-enriched waters are most likely brought up from the bottom to the surface.

Over the four seasons, we observed a predominant CO_2 efflux related to a higher biomass of heterotrophic bacterioplankton, indicating that their biomass can also be added to the surface by turbulence. A smaller bacterial biomass in the summer can be explained by stabilization of the water column and increasing competition for nutrients with phytoplankton (Fontes and Abreu 2009). In Peri Lake, higher PAR, chlorophyll *a* and DOC in the summer, summed to a higher abundance of filamentous cyanobacteria (Fontes et al. 2013; Tonetta et al. 2013), reinforced the existence of competition among microbes in the lake.

In conclusion, undersaturation and CO_2 influx was observed only in the summer. This was likely related to the summer conditions of higher water stratification and light incidence. The diel patterns in the CO_2 flux and pCO_2 in Peri Lake are similar to those found in northern temperate systems. A switch from predominantly atmospheric CO_2 emissions during most of the seasons to an atmospheric CO_2 sink in the summer, as observed in Peri Lake, has also been reported in other lakes (Fan et al. 2005; Xing et al. 2005; Trolle et al. 2012). Our results highlight the importance of heterotrophic bacterial biomass to pCO_2 variability in the oligotrophic Peri Lake, the necessity for further studies on diel and seasonal variability of pCO_2 concentrations associated with physical mechanisms of water column mixing and the integration of sediment-water interface incubations in lakes.

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5.6 References

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? Journal of Phycology 40:231-238

Chonudomkul D, Yongmanitchal W, Theeragool G, Kawachi M, Kasal F, Kaya K, Watanabe M (2004) Morphology, genetic diversity, temperature tolerance and toxicity of *Cylindrospermopsis raciborskii*

(Nostocales, Cyanobacteria) strains from Thailand and Japan. FEMS Microbiology Ecology 48:345-355

Coffin RB, Connolly JP, Harris PS (1993) Availability of dissolved organic-carbon to bacterioplankton examined by oxygen utilization. Marine Ecology Progress Series 101:9-22, doi:10.3354/meps101009

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 SF6. Limnology and Oceanography 43:647-656

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

Corlett RT. 2013. Where are the Subtropics? Biotropica 45:273-275

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

Duarte CM, Prairie YT (2005) Prevalence of heterotrophy and atmospheric CO_2 emissions from aquatic ecosystems. Ecosystems 8:862-870

Fan C, Hu W, Ford P, Chen Y, Qu W, Zhang L (2005) Carbon dioxide partial pressure and carbon fluxes of air-water interface in Taihu Lake, China. Chinese Journal of Oceanology and Limnology 23:29-38

Fontes MLS, Abreu P (2009) Spatio-temporal variation of bacterial assemblages in a shallow subtropical coastal lagoon in Southern Brazil. Microbial Ecology 58:140-152

Fontes MLS, Tonetta D, Dalpaz L, Antônio RV, Petrucio MM (2013) Dynamics of planktonic prokaryotes and dissolved carbon in a subtropical coastal lake. Frontiers in Microbiology. doi: 10.3389/fmicb.2013.00071

Fontes MLS, Marotta H, MacIntyre S, Petrucio MM (2015) Inter- and intra-annual variations of pCO_2 and pO_2 in a freshwater subtropical coastal lake. Inland waters 5:107-116

Golterman HL, Clymo RS, Ohnstad MAM (1978) Methods for physical and chemical analysis of freshwater. Blackwell Science, Oxford

Hennemann MC, Petrucio MM (2011) Spatial and temporal dynamic of trophic relevant parameters in a subtropical coastal lagoon in Brazil. Environmental Monitoring and Assessment 181:347-361

Jiang Y, Hu Y, Schirmer M (2013) Biogeochemical controls on daily cycling of hydrochemistry and δ13C of dissolved inorganic carbon in a karst spring-fed pool. Journal of Hydrology 478:157-168

Koroleff F (1976) Determination of nutrients. In Grasshoff K (ed) Methods of sea water analysis. Verlag Chemie Weinhein, pp 117-181

Kosten S, Roland F, Motta Marques DML, Van Nes EH, Mazzeo N, Sternberg LSL, Scheffer M, Cole JJ (2010) Climate-dependent CO_2 emissions from lakes. Global Biogeochemical Cycles 24:GB2007

Lorenzen CJ (1967) Determination of chlorophyll and pheopigments: Spectrophotometric equations. Limnology and Oceanography 12:343-346

Maberly SC, Barker PA, Stott AW, De Ville MM (2012) Catchment productivity controls CO_2 emissions from lakes. Nature Climate Change 3:391-394

MacIntyre S, Jonsson A, Jansson M, Aberg J, Turney DE, Miller SD (2010) Buoyancy flux, turbulence, and the gas transfer coefficient in a stratified lake. Geophysical Research Letters 37:L24604

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

Marotta H, Duarte CM, Sobek S, Enrich-Prast A (2009a) Large CO_2 disequilibria in tropical lakes. Global Biogeochemical Cycles 23:GB4022

Marotta H, Paiva LP, Petrucio MM (2009b) Changes in thermal and oxygen stratification pattern coupled to CO_2 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_2 in Brazilian coastal lakes. Biogeosciences 7:1607-1614

Marotta H, Ricci RMP, Sampaio PL, Melo PP, Enrich-Prast A (2012a) Variações em curto prazo do metabolismo e da pCO_2 na lagoa Rodrigo de Freitas: elevado dinamismo em um ecossistema tropical urbano. Oecologia Australis 16:391-407

Marotta H, Fontes MLS, Petrucio MM (2012b) Natural events of anoxia and low respiration index in oligotrophic lakes of the Atlantic Tropical Forest. Biogeosciences Discussion 9:4225-4244

Marotta H, Pinho L, Gudasz C, Bastviken D, Tranvik LJ, Enrich-Prast A (2014) Greenhouse gas production in low-latitude lake sediments responds strongly to warming. Nature Climate Change doi:10.1038/nclimate2222

Massana R, Gasol JM, Bjornsen PK, Blackburn N, Hagstrom A, Hietanen S, Hygum BH, Kuparinen J, Pedrós-Alió C (1997) Measurement of bacterial size via image analysis of epifluorescence preparations: description of an inexpensive system and solutions to some of the most common problems. Scientia Marina 61:397-407

Nimick DA, Gammons CH, Parker SR (2011) Diel biogeochemical processes and their effect on the aqueous chemistry of streams: A review. Chemical Geology 283:3-17

Norland S (1993) The relationship between biomass and volume of bacteria. In Kemp PF, Sherr BF, Sherr EB, Cole JJ. Handbook of methods in aquatic microbial ecology. Lewis pp 303-307

Pacheco FS, Roland F, Downing JA (2013) Eutrophication reverses whole-lake carbon budgets. Inland Waters, 4:41-48

Panzenbock M (2007) Effect of solar radiation on photosynthetic extracellular carbon release and its microbial utilization in alpine and Arctic lakes. Aquatic Microbial Ecology 48:155-168

Petrucio MM, Barbosa FAR (2004) Diel variations of phytoplankton and bacterioplankton production rates in four tropical lakes in the middle Rio Doce basin (southeastern Brazil). Hydrobiologia 513:71-76

Pinardi M, Rosseto M, Viaroli P, Bartoli M (2014) Daily and seasonal variability of CO_2 saturation and evasion in a free flowing and in a dammed river reach. Journal of Limnology 73:468-481

Porter KG, Feig YS (1980) The use of DAPI for identifying and counting aquatic microflora. Limnology and Oceanography 25:943-948

Raymond PA, Hartmann J, Lauerwald R et al. (2013) Global carbon dioxide emissions from inland waters. Nature 503:355-359

Read JS, Hamilton DP, Desai AR, Rose KC, MacIntyre S, Lenters JD, Smyth RL, Hanson PC, Cole JJ, Staehr PA, Rusak JA, Pierson DC, Brookes JD, Laas A, Wu CH (2012) Lake-size dependency of wind shear and convection as controls on gas exchange. Geophysical Research Letters 39: L09405

Sadro S, Nelson CE, Melack JM (2011) Linking diel patterns in community respiration to bacteriplankton in an oligotrophic high-elevation lake. Limnology and Oceanography 56:540-550

Sejr MK, Krause-Jensen D, Dalsgaard T, Ruiz-Halpern S, Duarte CM, Middelboe M, Glud RN, Bendtsen J, Balsby TJS, Rysgaard S (2014) Seasonal dynamics of autotrophic and heterotrophic plankton metabolism and PCO_2 in a subarctic Greenland fjord. Limnology and Oceanography 59:1764-1778

Staehr PA, Sand-Jensen K (2007) Temporal dynamics and regulation of lake metabolism. Limnology and Oceanography 52:108-120

Snoeyink VL, Jenkins D (1980) Water chemistry. Wiley, New York

Sobek S, Tranvik L, Cole, JJ (2005) Temperature independence of carbon dioxide supersaturation in global lakes. Global Biogeochemical Cycles 19: GB2003 doi:10.1029/2004GB002264

Strickland JDH, Parsons TR (1960) A manual of seawater analysis. Bulletin. Fisheries Research Board of Canada 125:1-18

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

Tans P (2013) National Oceanic and Atmospheric Administration. <URL:http://www.esrl.noaa.gov/gmd/ccgg/trends/>. Accessed 20 August 2013

Tonetta D, Petrucio MM, Laudares-Silva R (2013) Temporal variation in phytoplankton community in a freshwater coastal lake of southern Brazil. Acta Limnologica Brasiliensia 25:99-110

Tonetta D, Laudares-Silva R, Petrucio MM (i*n press*) Planktonic production and respiration in a subtropical lake dominated by cyanobacteria. Brazilian Journal of Biology.

Tranvik LJ, Downing JA, Cotner JB et al. (2009) Lakes and reservoirs as regulators of carbon cycling and climate. Limnology and Oceanography 54: 2298-2314.

Trolle D, Staehr PA, Davidson TA, Bjerring R, Lauridsen TL, Søndergaard M, Jeppesen E (2012) Seasonal dynamics of CO_2 flux across the surface of shallow temperate lakes. Ecosystems 15:336-347

Vachon D, Prairie YT (2013) The ecosystem size and shape dependence of gas transfer velocity versus wind speed relationships in lakes. Canadian Journal of Fisheries and Aquatic Sciences 70:1757-1764

Vera C, Higgins W, Amador J et al. (2006) Toward a Unified View of the American Monsoon Systems. Journal of Climate 19:4977-5000

Wanninkhof R, Knox M (1996) Chemical enhancement of CO_2 exchange in natural waters. Limnology and Oceanography 41:689-697

Weiss RF (1974) Carbon dioxide in water and seawater: The solubility of a non-ideal gas. Marine Chemistry 2:203-215

Xing YP, Xie P, Yang H, Ni LY, Wang YS, Rong KW (2005) Methane and carbon dioxide fluxes from a shallow hypereutrophic subtropical lake in China. Atmospheric Environment 39:5532-5540

Electronic supplementary material

Table 1 SM: Meteorological and limnological variables recorded in Peri Lake during two consecutive days in spring, summer, autumn and winter.

	Spring	Summer	Autumn	Winter
Accumulated rainfall (mm)*	0.7	170.0	182.1	0.4
Air temperature (ºC)	21.8 ± 1.38^{b} (20.1-24.3)	25.9 ± 2.02^{c} (23.0-29.0)	20.8 ± 1.01^{b} (19.0-22.0)	15.7 ± 3.59^{a} (12.0-21.0)
PAR (μmol m^{-2} s^{-1})	191.6 ± 238.98^{b} (0.0-774.5)	296.6 ± 345.99^{c} (0.0-944.0)	124.7 ± 134.88^{a} (0.0-337.2)	174.1 ± 273.79^{b} (0.0-896.6)
Wind (m s^{-1})	2.7 ± 1.97^{b} (0.0-6.7)	1.3 ± 0.69^{a} (0.0-2.0)	1.4 ± 1.50^{a} (0.0-3.7)	6.4 ± 2.28^{c} (3.1-11.0)
$p\mathrm{CO}_2$ (μatm)	888.7 ± 203.43^{c} (487.9-1181.3)	268.7 ± 120.30^{a} (88.8-470.5)	473.1 ± 118.82^{b} (320.3-676.7)	475.7 ± 106.40^{b} (359.1-755.9)
CO_2 flux (mmol m^{-2} h^{-1})	0.7 ± 0.32^{c} (0.1-1.3)	-0.2 ± 0.19^{a} (-0.5-0.1)	0.1 ± 0.13^{b} (-0.1-0.4)	0.3 ± 0.47^{b} (-0.1-1.7)
Water temperature (ºC)	21.2 ± 1.07^{b} (20.0-23.0)	27.2 ± 1.02^{c} (26.0-29.0)	20.5 ± 0.53^{b} (19.7-21.4)	17.5 ± 1.54^{a} (15.3-20.4)
pH	6.4 ± 0.11^{a} (6.3-6.6)	7.6 ± 0.24^{c} (7.2-7.9)	7.1 ± 0.12^{b} (7.0-7.3)	7.1 ± 0.07^{b} (7.0-7.3)
Alkalinity (mEq L^{-1})	0.04 ± 0.004^{a} (0.029-0.044)	0.13 ± 0.012^{b} (0.112-0.147)	0.11 ± 0.003^{b} (0.105-0.115)	0.13 ± 0.021^{b} (0.113-0.193)
Conductivity (μS cm^{-1})	62.7 ± 1.65^{a} (60.3-65.9)	76.6 ± 1.75^{c} (72.5-78.7)	67.9 ± 0.76^{b} (66.6-69.8)	59.5 ± 3.95^{a} (55.9-69.7)
Dissolved Oxygen (mg L^{-1})	9.1 ± 0.52^{b} (8.2-10.0)	7.7 ± 0.44^{a} (6.7-8.2)	8.6 ± 0.31^{a} (8.0-9.0)	9.2 ± 0.21^{b} (8.9-9.6)
Dissolved Inorganic Nitrogen (μg L^{-1})	15.7 ± 2.05^{b} (12.0-19.8)	14.5 ± 4.23^{a} (8.3-21.6)	35.4 ± 7.20^{d} (24.4-46.6)	24.3 ± 8.94^{c} (15.0-43.5)
Soluble Reactive Phosphorus (μg L^{-1})	1.9 ± 0.52^{a} (1.1-2.8)	1.6 ± 0.73^{a} (0.4-2.9)	3.4 ± 0.66^{b} (2.5-5.0)	1.0 ± 0.67^{a} (0.2-2.7)

Dissolved Organic Carbon (mg L^{-1})	3.7±0.26^{b} (3.5-4.5)	5.0±1.88^{b} (3.2-8.9)	3.4±0.29^{b} (3.0-4.0)	2.8±0.16^{a} (2.6-3.2)
Chlorophyll *a* (µg L^{-1})	6.1±0.84^{a} (4.6-7.4)	7.2±0.13^{b} (7.1-7.4)	4.9±1.96^{a} (2.1-9.6)	8.6±1.46^{b} (5.9-11.2)
Heterotrophic Biomass (µg Carbon L^{-1})	185.4±96.58^{b} (60.0-460.0)	51.5±11.44^{a} (40.0-80.0)	137.7±40.24^{b} (60.0-190.0)	189.4±81.90^{b} (70.0-320.0)

*Absolute values for seven-days of accumulated rainfall prior to sampling.

Other variables are average ± standard deviation, minimum and maximum values during 48 hours (n= 13 per season). Further details in Materials and methods section.

Similar lowercase letters represent the homogeneous groups after Tukey's post-hoc test for four seasons ($p<0.05$).

6 CAPÍTULO 2

Physical conditions driving the spatial and temporal variability in aquatic metabolism of a subtropical coastal lake

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Lagoa do Peri após um período de ausência de chuvas, em maio de 2012
Foto: acervo pessoal

6.1 Abstract

We investigated the importance of meteorological and lake physical conditions for temporal, horizontal and vertical differences in the concentration of dissolved oxygen (DO) and water temperature, and the derived daily estimates of gross primary production (GPP), ecosystem respiration (R) and net ecosystem production (NEP). Our study was conducted in a subtropical and polymictic lake in Southern Brazil, during a spring-summer transition. Metabolic rates were determined from two sites using the open water oxygen technique. At the central deep site, oxygen sondes were deployed at three depths to assess patterns in vertical variability. During 10 days, an additional DO and temperature sonde was placed near the shoreline allowing us to compare metabolic differences in the surface layers between the central pelagic and littoral site. While GPP was similar, R was significantly higher at the shallower littoral site, causing NEP to be lower, although NEP was still positive. The littoral site had less diel changes in DO and higher daily variability in all metabolic rates. Variability in GPP and R at the littoral site was related to temperature, wind speed and rainfall suggesting that short-term variability in metabolic rates in shallow areas are sensitive to resuspension of sediments caused by a less stable water column. A clear vertical gradient was furthermore found for the metabolic rates at the central deep part of the lake, related to the light extinction, with highest GPP around 0.3 m and decreasing with depth, while respiration showed the inverse pattern. Below subsurface, respiration prevailed at 5.0 m depth and was uncoupled to primary production. Under conditions with high light and temperature, and low wind speeds, the mixing depth became shallower, in turn increasing the water column stability at the deep pelagic site, which resulted in higher mean light available and higher GPP in the water column. Our results confirm that deployment of sensors in different sites and depths allows for spatially, as well as temporally more representative estimates of lake metabolism.

Keywords: Spatial heterogeneity; Daily variability; Stratification; Primary production; Respiration; Water column stability; High frequency

6.2 Introduction

Dissolved oxygen (DO) is used to determine ecosystem metabolism, which is an integrated descriptor of the production and degradation of organic matter in lakes (Del Giorgio et al., 1999;

Carignan et al., 2000; Cole and Caraco, 2001). The balance between gross primary production (GPP) and ecosystem respiration (R) results in the net ecosystem production (NEP = GPP – R), defining the environment as net autotrophic, when NEP is positive, or net heterotrophic, when NEP is negative (Cole et al., 2007; Staehr et al., 2010a; 2012a). The respiratory part of carbon cycling in lakes is greatly dependent on organic matter produced by primary producers, which in turn are sustained by inorganic matter mineralized by heterotrophic. This makes the GPP and R highly interdependent and well-correlated in aquatic systems (Cole et al., 2000). In eutrophic lakes, GPP and R are generally strongly correlated, since the organic matter from autotrophic production sustains the respiration rates. On the other hand, in oligotrophic lakes, the GPP is low and respiration typically depends on external inputs of organic matter (Hanson et al., 2003). In this way, the coupling between GPP and R depends on many external and internal variables from lakes, and the inputs from terrestrial environment and sediment can exert high influence in respiration, making the processes less coupled (Solomon et al., 2013). In recent years, several improvements have been made to estimate metabolic rates (Staehr et al., 2010a). The high frequency measurements of DO in free-water has brought new insights and understandings about the spatial and temporal variability in the aquatic ecosystems (Laas et al., 2012; Staehr et al., 2012b).

Many variables have been related to the spatial and temporal variability of the metabolic processes (Van de Bogert et al., 2012). Oxygen dynamics in lakes are under the influence of different benthic substrate types, wind speed and direction, presence of macrophytes, inputs from streams, and the surrounding terrestrial vegetation, which may affect the distribution of nutrients and organisms in the water column, consequently influencing the spatial heterogeneity (Laas et al., 2012; Muduli et al., 2012; They et al., 2013). Wind, light and temperature are associated to the vertical distribution of nutrients and organisms in water column (Serra et al., 2007). Littoral areas, in general shallower and protected by hills, can exhibit different gaseous flux dynamics (Cole and Caraco, 1998; Vachon et al., 2010) and generally are more influenced by benthic processes, terrestrial inputs and macrophytes than pelagic waters (Lauster et al., 2006; Staehr et al., 2012c). Rainfall events can promote increase in organic matter into lakes from terrestrial sources, leading to high respiration rates, especially at littoral waters, in turn promoting CO_2 efflux to the atmosphere (Rantakari and Kortelainen, 2005; Fontes et al., 2015).

Consequently, higher spatial heterogeneity and temporal variability are expected at littoral areas (Obrador and Petrus, 2013).

On a daily basis, temperature and light have a strong variation and influence the biological activity, consequently in the biogeochemical process (MacIntyre et al., 2010; Nimick et al., 2011; Jiang et al., 2013), and therefore daily changes in DO (Hanson et al., 2006). Shallow areas are more susceptive to this short-term variability since the low depth and proximity of sediments has a strong effect on water column conditions. In a study during 48 hours in a subtropical lake, Tonetta et al. (2015a) have recorded that the daily CO_2 dynamics was highly variable and related to organic carbon availability and bacterioplankton, but no spatial variation was studied by the authors. In another shallow subtropical lake, however, They et al. (2013) found spatial variability between pelagic and littoral areas, where lower respiration rates were recorded at littoral areas, related to the macrophytes presence. In this way, more studies in subtropical areas are needed to fill the gaps of this knowledge and to understand how both spatial and temporal variation are related to physical conditions in shallow subtropical lakes.

Significant vertical variability in DO and metabolic rates may occur in lakes where thermal stratification and mixing events influence the vertical transport of DO, nutrients and organisms in the water column (Lewis, 2010; Obrador et al., 2014). In stratified lakes, nutrients and organic matter are concentrated in the deepest part of the lakes, while light availability is high at the shallowest part (Sadro et al., 2011; Coloso et al., 2011). Consequently, net autotrophy occurs in the photic zone, net heterotrophy in the layers below the photic depth, and the metalimnion can be net auto- or heterotrophic depending on physical and limnological conditions (Staehr et al., 2012b). However, vertical patterns are very sensitive to short-term physical forcing influencing availability of inorganic, organic resources and light, as well as vertical and horizontal gas-exchanges (Staehr et al., 2010a). In a recent study from stratified tropical lakes, Brighenti et al. (2015) showed that metabolic rates were higher during the full mixing than during the stratified period. On the other hand, studies in temperate lakes have shown reduced rates of GPP and R during full mixing (Staehr et al., 2012b) and prevalence of heterotrophy when become stratified (Obrador et al., 2014).

In shallow lakes, vertical stratification can occur frequently, depending upon the balance between temperature driven gradient differences and mixing by wind (Rueda and Schladow, 2009). Peri

Lake, considered a shallow subtropical lake, under high seasonal variability, has a distinctive pattern of short-lived stratification. This ephemeral type of stratification and water column mixing may occur within hours, causing upwelling of waters rich in nutrients and organic matter, or just inorganic sediment and sand particles. Deployment of sensor recording DO at different depths and different places in a lake, makes possible to evaluate the importance of such ephemeral events on rates of primary production and respiration, thus providing more representative estimates of lake metabolism.

In this study, we estimated the GPP, R and NEP rates in a subtropical coastal lake at two sites (littoral and pelagic) to assess the horizontal variability, and in three depths at the pelagic site (subsurface, 1.0 m and 5.0 m depth) to assess the vertical variability, as well as the temporal variability. The aim of this study was to investigate the degree of spatial variability in volumetric metabolic rates in both pelagic and littoral sites. Furthermore, we evaluate how meteorological and lake physical conditions (rainfall, temperature, wind speed, light availability, and water stability), are related with metabolic variability, during a short period in spring-summer transition. We hypothesize that diel changes in DO and related rates of GPP will be highest near the surface, and decrease with depth as levels of light and temperature decreases and becomes less variable. In addition, we expect that GPP and R will be strongly coupled at subsurface and uncoupled at bottom waters, where R will prevail due to low light conditions. Finally, we expect that higher metabolic rates and higher day-to-day variability will occur at the shallower littoral site due to greater influence of sediment resuspension and respiration, and inputs of organic matter from the nearby terrestrial environment, resulting in uncoupled relation between GPP and R.

6.3 Material and Methods

Study site

This study was conducted in Peri Lake (27°44'S and 48°31'W), Southern Brazil. Peri Lake is a freshwater coastal lake, area of 5.07 km^2, average depth ~ 4 m, and maximum depth ~ 11 m, in a protected area of the Secondary Atlantic Rainforest, with a restricted human occupation. The lake is the main freshwater resource on the Santa Catarina Island (Figure 1), and it is characterized by macrophytes presence in southern littoral of the lake, where are located the two main tributaries (Cachoeira Grande and Ribeirão Grande Streams).

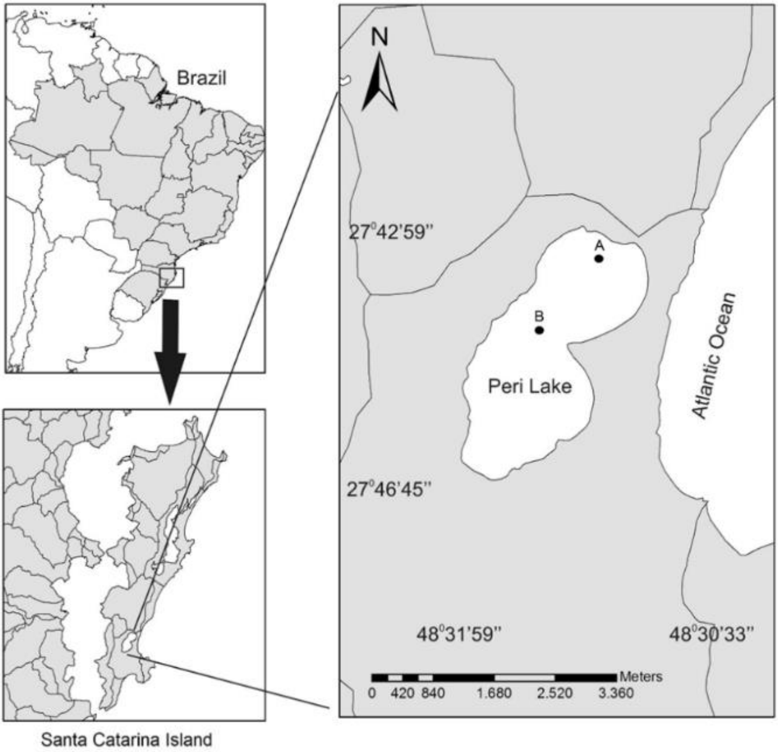

Figure 1: Location of the Peri Lake, Santa Catarina Island, Brazil. The letter A represents the littoral station, with 2.0 m depth, and the letter B represents the pelagic station sampled, with 7.0 m depth. Adapted from Fontes et al. (2013).

Important changes in Peri Lake have been recorded in recent years, as result of decrease in rainfall and water level (Fuentes and Petrucio, 2015). The chlorophyll *a*, mostly composed by filamentous cyanobacteria – *Cylindrospermopsis raciborskii*, and the $p\text{CO}_2$ have increased and water transparency has decreased, but, dissolved nutrients remain in low levels (Hennemann et al., unpublished data). Additionally, a long-term study has shown a slight difference between littoral and pelagic sites to some variables, e.g higher dissolved organic carbon, lower chlorophyll *a* and $p\text{CO}_2$ at littoral areas (Tonetta et al., unpublished data). During our study (October, 2014 – January, 2015), the lake had total phosphorus and nitrogen around 11.0 µg L^{-1} and 0.9

mg L^{-1}, respectively, water transparency ~ 1.0 m, and chlorophyll *a* around 20.9 µg L^{-1}. Dissolved organic carbon concentration was around 6.0 mg L^{-1}, and higher concentration was recorded in November/14 (10.9 mg L^{-1}).

Study design

Continuous measurements of water temperature and DO in free-water were made with MiniDO2T loggers® during 84 days in spring-summer transition at 10-15 min intervals, from October 22, 2014 to January 13, 2015. Loggers were placed at three depths (subsurface, 1.0 m and 5.0 m depth), at the pelagic – central point of the lake, with 7.0 m total depth (Letter B, Figure 1). We will refer to subsurface, to the sondes placed just under the surface, around ~ 0.3 m depth, in both pelagic and littoral sites. During 10 days, November 08-17, 2014, one additional logger was deployed at subsurface (~ 0.2 – 0.3 m) of the littoral site, with 2.0 m total depth (Letter A, Figure 1). Wind speed and air temperature were measured at 15 min intervals at the central part of the lake.

Underwater light conditions were measured at subsurface, 1 and 2 m depth, using underwater HOBO® light sensors. Photosynthetic active radiation (PAR) measurements in lux units were converted to µmol photons m^{-2} s^{-1} (Sager and McFarlane, 1997), to estimate the daily vertical light attenuation coefficient (K_d), the mean daily available light (E_{mean}) in the upper mixed layer, and the photic zone depth (Z_{eu}).

Additionally, temperature measurements at the central part, from HOBO® loggers placed at subsurface, 1, 2, 3, 4 and 5.0 m depth were used to calculate the water column stability index (N^2) and depth of the upper mixed layer (Z_{mix}). Light and DO loggers were cleaned and downloaded approximately every 25 days and no biofilm accumulation was observed.

Meteorological and lake physical conditions

The daily vertical light attenuation coefficient (K_d m^{-1}) was determined as the slope of a linear regression model of natural logarithm of irradiance (E_z, 400 – 700 nm) versus depth (z) as $\ln(E_z) = b + K_d\ z$. We calculated the K_d daily mean using measurements every 15 min, between 12:00 and 13:00 h, where slopes from regression with $R^2 < 0.8$ were excluded. The depth of the photic zone (Z_{eu}) was calculated for each day as 4.6 divided by K_d.

The mean daily available light at the upper mixed layer (E_{mean}, mol photons m^{-2} d^{-1}) was estimated according to Staehr and Sand-Jensen

(2007), as: $E_{mean} = \frac{E_0\,(1-\beta)(1-e^{-KdZmix})}{(KdZmix)}$, where E_0 is the mean daily light available at the surface, β is a constant (0.1), K_d is the vertical light attenuation coefficient, and Z_{mix} is the depth of epilimnion.

We assessed the water column stability index (N^2) each 30 min, from a temperature profile, by using the Brunt-Väisälä buoyancy frequency, which indicates the stratification strength (Read et al., 2011). The Z_{mix} depth was also determined at 30 min intervals, where Z_{mix} corresponds to the depth of epilimnion, which means the shallowest depth with a water-density gradient equal to or above a suitable threshold ~ 0.03 kg m^{-3} m^{-1} (Staehr et al., 2012b). Daily rainfall and air temperature were obtained from Instituto de Controle do Espaço Aéreo (ICEA), located 7 km away from the lake.

Metabolic rates

Data treatment prior to metabolism calculations included simple linear interpolation to correct the readings between intervals of downloaded data, to fix the outliers, and to obtain all variables every 30 min, followed by a temporal smoothing of the time series at each depth through a running average of 4 h.

We estimated gross primary production (GPP), respiration (R) and net ecosystem production (NEP) for each depth according Obrador et al. (2014), which includes biological fluxes, air-water gas exchange and DO exchange between depth layers driven by mixed-layer deepening and eddy diffusivity (Staehr et al., 2012b). The model assumes that the DO change between two consecutive time steps, in a given depth layer (i), as described by Eq. (1):

$\frac{\Delta O_{2(i)}}{\Delta t} = NEP_i + D_{z(i)} - D_{v(i)} - D_{s(i)}$ (Eq. 1); where NEP_i is the net ecosystem production, $D_{z(i)}$ is the flux between layers driven by mixed-layer deepening, $D_{v(i)}$ is the flux between layers driven by eddy diffusivity, and $D_{s(i)}$ is the air-water gas exchange, all expressed in mmol O_2 m^{-3} h^{-1}.

Metabolic rates were calculated using an inverse modeling procedure (Hanson et al., 2008), which calculates NEP_i from photosynthetically active radiation (PAR_i) and temperature at each specific depth i. The model includes a saturating response of photosynthesis to PAR (Jassby and Platt, 1976) and a thermo-dependent respiration, as described by Eq. (2):

$NEP_i = P_{max}\tanh\left(\frac{\alpha PAR_i}{P_{max}}\right) - R_{30}\theta^{(T_i-30)}$ (Eq. 2); where P_{max} is the maximum photosynthetic rate at saturating light (mmol O_2 m^{-3} h^{-1}), α is the photosynthetic efficiency (mmol O_2 m^{-3} h^{-1} [µmol photons m^{-2} s^{-1}]$^{-1}$), R_{30} is the respiration rate at 30ºC (mmol O_2 m^{-3} h^{-1}), and θ is a coefficient that stands for the thermal dependence of respiration (set to 1.07). PAR_i was obtained from continuous subsurface PAR measurements and from the light-attenuation coefficient in the water column (K_d m^{-1}). The first term in Eq. 2 corresponds to gross primary production (GPP_i, mmol O_2 m^{-3} h^{-1}), which is dependent of the light, and the second to ecosystem respiration (R_i, mmol O_2 m^{-3} h^{-1}), which is dependent of the temperature, for each depth layer. NEP was calculated as the daily difference between GPP and R (NEP = GPP – R, using positive values to R). Further details in Obrador et al. (2014).

A model combining Eqs. (1) and (2) was fitted to the DO data for 24 h periods using a numerical minimization algorithm in the non-linear function in the Statistical Analysis System (SAS) software. Thus, by fitting the model to the observed DO time series at each depth, we obtained, for every 24 h and every depth layer, estimates of the parameters P_{max}, α, and R_{30}. We calculated hourly metabolic rates for each depth (i; NEP_i, GPP_i, and R_i, in mmol O_2 m^{-3} h^{-1}) by applying the parameters. The daily metabolic rates (in mmol O_2 m^{-3} d^{-1}) were calculated as the average hourly rates multiplied by 24 h. To the littoral site, we applied the same approach, using the Z_{mix}, light and wind conditions from the central part of the lake, but considering the total depth as 2 m.

We assessed how the predicted DO fit to observed DO data through the coefficient of determination (R^2). Days with $R^2 < 0.4$ were excluded from further analyses, as visual inspections of daily DO time plots showed these to be noisy, unrelated to diel patterns in light and temperature condition and with a poor match between predicted and measured DO values, implying a strong influence by non-biological processes not included in our model (Eq. 1). For the 84 days of this study, 92% of the days at subsurface satisfied the model requirements, 87% at 1.0 m depth, and just 56% at 5.0 m depth. The excluded days were replaced by interpolation from two days before and two days after, when they did not represent more than 20% of variation among these days. The metabolic rates are showed as weekly mean and standard deviation, however we omitted the metabolic rates from week 42, at 5.0 m depth, because the R^2 between the predicted DO and observed DO values, were < 0.4 and we did not have previous days to compare the variability. Respiration rates are shown as negative values to ease interpretation, and for the statistical analysis, R values were considered positive.

Limnological conditions

We took water samples monthly at four depths (subsurface, 1.0 m, 3.0 m and 5.0 m depth), at central part of the lake, and filtered in Whatman GF/F for analysis of nitrite (Golterman et al., 1978), nitrate (Mackereth et al., 1978) and ammonia (Koroleff, 1976), which were summed and considered as dissolved inorganic nitrogen (DIN). Soluble reactive phosphorus (SRP) was determined according to Strickland and Parsons (1960), and dissolved organic carbon (DOC) in TOC analyzer (Shimadzu TOC-5000A). Chlorophyll *a* (chla) was extracted with 80% ethanol, corrected for pheophytin (Lorenzen, 1967).

Data analysis

We used the repeated measurements analysis of variance (RM_ANOVA) to identify significant difference in metabolic rates (GPP, R and NEP) among depths and sites, considering the successive sampled days, followed by Bonferroni t-test ($p<0.05$). To identify significant difference in limnological conditions among depths we used analysis of variance (ANOVA). If there was a significant difference among depths ($p<0.05$), Tukey's post-hoc test was used to determine which depth was different.

Pearson correlation analyses was performed between daily metabolic rates (GPP, NEP and R) and physical conditions over the course of 10 days to the littoral site and 84 days to the pelagic site, considering only the subsurface rates, to identify how these variables affect the metabolism at both sites. The physical conditions considered were water temperature, wind speed, rainfall, light (PAR, E_{mean} and Z_{eu}), Z_{mix}, and N^2. To achieve the requirement for parametric tests (normal distribution and equally of variances) all data were log(x+1)-transformed.

We fitted linear regression models to each depth and site, to describe the coupling between R and GPP from R^2 values, and to determine the background respiration level from intercept on the y-axis. We used the analysis of covariance (ANCOVA) to test differences in slopes among regression lines, from the three depths sampled at the pelagic site. All statistical tests were performed using the R Development Core Team (2011).

6.4 Results

Meteorological and lake physical conditions

During the studied period (October 22, 2014 to January 13, 2015), the environmental conditions were within the typical range of spring and summer in subtropical areas. Wind speed was on average 3.8 m s^{-1} (Figure 2a); air temperature was around 24ºC (17.9 – 35.5ºC), and the accumulated rainfall during 84 days was 212.9 mm. The high average light attenuation (K_d = 1.13 m^{-1}) caused a strong vertical gradient in light, from on average, 74 µmol photons m^{-2} s^{-1} at subsurface, to on average, 24 µmol photons m^{-2} s^{-1} at 1.0 m and at 5.0 m depth the light was around 0.36 µmol photons m^{-2} s^{-1} (Figure 2b).

From October to beginning of December water temperatures were very similar among the depths (Figure 2d), but in the transition from the middle of December to January water temperatures increased (Figure 2d), consistent with the beginning of summer and increases in air temperature. The higher temperature and lower wind speed (Figure 2a) promoted warmer superficial waters compared to the bottom waters, which promoted the increase in vertical stratification in oxygen saturation (Figure 2c). In December we recorded higher accumulated rainfall, corresponding to 60% of the rainfall recorded in the 84 days studied. Most of the rainfall was recorded after December 15th, explaining the drop in PAR in this period (Figure 2b).

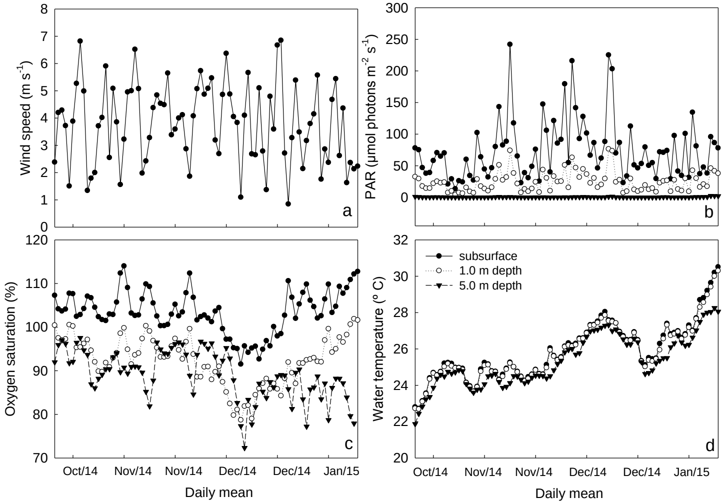

Figure 2: Daily mean of wind speed, PAR, oxygen saturation and water temperature, during spring-summer transition (2014-2015) in Peri Lake. Subsurface represents ~ 0.3 m depth.

Oxygen saturation and water temperature also decreased with depth (Figures 2c and d). The temperature contour plot showed consistent daily changes in temperature with frequent changes in Z_{mix}, where most of the time the lake was completely mixed (71%), undergoing ephemeral stratification especially during the final warm period (Figure 3). The Z_{eu} varied between 3 and 6 m (average 4 m), and was shallower than Z_{mix} during 83% of the time, suggesting that primary production at 5.0 m was strongly light limited. Additionally, the low wind speeds in the last three weeks contributed to decrease in Z_{mix} and increase in the mean daily available light (E_{mean}); and the water stability (N^2). Rainfall and wind speed showed negative correlation with the water stability, while positive correlation was found with water temperature (Table 1).

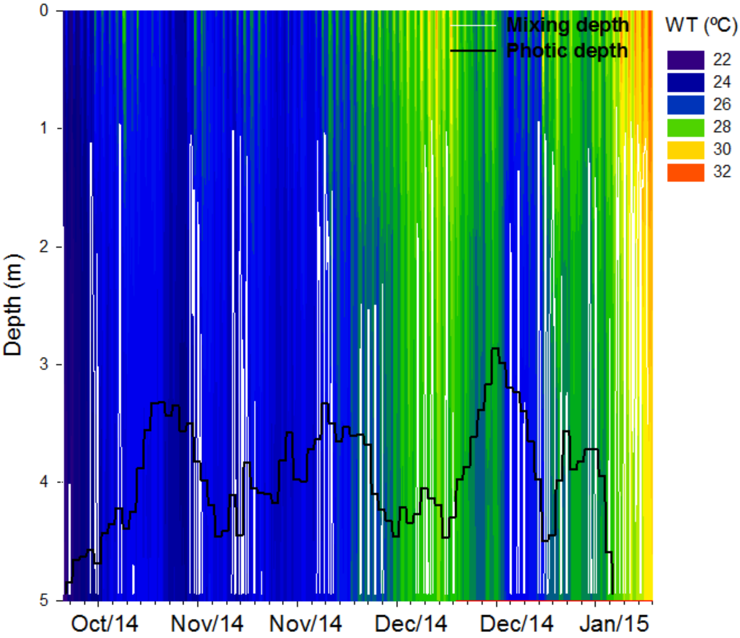

Figure 3: Water temperature daily profile at pelagic site during 84 days, measured each 30 min, at central part of the Peri Lake. White line represents the mixing zone depth, and black line represents the photic zone depth, during spring-summer transition in 2014-2015.

Table 1: Pearson correlation coefficients for daily metabolic rates and physical conditions over the course of 84 days to subsurface of pelagic site and 10 days to littoral site. Bold numbers were significant ($p<0.05$). E_{mean}: mean light available; N^2: Brunt-Väisälä buoyancy frequency; PAR: photosynthetically active radiation; Z_{eu}: photic zone; Z_{mix}: mixing zone; WT: water temperature.

Site	Variable	R	NEP	E_{mean}	N^2	Rainfall	Wind Speed	PAR	Z_{eu}	Z_{mix}	WT
Pelagic (n=84)	GPP	**0.53**	**0.29**	0.19	**0.37**	-0.13	-0.08	0.16	-0.04	**-0.40**	0.15
	R		**-0.49**	0.00	0.13	**-0.25**	0.21	-0.02	0.13	-0.11	0.05
	NEP			0.22	**0.35**	0.03	**-0.29**	0.17	-0.12	**-0.40**	-0.05
	E_{mean}				**0.38**	-0.34	0.07	**0.95**	0.23	**-0.30**	**0.26**
	N^2					-0.31	**-0.52**	0.19	0.16	**-0.95**	0.17
	Rainfall						-0.09	**-0.31**	**-0.41**	0.20	0.11
	Wind speed							0.21	-0.04	**0.50**	-0.04
	PAR								0.09	-0.09	**0.29**
	Z_{eu}									-0.09	-0.15
	Z_{mix}										-0.08
Littoral (n=10)	GPP	**0.86**	0.08	-0.10	0.09	0.10	-0.38	-0.06	-0.23	-0.51	-0.34
	R		0.47	-0.10	-0.12	0.31	-0.16	-0.07	-0.19	-0.28	-0.36
	NEP			-0.15	-0.06	0.40	-0.01	-0.22	0.07	0.39	-0.10
	E_{mean}				0.26	-0.34	-0.17	**0.96**	-0.05	0.09	-0.14
	N^2					**-0.67**	**-0.87**	0.04	0.19	0.10	0.60
	Rainfall						0.40	-0.19	-0.47	0.17	-0.44

Wind speed	-0.02	0.06	0.20	-0.28
PAR		-0.19	-0.05	-0.35
Z_{eu}			0.33	0.31
Z_{mix}				0.48

Table 2: Mean ± standard deviation (mmol O_2 m^{-3} d^{-1}) and coefficient of variation (%) of metabolic rates, from three depths at the pelagic site, sampled during 84 days, from spring-summer transition in Peri Lake. Lowercase letters indicate the significant difference among depths according to repeated measurements ANOVA.

depth	GPP	R	NEP
Subsurface	$40.9^{a} \pm 13.68$ (33)	$13.9^{b} \pm 14.38$ (103)	$26.9^{c} \pm 12.19$ (45)
1.0 m depth	$35.1^{a} \pm 15.77$ (45)	$46.9^{a} \pm 20.30$ (43)	$-11.7^{b} \pm 18.39$ (157)
5.0 m depth	$0.7^{b} \pm 1.57$ (237)	$53.4^{a} \pm 22.43$ (42)	$-52.7^{a} \pm 22.95$ (44)

Vertical variability in metabolism and limnological conditions

Estimates of GPP were the highest near the surface and decreased with depth. Conversely, R was the lowest at subsurface increasing with depth. The balance between GPP and R resulted in net autotrophy near the surface (just two days were slightly negative NEP), and predominant net heterotrophy at 1.0 and 5.0 m depth (Table 2; Figure 4). The day-to-day variability in respiration was higher at 5.0 m depth (overall SD = 22.43 mmol O_2 m^{-3} d^{-1} vs 14.38 mmol O_2 m^{-3} d^{-1} at subsurface), and similar to 1.0 m depth (SD = 20.30 mmol O_2 m^{-3} d^{-1}), however no significant difference was found in day-to-day variability of R ($p=0.12$) and NEP ($p=0.49$). Additionally, GPP showed a higher coefficient of variation at 5.0 m depth (Table 2), resulting in a significant difference among the days ($p<0.001$), and a tendency to increase at all depths, during the last three weeks of the studied period (Figure 4).

Limnological conditions were quite similar among depths, and we recorded low dissolved inorganic nitrogen at 1.0 m and low soluble reactive phosphorus at 5.0 m depth. Conversely, the same depths presented slight higher chlorophyll *a* concentration, and dissolved organic carbon showed higher values at subsurface and 1.0 m depth, even though all variables were not significant among the depths ($p>0.05$; Table 3).

Table 3: Limnological conditions (mean ± standard deviation) monthly sampled, from October to January 2015, at four depths in a deepest part of Peri Lake. Similar lowercase letters represent the not significant difference among depths, according to ANOVA for four depths ($p>0.05$). DIN: dissolved inorganic nitrogen; SRP: soluble reactive phosphorus, Chla: chlorophyll *a*; DOC: dissolved organic carbon.

Variable	subsurface	1.0 m depth	3.0 m depth	5.0 m depth
DIN (µg L^{-1})	$10.3^a \pm 4.11$	$9.4^a \pm 3.35$	$10.2^a \pm 1.60$	$10.9^a \pm 1.49$
SRP (µg L^{-1})	$1.3^a \pm 0.35$	$1.7^a \pm 1.04$	$1.7^a \pm 0.64$	$1.2^a \pm 0.37$
Chla (µg L^{-1})	$20.9^a \pm 3.37$	$21.0^a \pm 6.84$	$20.7^a \pm 6.86$	$21.1^a \pm 4.50$
DOC (mg L^{-1})	$6.5^a \pm 4.43$	$6.6^a \pm 4.51$	$5.6^a \pm 2.67$	$5.3^a \pm 1.85$

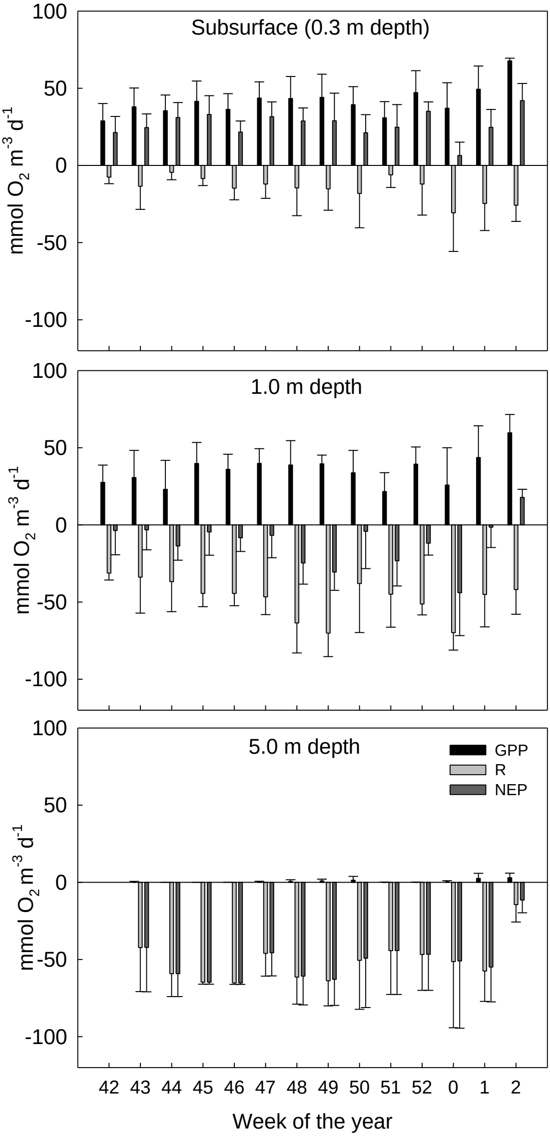

Figure 4: Weekly rates of GPP, R and NEP (mmol O_2 m^{-3} d^{-1}) at three depths from the pelagic site, during spring-summer transition, in Peri Lake. Bars represent the mean and standard deviation

Horizontal variability in metabolism

Both littoral and pelagic sites showed the same daily pattern of DO and temperature with increases during daytime and decreases after sunset (Figures 5a and b), with similar coefficient of variability, even though the pelagic site was slightly warmer and DO saturated (Table 4). GPP was similar between the pelagic and littoral subsurface sites (p=0.55), while R and NEP showed significant difference (p<0.001), with much higher R at the littoral site and consequently significantly lower NEP (Figures 5c and d). All days were net autotrophic at the pelagic site, while negative NEP occurred in two days at the littoral site, coinciding with periods of high rainfall and wind speed, and lower temperatures. Additionally, the littoral site showed higher day-to-day variability to metabolic rates than the same days in the pelagic site (Table 4; Figures 5c and d).

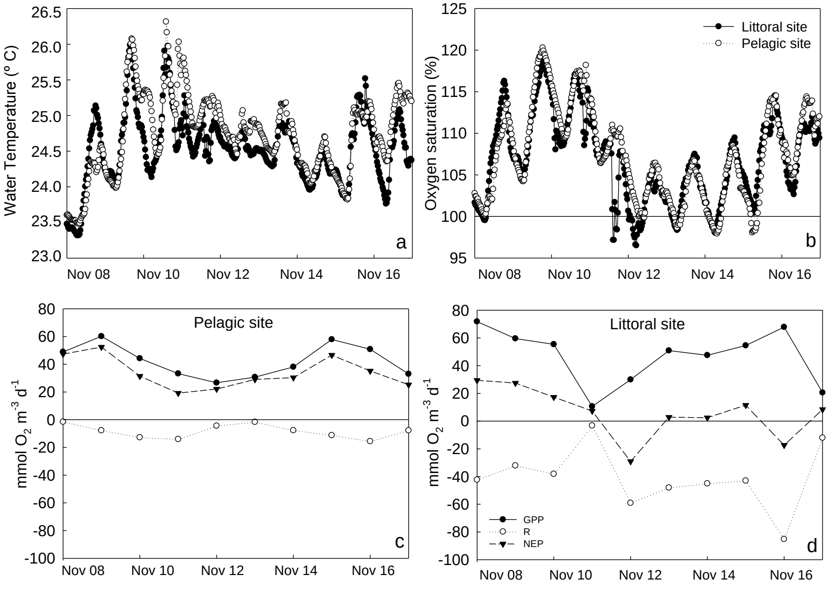

Figure 5: Day-to-day variability of water temperature, oxygen saturation and metabolic rates, during 10 days at subsurface (~ 0.3 m depth) from pelagic and littoral sites. The horizontal line in b represents the equilibrium with atmosphere.

Drivers of R and GPP

GPP and R rates were correlated at subsurface (R^2= 0.39; $p<0.05$), decreasing at 1.0 m (R^2= 0.25; $p<0.05$) and 5.0 m depth (R^2= 0.05; $p<0.05$), where the background respiration was the highest (Figure 6; Table 5). However, at the littoral site the coupling between R to GPP was stronger than at pelagic site (R^2= 0.42; $p<0.05$) and presented low background respiration (Table 5). The slope of the R vs GPP was not significantly different between subsurface and 1.0 m depth (p=0.97), while at 5.0 m depth the slope was negative and was significant different from the subsurface (p=0.001).

Table 4: Oxygen saturation, water temperature and metabolic rates at subsurface of pelagic and littoral site in Peri Lake, sampled during 10 days. Lowercase letters indicate the significant difference between sites according to repeated measurements ANOVA. SD: standard deviation. CV: Coefficient of variation.

	Pelagic site			Littoral site		
	Oxygen saturation					
Mean ± SD (%)	$107.1^b \pm 5.28$			$106.4^a \pm 4.97$		
CV (%)	4.9			4.7		
	Water temperature					
Mean ± SD (ºC)	$24.7^b \pm 0.63$			$24.5^a \pm 0.53$		
CV (%)	2.5			2.2		
	GPP	NEP	R	GPP	NEP	R
Mean ± SD (mmol O_2 m^{-3} d^{-1})	$42.2^a \pm 11.19$	$34.4^b \pm 10.88$	$7.8^a \pm 5.13$	$46.8^a \pm 20.18$	$6.0^a \pm 18.18$	$40.8^b \pm 22.84$
CV (%)	27	32	65	43	303	56

Table 5: Summary of linear regression analysis between daily rates of GPP and R to each site sampled.

	R^2	Slope	Intercept	p-value
Subsurface	0.39	0.6554	-12.848	0.001
1.0 m depth	0.25	0.6488	24.084	<0.001
5.0 m depth	0.05	-4.227	56.163	<0.001
Littoral site	0.42	0.7343	6.4397	0.007

At the pelagic site, the strongest correlations observed to GPP were with Z_{mix} (r=-0.40; p<0.05) and water stability (r=0.37; p<0.05). R was significant only with rainfall (r=-0.25; p<0.05). Light, represented by PAR and E_{mean}, and water temperature showed weak positive correlations with GPP (Table 1). High R rates at the littoral were recorded in days with rainfall, even though this correlation was not significant (r=0.31; p>0.05); suggesting that rainfall exerted direct influence in respiration at littoral areas, since at the pelagic area, this relationship was negative (Table 1). The more important correlations to GPP and R at the littoral site were with water temperature, wind speed and Z_{mix}, all negatively correlated, although not significant (Table 1).

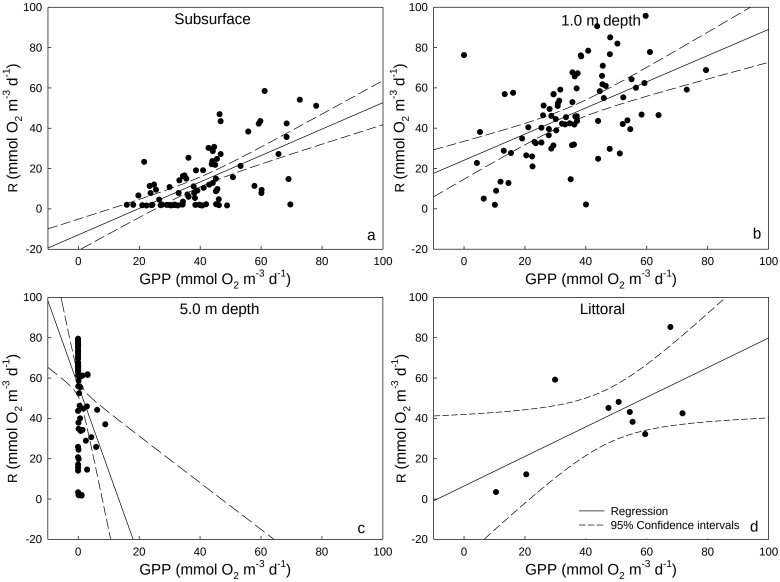

Figure 6: Linear regression analysis between daily rates of GPP and R in Peri Lake, at four sites sampled. Black lines are the regression lines and dashed lines represent the 95% confidence intervals. Subsurface and littoral sites were sampled at ~ 0.3 m depth.

6.5 Discussion

Vertical and horizontal variability in metabolic rates

Using high-frequency measurements of dissolved oxygen and temperature, we observed significant vertical variability in metabolic rates despite the homogeneous conditions of dissolved organic carbon, nutrients and chlorophyll *a* in the water column. This suggest that vertical differences in GPP and less in R were influenced by decreasing light levels and periodic water column stratification patterns. GPP rates were however similar between the subsurface (~ 0.3 m) and 1.0 m depth, which both were above the ephemeral stratification layer.

In monomictic or dimictic systems with well-defined mixing periods, changes in stratification usually has a strong impact on rates of primary production due to depletion of nutrients during summer, while respiration and primary production are strongly influenced by intrusion of bottom waters rich in DOC and nutrients. GPP and R can therefore vary significantly from day-to-day during transition from stratification to full mixing depending on the magnitude of mixing, the quantity and quality of the DOC, and nutrient inputs (Staehr et al., 2012b; Brighenti et al., 2015). The efficient deep and frequent mixing events in Peri Lake is very likely to promote light limitation of primary production, and introduce organic matter for elevated respiration, although inputs of nutrients-rich bottom waters into the surface layers may also stimulate photosynthesis here (Staehr et al., 2010b). Calm weather conditions which favor a stable water column and lasting stratification, will on the other hand promote settlement of particles, which increases light availability and is expected to raise primary production. Much of the observed variability in GPP is therefore likely caused by wind driven changes in water column stability and stratification especially at deeper waters, where most of light is more limiting. While the ephemeral stratification adds a large day-to-day variability in metabolic rates from Peri Lake, the coefficients of variability at the subsurface, were lower (GPP, CV = 33 %) in comparison to found by Van de Bogert et al. (2012) (GPP, CV = 65 % in Sparkling Lake); and Staehr et al. (2010b) (GPP, CV = 95 and 66 % in Slotssø and Gribssø Lakes, respectively).

The predominant net autotrophic condition at subsurface, changed at 1.0 m depth, where net heterotrophy occurred on several days, reaching constantly negative NEP values at 5.0 m depth. This vertical pattern is similar to those observed for relatively turbid polymictic lakes (Staehr et al., 2012b; Obrador et al., 2014), but differs from clear-water lakes, where the light penetrates below the mixed layer depth, increasing the primary production in deeper waters (Coloso et al., 2008). The net autotrophic at subsurface from Peri Lake was consistent with findings in Tonetta et al. (2015a), estimating CO_2 flux over 48 h, where under summer conditions (high temperature and light) the lake was net autotrophic. The vertical gradient in the balance between GPP and R is also related to restrictions on the photosynthetic capacity of phytoplankton by light and to some degree nutrients (Kehoe et al., 2015) combined with more homogeneous distribution of R (Coloso et al., 2008; Staehr et al., 2012b; Obrador et al., 2014).

Our results also confirm previous findings using bottles incubation, where the highest primary production was recorded at subsurface, decreasing with depth (Tonetta et al., 2015b). Furthermore, the authors presented that the highest respiration rates occurred at 1.0 m depth, and did not increase with depth, showing a more homogeneous condition to the pelagic metabolism along the different depths. Comparing both methodologies, bottle incubations and free-water, is possible to infer that the high respiration near the bottom indicates the importance of other process, especially benthic processes. In some lakes, benthic processes can account for ~ 40% of epilimnetic GPP and R, but it depends on the lake area and depth, and the influence of wind speed promoting sediment resuspension (Van de Bogert et al., 2007). The sinking of particulate matter produced in the shallow waters may cause respiration to increase with depth (Staehr et al., 2010b), and the elevated R at 5.0 m, despite of lower DOC concentrations, suggests a strong influence from benthic respiration. The relative importance of benthic and pelagic processes however, needs to be confirmed by benthic chamber-based measurements of metabolism.

Peri Lake had overall high wind speeds (mean of 4 m s^{-1}) during our measurements, which should efficiently mix the lake both vertically and horizontally. According to Van de Bogert et al. (2007), the high wind velocity was responsible to the low variability in GPP and R among sites, and 2.75 m s^{-1} was set up as a threshold to this homogeneity. The horizontal homogeneity was observed in the near surface rates of GPP, which were similar between littoral and pelagic. Respiration rates were on the contrary significantly higher at the littoral site, suggesting either elevated influence from benthic processes at the shallower littoral site or elevated R at the littoral site due to inputs of organic allochthonous material carried by rainfall, as supported by slightly higher DOC concentrations at the littoral compared to the surface pelagic site.

Coupling between R and GPP

The similar slope in the coupling R vs GPP, observed between subsurface and 1.0 m depth, in Peri Lake, implies that respiration was equally dependent on the photosynthetically active phytoplankton under high light conditions at these depths. Elevated respiration observed below the photic zone is dependent on a combination of organic matter from terrestrial origin, as well as sinking of autochthonous matter, and sedimentation of algal particles (Reynolds, 1989), resulting in a negative and different slope from the other depths sampled. We expect that the high level of mixing observed in Peri lake contributed to much of the variation in DO observed at the 5.0 m depth, although other processes, such as sediment respiration or groundwater intrusion may also be important (Kling et al., 1991; Fontes et al., 2015). The proximity with the bottom of the lake is therefore likely to promote noise in the DO signal here. We investigated how much the physically driven vertical fluxes in DO could influence the NEP estimates in each depth strata. Overall, the air-water exchange and vertical flux driven by eddy diffusivity (D_s and D_v, respectively) were more important than the flux driven by mixed-layer deepening (D_z), but still the biological processes accounted to 52% of the NEP at subsurface, where D_v contributed 36%; 44% at 1.0 m depth (D_s contributed 36%); and biological processes accounted to 84% at 5.0 m depth. This implies that the predominant and stable respiration rates and the light limited and low primary production at 5.0 m depth, with most of the days with no GPP or close to zero, resulted in R uncoupled to GPP.

In studies across gradients in trophic status, Solomon et al. (2013) suggested a R-GPP slope around 0.8 and 1.0 for oligotrophic systems, and lower values in eutrophic systems. We found slopes around 0.65 in the near surface waters, which implies in a system near to eutrophic conditions. This confirms a recent study which based on sediment cores analyses (Hennemann et al., 2015), showed that Peri Lake is developing towards a more eutrophic status.

A higher slope of 0.73 was found at the littoral site, where the R and GPP were highly correlated. At this site, the GPP were very similar to R rates, mean 46.8 and 40.8 mmol O_2 m^{-3} d^{-1}, respectively. This substantial increase in R at the littoral site in relation to the pelagic site, suggests that more carbon to respiration is available at the littoral, since similar GPP rates were found in both sites, which suggests this carbon is allochthonous. According to Lisboa et al. (2014) higher allochthonous organic matter inputs from the catchment area, in Peri Lake, occur during rainfall periods, and DOC concentration from a monitoring program has shown that the littoral site has slightly more DOC than pelagic (around 4.43 and 4.30 mg L^{-1}, respectively). Additionally, we observed that during the few days sampled at littoral site, elevated GPP and R occurred in days with rainfall, suggesting that rainfall could provide nutrients and organic matter into the system, by external influence or resuspension.

Temporal variability

Several factors may have added observed higher temporal variability in GPP and NEP at the littoral site, such as macrophytes presence (Obrador and Petrus, 2013; They et al., 2013); sediments heterogeneity (Lauster et al., 2006); wind speed creating spatial patchiness of nutrients and organisms (Van de Bogert et al., 2012), and rainfall introducing allochthonous organic matter (Marotta et al., 2010). Our methodology, however, did not allow us to access the direct importance of these variables for the observed temporal variability observed. However, our correlation analysis suggested that rainfall, wind speed, temperature and Z_{mix} had some influence on the elevated rates of littoral respiration.

Higher temporal variability in Z_{mix}, Z_{eu} and N^2, were observed under stronger winds and heavier rains, conditions which correlated with higher day-to-day variability in in metabolic rates. An interesting result emerged from the last week of sampling, where PAR and wind speed tended to decrease, due to the rainfall days, and temperature increased, which boosted the strength and duration of stratification of the water column. These changes promoting a shallower mixing depth, and particles settlement, besides the warmer water column, which favored the higher light available in deeper waters, consequently the GPP tended to increase in all depths sampled during this period. This behavior in GPP showed a tendency of the lake to be more autotrophic during the beginning of the summer. Opposite result was found by Obrador et al. (2014), when net heterotrophy increases when the lakes became stratified.

Our findings in Peri Lake showed that periods with full mixing were characterized by lower GPP, suggesting an impact of resuspended particles from bottom waters. Furthermore, during low wind speeds, there is a shallower mixing depth, and the more stable water column reduces resuspension of sediment and improves the water clarity, favoring the increase in phytoplankton productivity (Brookes et al., 2013; Woolway et al., 2015). The positive effect of water column stability was, however challenged in a recent study from stratified tropical lakes (Brighenti et al., 2015). Here we showed that metabolic rates were lower during the fully mixing than during the stable stratified period, as observed in temperate lakes (Staehr et al., 2012b).

As previously discussed, we observed no direct effect of DOC concentration on R when considering the vertical gradient at the center of the lake. However, some interesting findings emerged for the temporal variability. For instance, in November, DOC reached 11 mg L^-

^{1}, compared to an average level of 4-5 mg L^{-1}. The elevated DOC levels during weeks 48 and 49 coinciding with a slightly increase in respiration at 1.0 m depth, from on average 45 mmol O_2 m^{-3} d^{-1} during week 47, to 70 mmol O_2 m^{-3} d^{-1} during week 49. High variability respiration may furthermore be related to high variability observed in nutrients, chlorophyll *a* and DOC quality (Hanson et al., 2003), however, further sampling of these conditions are needed to confirm such relationships.

6.6 Conclusion

We found considerable spatial variation in lake primary production and respiration, governed by gradients in light, organic matter and proximity to land. During a short period in spring-summer transition, GPP was similar between littoral and pelagic areas, but respiration was higher at the near shore littoral site. At the center of the lake, we found a clear vertical gradient for the metabolic rates, with highest GPP and net autotrophy occurring near surface, and decreasing with depth, due to the light extinction. On the other hand, respiration increased with depth, where the bottom waters were predominantly net heterotrophic, suggesting a greater influence of benthic processes on the DO dynamics.

The nutrients, carbon and chlorophyll *a* concentrations in Peri Lake were similar among the depths sampled, suggesting a stronger importance of the physical conditions in driving the metabolic variability. Temporally, under high light and temperatures, and low wind speeds, the mixing depth became shallower, water column stability as well as the light availability increased in the water column, promoting higher GPP. Our results supports previous findings that complex models with greater integration of physical and limnological processes are needed, to better identify the underlying drivers of short-term temporal variability, in lakes with intense mixing regime (Coloso et al., 2011). Deployment of sensors in different sites and depths are therefore needed to obtain spatially, as well as temporally, more representative estimates of lake metabolism.

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6.7 References

Brighenti, L.S., Staehr, P.A., Gagliardi, L.M., Brandão, L.P.M., Elias, E.C., Mello, N.A.S.T., Barbosa, F.A.R., Bezerra-Neto, J.F., 2015. Seasonal changes in metabolic rates of two tropical lakes in the Atlantic Forest of Brazil. Ecosystems 18, 589–604.

Brookes, J.D., O'Brien, K.R., Burford, M.A., Bruesewitz, D.A., Hodges, B.R., McBride, C., Hamilton, D.P., 2013. Effects of diurnal vertical mixing and stratification on phytoplankton productivity in geothermal Lake Rotowhero, New Zealand. Inland Waters 3, 369–376.

Carignan, R., Planas, D., Vis, C., 2000. Planktonic production and respiration in oligotrophic Shield lakes. Limnol. Oceanogr. 45, 189–199.

Cole, J.J., Caraco, N.F., 1998. Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF6. Limnol. Oceanogr. 43, 647–656.

Cole, J.J., Caraco, N.F., 2001. Carbon in catchments: connecting terrestrial carbon losses with aquatic metabolism. Mar. Fresh. Res. 52, 101–110.

Cole, J.J., Pace, M.L., Carpenter, S.R., Kitchell, J.F., 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. Limnol. Oceanogr. 45, 1718–1730.

Cole, J.J., Prairie, Y.T., Caraco, N.F., McDowell, W.H., Tranvik, L.J., Striegl, R.G., Duarte, C.M., Kortelainen, P., Downing, J.A., Middelburg, J.J., Melack, J., 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. Ecosystems 10, 171–184.

Coloso, J.J., Cole, J.J., Hanson, P.C., Pace, M.L., 2008. Depth-integrated, continuous estimates of metabolism in a clear-water lake. Can. J. Fish. Aquat. Sci. 65, 712–722.

Coloso, J.J., Cole, J.J., Pace, M.L., 2011. Difficulty in discerning drivers of lake ecosystem metabolism with high frequency data. Ecosystems 14, 935–948.

Del Giorgio, P.A., Cole, J.J., Caraco, N.F., Peters, R.H., 1999. Linking planktonic biomass and metabolism to net gas fluxes in northern temperature lakes. Ecology 80, 1422–1431.

Fontes, M.L.S., Dalpaz, L., Tonetta, D., Antônio, R.V., Petrucio, M.M., 2013. Dynamics of planktonic prokaryotes and dissolved carbon in a subtropical coastal lake. Front. Microbiol. 4, 71.

Fontes, M.L.S., Marotta, H., MacIntyre, S., Petrucio, M.M., 2015. Inter- and intra-annual variations of $p\mathrm{CO}_2$ and $p\mathrm{O}_2$ in a freshwater subtropical coastal lake. Inland Waters 5, 107–116.

Fuentes, E.V., Petrucio, M.M., 2015. Water level decrease and increased water stability promotes phytoplankton growth in a mesotrophic subtropical lake. Mar. Fresh. Res. 66, 711–718.

Golterman, H.L., Clymo, R.S., Ohnstad, M.A.M., 1978. Methods for Physical and Chemical Analysis of Freshwater. Blackwell Science, Oxford.

Hanson, P.C., Bade, D.L., Carpenter, S.R., 2003. Lake metabolism: relationships with dissolved organic carbon and phosphorus. Limnol. Oceanogr. 48, 1112–1119.

Hanson, P.C., Carpenter, S.R., Armstrong, D., Stanley, E.H., Kratz, T.K., 2006. Lake dissolved inorganic carbon and dissolved oxygen: changing drivers from days to decades. Ecol. Monogr. 76, 343–363.

Hanson, P.C., Carpenter, S.R., Kimura, N., Wu, C., Cornelius, S.P., Kratz, T.K., 2008. Evaluation of metabolism models for free-water dissolved oxygen methods in lakes. Limnol. Oceanogr. Methods 6, 454–465.

Hennemann, M.C., Simonassi, J.C., Petrucio, M.M., 2015. Paleolimnological record as an indication of incipient eutrophication in an oligotrophic subtropical coastal lake in Southern Brazil. Environ. Monit. Assess. 187, 513.

Jassby, A.D., Platt, T., 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. 21, 540–547.

Jiang, Y., Hu, Y., Schirmer, M., 2013. Biogeochemical controls on daily cycling of hydrochemistry and δ13C of dissolved inorganic carbon in a karst spring-fed pool. J. Hydrol. 478, 157–168.

Kehoe, M., O'Brien, K.R., Grinham, A., Burford, M.A., 2015. Primary production of lake phytoplankton, dominated by the cyanobacterium *Cylindrospermopsis raciborskii*, in response to irradiance and temperature. Inland Waters 5, 93–100.

Kling, G.W., Kipphut, G.W., Miller, M.C., 1991. Arctic streams and lakes as conduits to the atmosphere: implications for tundra carbon budgets. Science 251, 298–301.

Koroleff, F., 1976. Determination of nutrients, in: Grasshoff, K. (Ed.), Methods of Sea Water Analysis. Verlag Chemie Weinhein, pp. 117–181.

Laas, A., Nõges, P., Kõiv, T., Nõges, T., 2012. High-frequency metabolism study in a large shallow temperate lake reveals seasonal switching between net autotrophy and net heterotrophy. Hydrobiologia 694, 57–74.

Lauster, G., Hanson, P., Kratz, T., 2006. Gross primary production and respiration differences among littoral and pelagic habitats in northern Wisconsin lakes. Can. J. Fish. Aquat. Sci. 63, 1130–1141.

Lewis, W., 2010. Biogeochemistry of tropical lakes. Verh. Int. Verein. Limnol. 30, 1595–1603.

Lisboa, L.K., Silva, A.L.L., Siegloch, A.E., Gonçalves, J.F.J., Petrucio, M.M., 2014. Temporal dynamics of allochthonous coarse particulate organic matter in a subtropical Atlantic Rainforest Brazilian stream. Mar. Fresh. Res. 66, 674–680.

Lorenzen, C.J., 1967. Determination of chlorophyll and pheopigments: Spectrophotometric equations. Limnol. Oceanogr. 12, 343–346.

MacIntyre, S., Jonsson, A., Jansson, M., Aberg, J., Turney, D.E., Miller, S.D., 2010. Buoyancy flux, turbulence, and the gas transfer coefficient in a stratified lake. Geophys. Res. Lett. 37, 2–6.

Mackereth, F.J.H., Heron, J.E., Talling, J.F., 1978. Water Analysis: Some Revised Methods for Limnologists. Freshwater Biological Association, Michigan.

Marotta, H., Duarte, C.M., Pinho, L., Enrich-Prast, A., 2010. Rainfall leads to increased $p\mathrm{CO_2}$ in Brazilian coastal lakes. Biogeosciences 7, 1607–1614.

Muduli, P.R., Kanuri, V.V., Robin, R.S., Kumar, B.C., Patra, S., Raman, A.V., Rao, G.N., Subramanian, B.R., 2012. Spatio-temporal variation of CO_2 emission from Chilika Lake, a tropical coastal lagoon, on the east coast of India. Estuar. Coast. Sh. Sci. 113, 305–313.

Nimick, D.A., Gammons, C.H., Parker, S.R., 2011. Diel biogeochemical processes and their effect on the aqueous chemistry of streams: A review. Chem. Geol. 283, 3–17.

Obrador, B., Petrus, J.L., 2013. Carbon and oxygen metabolism in a densely vegetated lagoon: implications of spatial heterogeneity. Limnetica 32, 321–336.

Obrador, B., Staehr, P.A., Christensen, J.P.C., 2014. Vertical patterns of metabolism in three contrasting stratified lakes. Limnol. Oceanogr. 59, 1228–1240.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <URL:http://www.R-project.org/>.

Rantakari, M., Kortelainen, P., 2005. Interannual variation and climate regulation of the CO_2 emission from large boreal lakes. Glob. Chang. Biol. 11, 1368–1380.

Read, J.S., Hamilton, D.P., Jones, I.D., Muraoka, K., Winslow, L.A., Kroiss, R., Wu. C.H., Gaiser, E., 2011. Derivation of lake mixing and stratification indices from high-resolution lake buoy data. Environ. Model. Softw. 26, 1325–36.

Reynolds, C.S., 1989. Physical determinants of phytoplankton succession, in: Sommer, U. (Ed.), Plankton Ecology. Spring-Verlag, New York, pp.9–56.

Rueda, F., Schladow, G., 2009. Mixing and stratification in lakes of varying horizontal length scales: Scaling arguments and energy partitioning. Limnol. Oceanogr. 54, 2003–2017.

Sadro, S., Nelson, C.E., Melack, J.M., 2011. Linking diel patterns in community respiration to bacterioplankton in an oligotrophic high-elevation lake. Limnol. Oceanogr. 56, 540–550.

Sager, J.C., McFarlane, J.C., 1997. Radiation, in: Langhans, R.W., Tibbitts, T.W. (Eds.), Plant Growth Chamber Handbook. Iowa Agriculture and Home Economics Experiment Station Special Report no. 99, Ames, IA. Iowa State Univ. Press, pp. 1–29.

Serra, T., Vidal, J., Casamitjana, X., Soler, M., Colomer, J., 2007. The role of surface vertical mixing in phytoplankton distribution in a stratified reservoir. Limnol. Oceanogr. 52, 620–634.

Solomon, C.T., Bruesewitz, D.A., Richardson, D.C., Rose, K.C., Van de Bogert, M.C., Hanson, P.C., Kratz, T.K., Larget, B., Adrian, R., Babin, B.L., Chiu, C., Hamilton, D.P., Gaiser, E.E., Hendricks, S., Istvanovics, V., Laas, A., O’Donnell, D.M., Pace, M.L., Ryder, E., Staehr, P.A., Torgersen, T., Vanni, M.J., Weathers, K.C., Zhu, G., 2013. Ecosystem respiration: drivers of daily variability and background respiration in lakes around the globe. Limnol. Oceanogr. 58, 849–866.

Staehr, P.A., Sand-Jensen, K., 2007. Temporal dynamics and regulation of lake metabolism. Limnol. Oceanogr. 52, 108–120.

Staehr, P.A., Bade, D., Van de Bogert, M.C., Koch, G.R., Williamson, C., Hanson, P., Cole, J.J., Kratz, T., 2010a. Lake metabolism and the diel oxygen technique: State of the science. Limnol. Oceanogr. Methods 8, 628–644.

Staehr, P.A., Sand-Jensen, K., Raun, A.L., Nilsson, B., Kidmose, J., 2010b. Drivers of metabolism and net heterotrophy in contrasting lakes. Limnol. Oceanogr. 55, 817–830.

Staehr, P.A., Testa, J.M., Kemp, W.M., Cole, J.J., Sand-Jensen, K., Smith, S.V., 2012a. The metabolism of aquatic ecosystems: history, applications, and future challenges. Aquat. Sci. 74, 15–29.

Staehr, P.A., Christensen, J.P.A., Batt, R., Read, J., 2012b. Ecosystem metabolism in a stratified lake. Limnol. Oceanogr. 57, 1317–1330.

Staehr, P.A., Baastrup-Spohr, L., Sand-Jensen, K., Stedmon, C., 2012c. Lake metabolism scales with lake morphometry and catchment conditions. Aquat. Sci. 74, 155–169.

Strickland, J.D.H., Parsons, T.R., 1960. A Manual of Seawater Analysis. B. Fish. Res. Board Can. 125, 1–18.

They, N.H., Motta-Marques, D., Souza, R.S., 2013. Lower respiration in the littoral zone of a subtropical shallow lake. Front. Microbiol. 4, 434.

Tonetta, D., Fontes, M.L.S., Petrucio, M.M., 2015a. Linking summer conditions to CO_2 undersaturation and CO_2 influx in a subtropical coastal lake. Limnology 16, 193–201.

Tonetta, D., Laudares-Silva, R., Petrucio, M.M., 2015b. Planktonic production and respiration in a subtropical lake dominated by cyanobacteria. Braz. J. Biol. 75, 460–470.

Vachon, D., Prairie, Y.T., Cole, J.J., 2010. The relationship between near-surface turbulence and gas transfer velocity in freshwater systems and its implications for floating chamber measurements of gas exchange. Limnol. Oceanogr. 55, 1723–1732.

Van de Bogert, M.C., Carpenter, S.R., Cole, J.J., Pace, M.L., 2007. Assessing pelagic and benthic metabolism using free water measurements. Limnol. Oceanogr. Methods 5, 145–155.

Van de Bogert, M.C., Bade, D.L., Carpenter, S.R., Cole, J.J., Pace, M.L., Hanson, P.C., Langman, O.C., 2012. Spatial heterogeneity strongly affects estimates of ecosystem metabolism in two north temperate lakes. Limnol. Oceanogr. 57, 1689–1700.

Woolway, R.I., Jones, I.D., Feuchtmayr, H., Maberly, S.C., 2015. A comparison of the diel variability in epilimnetic temperature for five lakes in the English Lake District. Inland Waters 5, 139–154.

7 CAPÍTULO 3

Changes in CO_2 dynamics are related to the water level variations in a subtropical lake

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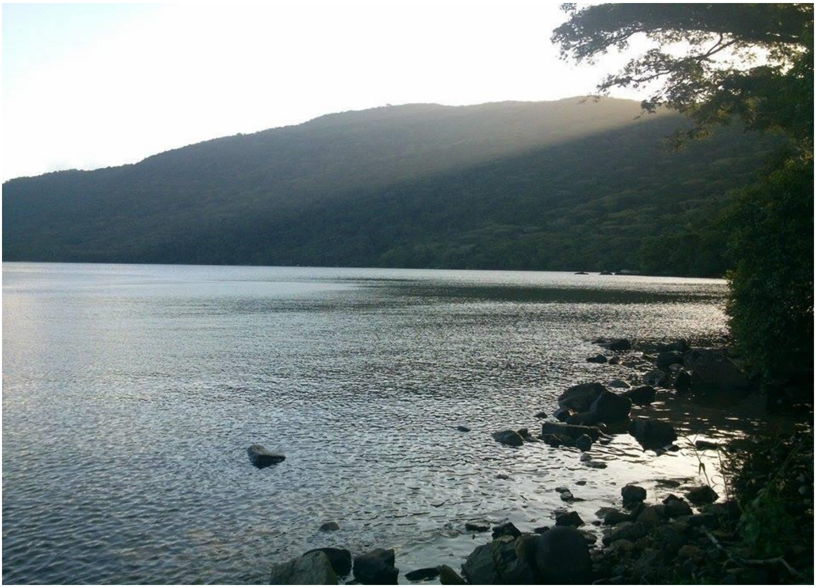

Lagoa do Peri, vista da porção oeste em maio de 2014
Foto: acervo pessoal

7.1 Abstract

Lakes are important sites for carbon cycling and sensitive to environmental changes. We investigated the implications of low rainfall and reduced water level for changes in nutrients and chlorophyll-a in a subtropical lake, and how these changes affected the dynamics of CO_2. Based on eight consecutive years of monthly monitoring of pH, alkalinity, oxygen and temperature we calculated the pCO_2 and CO_2 flux. Peri Lake featured reduction in rainfall in 2012 causing 0.36 m lower water level during that year. Low water level in the following years together with increases in chlorophyll-a and organic carbon reduced the water transparency leading to predominant CO_2 emission to the atmosphere. Our analyses suggest that changes in water level strongly affected levels of organic carbon, nutrients, chlorophyll-a, which in turn enhanced CO_2 air-water fluxes. Additionally, a generalized linear model showed that nutrients and temperature with one-month time lag provided a useful tool to predict changes in CO_2. The predicted pCO_2 values were similar to the observed in 2015 and showed the predominant CO_2 supersaturation in Peri Lake. We conclude that meteorological conditions such as low rainfall significantly enhance the CO_2 flux through changes in the water conditions.

Keywords: rainfall; carbon cycling; climatic changes; nutrients; chlorophyll-a; Peri Lake

7.2 Introduction

Biogeochemical changes associated with inputs and turnover of nutrients and carbon from the watershed can effectively change the net balance between primary production from autotrophic organism, and respiration from heterotrophic organisms (Cole et al., 2007). The metabolic activities are important for the processing of organic matter in lakes, which are known to be *hot spots* for production, degradation, storage and release of carbon (Tranvik et al., 2009). The balance between uptake and release of CO_2 reflects if the ecosystem is a net source or sink of carbon in relation to the atmosphere (Cole et al., 2007). CO_2 supersaturation in lakes is assumed to be the result from higher biological processing of organic matter, by respiration, over primary production, typical condition for lakes that receive allochthonous organic matter to sustain high respiration rates (Duarte & Prairie, 2005).

Other processes, however, can contribute to the CO_2 supersaturation in water, such as photooxidation (Granéli et al., 1996), CO_2 production in sediments (Duarte & Prairie, 2005), weathering of minerals in the catchment area (Marcé et al., 2015), mineralization of organic carbon from terrestrial sources (Maberly et al., 2012), and CO_2 from soil respiration (Weyhenmeyer et al., 2015). Therefore, aquatic systems and its metabolic rates are very sensitive to physical and chemical changes in the surrounding watershed (Williamson et al., 2009).

A few variables are expected to strongly influence the metabolic activity and the level of CO_2 saturation in lakes. Dissolved organic carbon (DOC) represents direct effects on bacterial respiration and photochemical oxidation of organic matter, and indirectly influence on the light availability for primary producers (Kirk, 1994; Sobek et al., 2007). DOC is either produced within the ecosystem (autochthonous) or imported via rainfall or as particles from the watershed (allochthonous), and the amount and lability of DOC has been found to affect the net carbon balance in aquatic ecosystems (Rantakari & Kortelainen, 2005; Muduli et al., 2012). During summer, the high light and temperature, together with inputs of nutrients increase primary production, thus lakes with high phosphorus, are often chlorophyll-a rich, and undersaturated in CO_2 (Balmer & Downing, 2011; Trolle et al., 2012; Jones et al., 2016). Other factors influencing CO_2 supersaturation include wind speed, which affects the gas exchange between water and air (Vachon & Prairie, 2013), and the size of the lake (Weyhenmeyer et al., 2015). Small lakes can present higher respiration than primary production, as observed by Staehr et al. (2012), or, in other cases undersaturation can be observed in small environments, as highlighted by Jones et al. (2016), studying the influence of morphology and hydrology in carbon fluxes.

Although tropical and subtropical areas are understudied compared to temperate and boreal lakes, it is possible to describe some overall conditions determining the level of CO_2 saturation in tropical lakes. For example, Pinho et al. (2016) in a study compiling several Brazilian systems found no correlation between DOC and pCO_2, suggesting the temperature influence in the biological processes and importance of other CO_2 sources to warm tropical lakes as recorded in boreal lakes (Weyhenmeyer et al., 2015). Other studies have shown the rainfall influence the aquatic metabolism through inputs of organic matter which stimulate respiration (Marotta et al., 2010a; Pacheco et al., 2015), while inputs of nutrients, mainly from anthropogenic activities, decrease the CO_2 concentration by increasing primary production (Pacheco et al., 2013; Peixoto et al., 2013). Besides the observed high CO_2 variability in tropical lakes, these systems generally contribute with high CO_2 emissions to the atmosphere (Marotta et al., 2009). Raymond et al. (2013) estimated that tropical lakes consist in 2.4 % of the global lake area and contribute for 34 % of the global lake carbon emission. Since tropical lakes are exposed to higher sunlight incidence and present different physical and biological dynamics than temperate lakes (Schiemerand & Boland, 1996), it is important to understand the importance of environmental drivers of CO_2 fluxes and carbon cycling in tropical lakes.

Changes in rainfall and temperature, associated with climate changes, are likely to affect several physical conditions in lakes (Roland et al., 2012). In the southeastern part of Brazil, expectations are for decreasing rainfall and increasing temperatures (IPCC, 2014). This combination will likely reduce water levels and warm the waters with potential effects on biological communities' structure and functions (Yvon-Durocher et al., 2010; Jeppesen et al., 2015). The overall aim of this study is to investigate the effects of changes in rainfall, temperature and water level on water chemistry (nutrients, DOC and chlorophyll-a) and CO_2 dynamics of a subtropical coastal lake in Brazil. We tested the hypothesis that reduction of rainfall causes a decrease in $p\mathrm{CO}_2$ and CO_2 flux due to related changes in water level and nutrients. Additionally, we predicted the $p\mathrm{CO}_2$ values for the coming years comparing with observed values in Peri Lake.

7.3 Material and Methods

Study site

This study was performed in Peri Lake (27°44'S and 48°31'W), with a surface area of 5.07 km^2, maximum depth of 11 m and mean depth of 4 m. The lake is situated in the southern region of Santa Catarina Island, Brazil, in a protected area of the Secondary Atlantic Rainforest, with low human impact – only recreational activities are allowed in a restrict area. Peri Lake has two main tributaries (Cachoeira Grande and Ribeirão Grande streams), and one channel (Sangradouro river) connecting the lake with the ocean, where there is no direct influence of the sea in the water lake (Fig. 1).

The lake is a freshwater system (salinity of zero and conductivity around 70 µS cm^{-1}), with vertical light attenuation coefficient around 1.1 m^{-1}, mean daily available light around 0.01 mol photons m^{-2} d^{-1}, euphotic zone and mixing zone depths around 4.1 m and 6.0 m, respectively (Tonetta et al., 2016). Peri Lake is the main freshwater resource in Santa Catarina Island, and small stands of aquatic macrophytes are present in littoral area, near the outfall from Cachoeira Grande and Ribeirão Grande streams. The most frequent and abundant species are *Schoenoplectus californicus, Nymphoides indica, Panicum* sp., *Typha* sp. and *Echinochloa polystachya* (*in situ* observation).

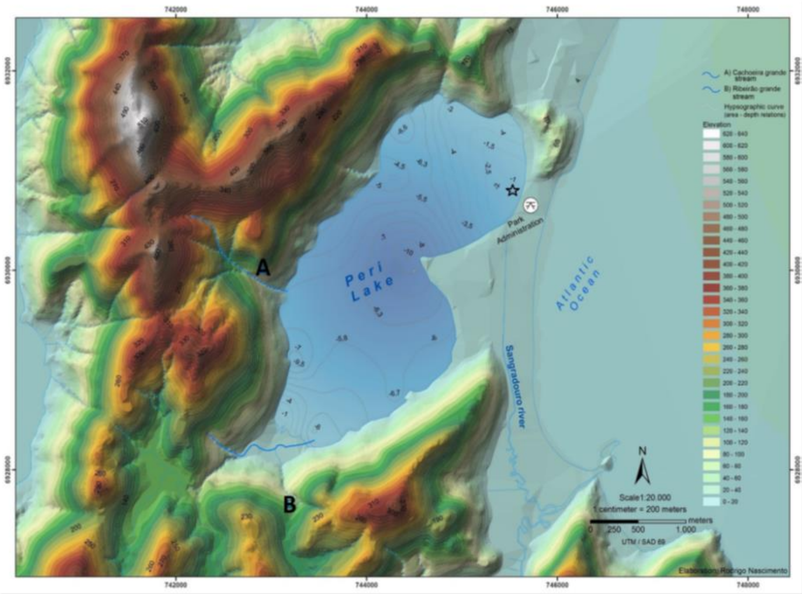

Figure 1: Bathymetric map of the Peri Lake with hypsographic curve and elevation of the coastal Lake Peri Park area. Letter A represents Cachoeira Grande Stream and B represents Ribeirao Grande stream. The star symbol indicates the recreational area, near the beginning of Sangradouro River. Adapted from Fontes et al. (2015).

Sampling

We collected water samples monthly, in the morning (9:00–11:00 local time, UTC/GMT -3 h) to avoid any bias from daily variations in our data set, from March 2007 to February 2015, totalizing 96 months and 600 samples, including vertical and horizontal samplings.

We collected water from four depths in central part of the lake, with 8.2 m total depth, according to light extinction (surface representing 100% of the light incident; 1.0 m depth representing 10% of the light incident; 3.0 m representing 1% of the light incident and 6.0 m depth representing the aphotic zone). Additionally, from March 2007 to March 2013, we collected water samples at 1.0 m depth, from stations near the outfall of the streams Cachoeira Grande (2.9 m total depth) and Ribeirão Grande (2.2 m total depth), but free of macropytes; and near the recreational area (1.5 m total depth). Except for CO_2 flux, which was estimated only from the surface samplings at the central part of the lake, the monthly values shown in the graphs represent the mean of all depths and sites sampled in one month, since the analyses of variance showed no significant difference among depths and sites (ANOVA, $p=0.92$). Hennemann and Petrucio (2011) conducting analyses of variance to chlorophyll-a and nutrients observed no significant difference among the same sites sampled in this study. Additionally, in a recent work, Tonetta et al. (2016) and Hennemann and Petrucio (2016) have shown the constant mixing of the lake and no vertical significant variation in chlorophyll-a, organic carbon and nutrients.

Analytical methods

Water temperature and dissolved oxygen were recorded *in situ* at all sites using a calibrated probe (model YSI-85). At the same time, the water transparency was determined by Secchi disk. Three liters of lake water were collected at each sampled site, and filtered through glass fiber filters (0.7 µm, Whatman GF/F) for extraction of chlorophyll-a with 90% acetone, corrected for pheophytin (Lorenzen, 1967). DOC was determined in acidified water samples using a high-temperature catalytic oxidation method on a TOC-5000 analyser (Shimadzu Scientific Instruments, Kyoto, Japan). Total nitrogen and total phosphorus were determined from unfiltered waters according to Valderrama (1981).

We obtained meteorological data from ICEA (Instituto de Controle do Espaço Aéreo), located 7 km away from the lake, and water level from CASAN (Companhia Catarinense de Água e Esgoto). Daily measurements were used to estimate the monthly-accumulated rainfall (mm), and monthly mean water level, from March 2007 to February 2015.

For estimates of pCO_2 in the water, we determined alkalinity through titration of 50 mL of lake water, adding sulfuric acid 0.01N and using a pHmeter (model Digimed DM-22). Equilibrium constants for inorganic carbon dissolution and speciation were corrected for temperature (Stumm & Morgan, 1996) and ionic strength was estimated from conductivity (Snoeyink & Jenkins, 1980), where ionic strength is $\sim 1.6 \times 10^{-5} \cdot$specific conductivity ($\mu S\ cm^{-1}$). The average pH from our data set was around 7.0 and only 7.5% of the samples showed pH lower than 6.0. In those cases, we excluded and interpolated the missing values to avoid CO_2 overestimates (Abril et al., 2015). We calculated pO_2 from temperature and dissolved oxygen (Garcia & Gordon, 1992) to evaluate the relationship with pCO_2.

CO_2 flux across air-water interface was estimated based on the diffusive model of Stumm & Morgan (1996): J_{CO2}(mol cm^{-2} h^{-1}) = $k \cdot \beta \cdot$ ([$CO_{2(aq)}$] – $K_H \cdot pCO_{2(air)}$) in order to determine if the lake was a source or sink of carbon. The model uses the gas transfer coefficient (k) based on wind speed (k=2.07+(0.215xU$^{1.7}$)), the chemical enhancement of diffusion (β), estimated from water temperature, pH, ionic strength, and wind speed (Bade & Cole, 2006), and the difference between the equilibrium and CO_2 concentrations in water surface in µmol L^{-1} (Cole & Caraco, 1998). Data from the Mauna Loa Observatory were used to access the atmospheric CO_2 concentration (Dlugokencky & Tans, 2016).

Statistical analyses

The sites and depths sampled in one month were considerated replicates to comparisons among months and years and ANOVA was conducted with data log (x+1) transformed. When significant, the differences were tested with post hoc Tukey-HSD test for multiple comparisons (n=600; significance level at $p<0.05$). A Pearson correlation analysis was performed to all variables log (x+1) transformed to identify how these variables affect each other and CO_2 flux, using only data from surface samples (n=96). A linear regression was performed between pCO_2 and pO_2 to determine the coupling between both gases.

Generalized linear model (GLM) was fitted to examine the potential association of pCO_2 with limnological and meteorological variable along the eight years of the study. We included the effect of the variables considering one-month lag time, where we investigated how the variable measured in the previous month could affect the pCO_2 in the next month. We applied the probability distribution model Gamma, with a log link function, which relates the mean value of one variable to its linear predictor (Crawley, 2012), using the *mass* package for model selection based on AIC (Venables & Ripley, 2002). A pseudo-determination coefficient (pseudo-R^2) was calculated to examine the fraction of the total variability explained by the selected model. This coefficient was calculated as 1 – (residual deviance/null deviance) according to Zuur et al. (2009).

The pCO_2 time series from March 2007 to February 2015 was used to predict pCO_2 values for 2015 and 2016 based on forecasting from ARIMA (autoregressive integrated moving averages) using the *forecast* package to predict potential changes in next years (Hyndman, 2016). The predicted values were plotted together with the values observed from pH and alkalinity along 2015-2016, which were not included in our results description and previous analyses.

7.4 Results

Water temperature varied monthly from 18.0 ± 1.58 ºC (mean ± standard deviation) in July to 28.2 ± 0.87 ºC in February, but with no significant difference between annual mean temperatures among years ($p>0.05$; Table 1). Rainfall however, differed significantly among years ($p<0.05$; Figure 2a), with the highest accumulated rainfall in 2011 with 2,197 mm; and the lowest in 2009 and 2012, 945 and 939 mm, respectively. In general, June was the driest month with 63 ± 36 mm, while January was the wettest (213 ± 157 mm). The low rainfall levels occurring during 2012 was identified as responsible for the reduction of 0.36 m in the water level of Peri Lake, as compared to 2011, which was the year with the highest water level (2.82 m; $p<0.05$). The water level remained low during 2013 and 2014, which also had low annual rainfalls (Figure 2b).

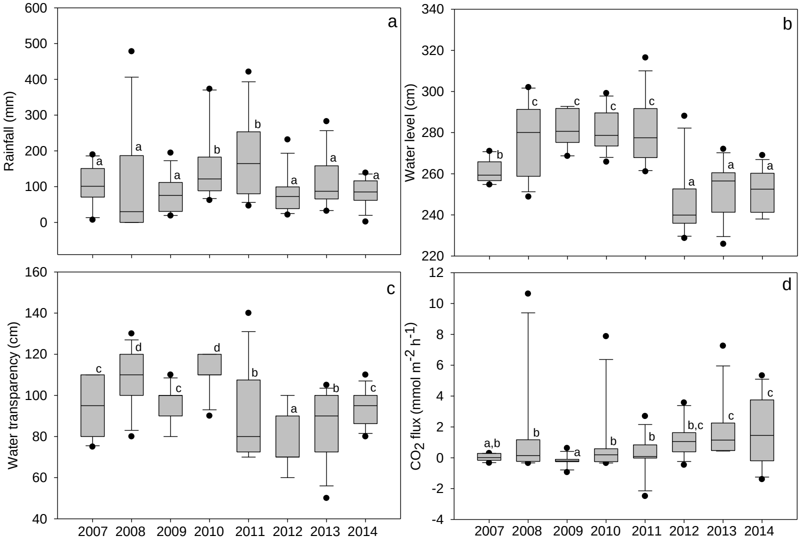

Figure 2: Annual variation of limnological variables in Peri Lake, for 2007–2014 period. Median, 10th, 25th, 75th and 90th percentiles as vertical boxes with error bars. Lower-case letters indicate significant difference between years, according to post hoc Tukey-HSD test.

During years of low rainfall and water level we also observed less transparent waters, especially during the dry 2012 (0.77 ± 0.14 m; Figure 2c), constrasting with the highest water transparency in 2010 (1.11 ± 0.10 m; $p<0.05$). CO_2 fluxes were generally positive except for 2009 where negative fluxes occured (-0.20 ± 0.35 mmol m^{-2} h^{-1}). CO_2 outgassing increasing significantly along the years with the highest flux measured in 2013 (1.76 ± 1.91 mmol m^{-2} h^{-1}; $p<0.05$; Figure 2d). Considering monthly variations in CO_2 fluxes, these were generally lowest in November (0.1 ± 0.57 mmol m^{-2} h^{-1}) and highest in August (2.3 ± 3.42 mmol m^{-2} h^{-1}). Overall, Peri Lake showed positive CO_2 flux in 65 % of the months sampled.

$p\mathrm{CO_2}$ was highly variable monthly (36 – 10,337 µatm; $p<0.05$) and was predominantly above the equilibrium with atmosphere (390 µatm; Figure 3a). Only during 2009, the $p\mathrm{CO_2}$ values were predominantly below atmospheric equilibrium (232 ± 177 µatm). On average, lower $p\mathrm{CO_2}$ was recorded in November (462 ± 398 µatm) and higher in April (3,010 ± 4,417 µatm). After 2009, the $p\mathrm{CO_2}$ increase significantly until 2012 (2,215 ± 3,020), decreasing to 1,403 ± 2,061 in 2013, and increasing again to 1,876 ± 3,061 in 2014 ($p<0.05$; Table 1). While Peri Lake was mostly CO_2 supersatured during the sampled months, oxygen saturation was below the equilibrium in 83% of the months (Figure 3c) and was significant different among years ($p<0.05$; Table 1). The highest oxygen saturation was observed in 2007 and the lowest in 2011 and 2012.

Chlorophyll-a and nutrients levels varied considerably between months (Figures 3b and 3d) with significant differences among years ($p<0.05$; Table 1), and chlorophyll-a showed a general trend of increasing until 2014. Monthly DOC ranged from 2.7 to 11.0 mg L^{-1} and chlorophyll-a from 4.6 to 55.3 µg L^{-1} (Figure 3b). High DOC was recorded in 2012 and high chlorophyll-a in 2013, while the lowest DOC was in 2010 and the lowest chlorophyll-a in 2007 (Table 1). Total phosphorus and total nitrogen showed the highest concentration in 2012 (Figure 3d; Table 1), with TN:TP ratio on average 70 ± 23. The lowest total phosphorus was recorded in 2007, while total nitrogen was the lowest in 2011, when the TN:TP ratio was on average 24 ± 10, the lowest TN:TP ratio along 2007-2015. Peri Lake was potentially P limited during the majority of the months (TN:TP ratio was lower than 50 only in 2008, 2010 and 2011). In general, both low TP and TN occurred in June (11.2 ± 3.47 µg L^{-1} and 563.2 ± 212.58 µg L^{-1}, respectively), while high TP was recorded in September (16.0 ± 5.06 µg L^{-1}) and high TN in August (789.7 ± 370.22 µg L^{-1}).

Table 1: Annual mean and standard deviation to all parameters sampled along 96 months in Peri Lake. Lower-case letters indicate the significant difference between years, according post hoc Tukey-HSD test.

Year	$p\text{CO}_2$ (µatm)	DO (%)	DOC (mg L^{-1})	Chl-a (µg L^{-1})	TN (µg L^{-1})	TP (µg L^{-1})	WT (ºC)
2007*	472^{b} ± 269	109^{d} ± 14	NS	14.0^{a} ± 5.60	790.3^{d} ± 185.11	10.7^{a} ± 4.83	22.3^{a} ± 3.69
2008	$1,857^{c}$ ± 3,283	91^{b} ± 15	NS	19.0^{b} ± 5.83	644.6^{c} ± 193.52	15.1^{b} ± 3.58	23.1^{a} ± 3.17
2009	232^{a} ± 177	95^{c} ± 7	3.6^{a} ± 0.39	18.3^{b} ± 5.86	818.1^{d} ± 181.11	13.5^{b} ± 2.31	23.3^{a} ± 3.89
2010	$1,210^{b}$ ± 2,207	94^{c} ± 14	3.1^{a} ± 0.31	19.6^{b} ± 3.16	378.9^{a} ± 157.85	11.9^{a} ± 5.34	22.3^{a} ± 3.26
2011	$1,851^{c}$ ± 3,293	90^{b} ± 12	3.3^{a} ± 0.56	26.1^{c} ± 5.38	353.3^{a} ± 129.84	15.2^{b} ± 2.17	22.2^{a} ± 4.13
2012	$2,215^{c}$ ± 3,020	90^{b} ± 11	5.6^{c} ± 1.14	32.3^{d} ± 9.44	$1,009.9^{d}$ ± 366.25	15.7^{b} ± 6.80	23.3^{a} ± 4.04
2013	$1,403^{b}$ ± 2,061	$93^{b,c}$ ± 6	$4.8^{b,c}$ ± 0.80	43.9^{e} ± 6.27	677.4^{c} ± 254.24	12.2^{a} ± 6.52	22.6^{a} ± 3.22
2014	$1,876^{c}$ ± 3,061	91^{b} ± 9	5.3^{c} ± 1.92	23.4^{b} ± 10.17	514.6^{b} ± 290.06	11.2^{a} ± 4.08	23.0^{a} ± 3.69
2015**	1,861 ± 1,255	92 ± 5	4.3 ± 0.32	30.2 ± 5.21	988.1 ± 182.96	18.6 ± 6.04	29.1 ± 0.37

DO: saturation of dissolved oxygen; DOC: dissolved organic carbon; Chl-a: chlorophyll *a*; TN: total nitrogen; TP: total phosphorus; WT: water temperature.

NS: not sampled. *10 months sampled. **the 2 months sampled were not included in the statistical analyses

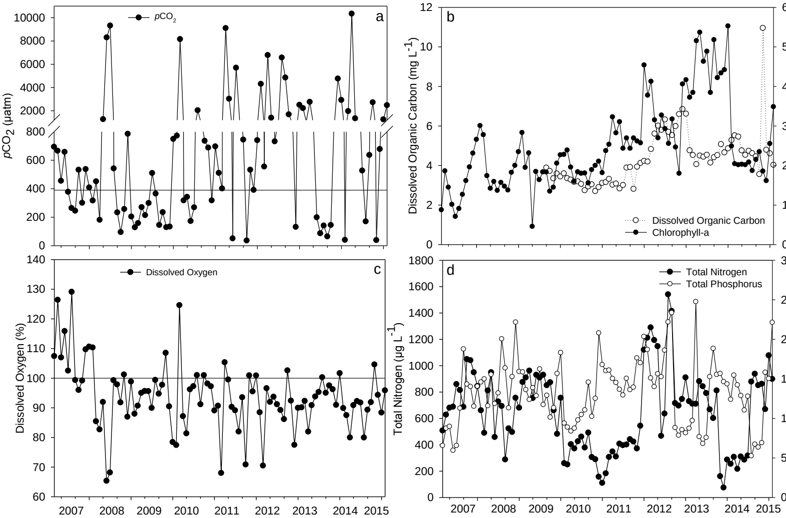

Figure 3: Monthly variation of limnological variables in Peri Lake, for 2007–2015 period. Each dot represents the monthly mean of all sites sampled in the lake – see methods. The line in panels a and c represents the equilibrium with atmosphere.

Decreases in rainfall yielded a positive relationship with decreasing water levels (r=0.32; p<0.05) and negatively correlated with DOC (r=-0.37; p<0.05). Water level correlated to many limnological variables suggesting water level to be a key environmental driver of water chemistry, including the negative correlation with CO_2 flux (r=-0.29; p<0.05). Other negative correlations with water level included DOC, TN and chlorophyll-a, while water level showed positive correlation with water transparency (Figure 4). Besides, CO_2 flux was positively correlated with chlorophyll-a and negatively with water transparency. We explored the coupling between pCO_2 and pO_2 through linear regression and found a weak and none significant correlation between the gases ($r^2 = 0.02$; p=0.13; Figure 5).

The correlations between all variables and pCO_2, further investigated with GLM, gave to us a model with 19 % of explanation and suggests that pCO_2 was related to water level and water temperature. For water temperature, the model showed that both temperatures measured in the month sampled and in the month before influence the pCO_2. Nutrients were also important to the model, however, only when one month of lag time was considered (Table 2). A forecast model was able to predicted the pCO_2 values to 2015 and 2016, showing a persistent CO_2 supersaturaion, as well as the values were similar to the observed in Peri Lake, based on pH and alkalinity measurements (Figure 6).

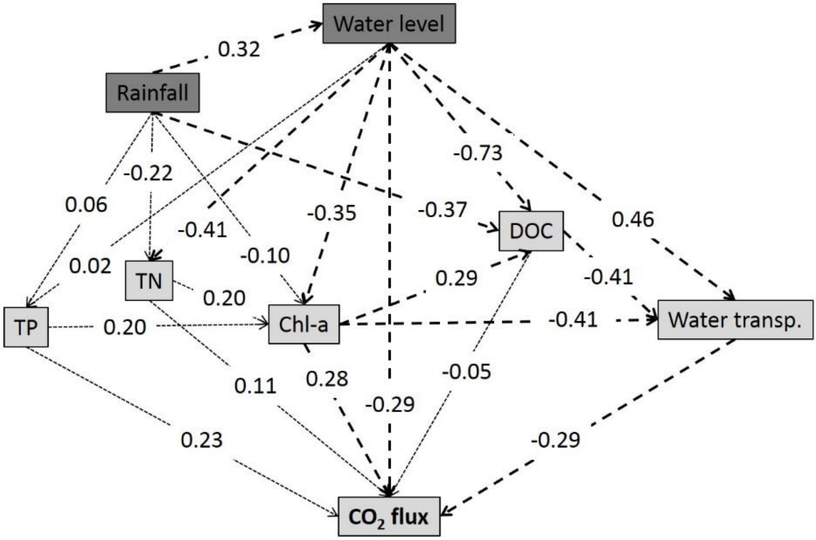

Figure 4: Diagram from Pearson's correlation coefficients to parameters direct and indirectly related to CO_2 flux in Peri Lake. TP: total phosphorus; TN: total nitrogen; Chl-a: chlorophyll-a; DOC: dissolved organic carbon. Dashed line represents significant correlation at p<0.05 and dotted line represents non-significant correlation.

Table 2: Generalized linear model results for pCO_2, in which the variables were also analyzed considering one-month lag time (.lg1) and the pseudo-R^2 was 19.0 %.

	Estimate	Std. Error	t value	p
Intercept	12.2777933	2.4341432	5.044	0.000002
Water level	-0.0221875	0.0079373	-2.795	0.00635
Water temperature	-0.1597450	0.0660435	-2.419	0.01761
Phosphorus.lg1	0.0842993	0.0358589	2.351	0.02094
Water temperature.lg1	0.1653238	0.0653296	2.531	0.01314
Nitrogen.lg1	-0.0008166	0.0005074	-1.609	0.11110

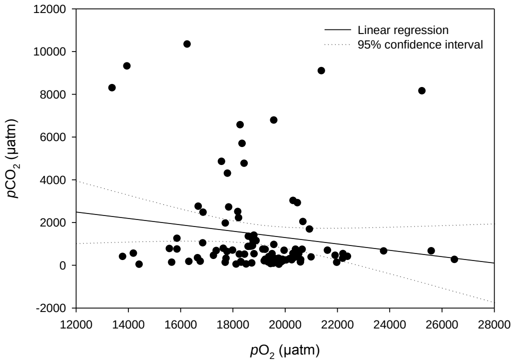

Figure 5: Linear regression between *p*CO_2 and *p*O_2 along 96 months in Peri Lake. $r^2 = 0.02$; $p = 0.13$; $y = –0.149*x + 4278.46$.

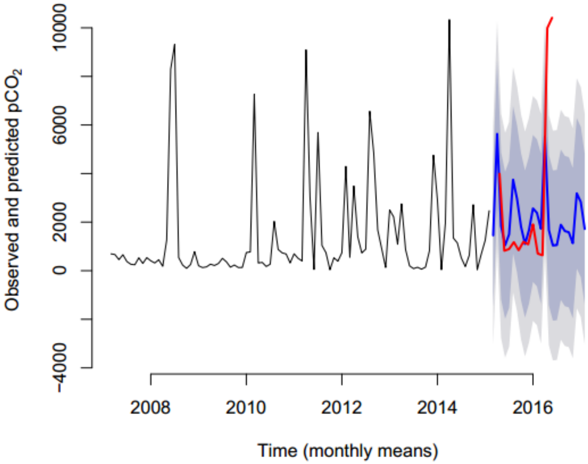

Figure 6: Observed *p*CO_2 from March 2007 to February 2015 (black line) and predicted values for 2015–2016 (blue line). The red line represents the *p*CO_2 values observed from pH and alkalinity measured in Peri Lake along 2015–2016. The shaded areas are the confidence intervals of 80 and 95%.

7.5 Discussion

Peri Lake was predominantly supersaturated with CO_2, suggesting a high decomposition of both allochthonous and autochthonous organic carbon. High respiration rates were identified in bottle incubations and in free-water measurements (Tonetta et al., 2015; 2016), corroborating with the high processing of carbon through biological activity in Peri Lake. Except in 2009, where CO_2 influx from the atmosphere was predominant, CO_2 supersaturation was recorded in all years, and along 2012–2014 the CO_2 flux to the atmosphere was intensified mainly due to the low rainfall, which reduced water level in those years. Similar rainfall effects were observed by Tsai et al. (2016), where absence of rainfall decreased the water level, as well as changed the lake trophic status.

Although clearly correlations do not give insight in causal relationships, various mechanisms could contribute to strong effects of water level in the overall changes in Peri Lake. For example, elevated pCO_2 and CO_2 emission during low water levels could be related to a stronger benthic-pelagic coupling, where elevated water and sediment temperatures increase benthic respiration and thereby CO_2 production (Vadeboncoeur et al., 2008). In some lakes the benthic contribution can represent 80% of the whole metabolism, depending on morphometry and trophic state (Vadeboncoeur et al., 2003). Our findings about the absent vertical difference in CO_2 concentration suggest that the lower water volume and the ephemeral nature of the stratification in Peri Lake cause a more effective full mixing of the lake (Tonetta et al., 2016), where CO_2 in the deepest part becomes more effectively mixed into the upper parts of the water column. Furthermore, the high CO_2 flux during months of low water level was similar to recorded by Jones et al. (2016), where the high water residence time determined the trophic state of the aquatic systems, in turn, CO_2 flux was higher when the systems presented a lower water column depth.

The pCO_2 values recorded in this study are within the range of other tropical and subtropical lakes (Kosten et al., 2010; Marotta et al., 2010b; Muduli et al., 2012); and other lakes around the world (Duarte & Prairie 2005; Sobek et al., 2007). In a recent study, Pinho et al. (2016) found that pCO_2 in Brazilian lakes were predominantly supersatured ranging from 900 to 8,300 µatm. Generally, in tropical lakes the rainfall has a great importance to the CO_2 concentration, since it can carry organic matter to the lakes that sustain the respiration (Marotta et al., 2010a). In our analyses, DOC did not correlated with CO_2 flux, corroborating the results from Kosten et al. (2010) and Pinho et al.

(2016) that also did not recorded correlation between DOC and pCO_2 in tropical lakes. In warmer lakes is expected that temperature stimulate respiration more than primary production (Yvon-Durocher et al., 2010) and the lack of relationship between DOC and CO_2 however, suggests that heterotrophy is not related to the dissolved organic part of the organic matter. Therefore, the particulate organic matter in the water column and/or in the sediment may be more important contributing to the high light extinction in the water column, more respiration in both compartiments and photooxidation near the surface.

The decoupling between primary production and respiration suggested by the weak correlation between CO_2 and O_2 imply in high sediment respiration rates producing large amounts of CO_2 from the bottom to the surface, as recorded by Tonetta et al. (2016). Additionally, the catchment area can contributed with high CO_2 since the Streams surrounding Peri Lake receive high amount of terrestrial organic matter (Lisboa et al. 2014). Thus, these processes can contribute to the CO_2 supersaturation in the lake without affect the O_2 concentrations, as mentioned by Fontes et al. (2015). Tonetta et al. (2016) found that under turbid low light conditions in Peri Lake, the coupling between primary production and respiration was weakened, as primary production became light limited while ecosystem respiration remained high. This suggest that respiration in the benthic compartment influences the overall imbalance between primary production and respiration in pelagic waters, resulting in excess production of CO_2 under conditions of low transparency occurring at low water levels. If the sediment becomes anaerobic, organic matter in the sediment will release methane, which is partly or completely oxidized by methanotrophic bacteria to CO_2 in the water column (Kortelainen et al., 2000). Other processes, however, could be taken into account, such as photochemical DOC degradation by high light levels in subtropical areas (Bertilsson & Tranvik, 2000), in turn increasing CO_2 via direct DOC oxidation, where no oxygen is envolved in the process (Torgensen & Branco, 2007); and indirectly through stimulation of bacterial respiration by the photodegraded DOC (Amado et al., 2006). DOC from algae is more available to bacteria compared to the DOC originated from the forest, which is more suitable to photochemical reactions (Amado et al., 2006). Given the positive correlation between DOC and chlorophyll-a (Figure 4) DOC in Peri Lake seems to be mainly from autochthonous origin. However, some allochthonous DOC will likely also enter the lake from decomposition of the riparian vegetation. Fontes et al. (2013) found that the heterotrophic bacteria biomass regulated CO_2 concentrations in Peri

Lake. Since bacterial production and respiration are generally higher in the tropics (Amado et al., 2013), we could expect that light and bacteria cooperate in order to enhance the carbon degradation and CO_2 supersaturation (Farjalla et al., 2009).

Phosphorus showed a positive, even though not significant, correlation with CO_2, and both nitrogen and phosphorus varied significantly over time in Peri Lake. Interestingly, introducing a lag time of one month in our GLM analysis raised the importance of nutrients to predict levels of pCO_2, probably because nitrogen and phosphorus stimulate phytoplankton growth with some time delay. The high CO_2 flux in months of high chlorophyll-a in Peri Lake contrast to the general findings in other tropical and temperate lakes, where CO_2 evasion declines with increasing lake productivity (Trolle et al., 2012; Pacheco et al., 2013; Peixoto et al., 2013). For example, Trolle et al. (2012), analyzing 151 lakes, found that the CO_2 uptake rates were higher in lakes with high chlorophyll-a, changing from CO_2 source to sink as lakes became more eutrophic. Conversely, a study from the Cochin estuary found that organic enrichment caused a deterioration in water quality, and the environment was a CO_2 source to the atmosphere (Gupta et al., 2009). Other studies have shown that even in eutrophic lakes the CO_2 supersaturation can still be recorded. For example in a tropical reservoir despite the high primary production in pelagic waters, high rates of organic carbon mineralization were recorded in the water and sediment, rending to the lake a strong CO_2 emission to the atmosphere (Almeida et al., 2016).

The increase in chlorophyll-a in Peri Lake as water level decreased could contributed to the high decomposition of these autochthonous organic matter in the water column, increasing the CO_2 concentration. Besides the decrease in photic zone by the increase of particulate matter could limit the primary production. In a mesocosm experiment Marotta et al. (2012), observed that CO_2 emissions persisted following the eutrophication of humic waters. While nutrients and chlorophyll-a were related to the CO_2 fluxes, the overall low power of the GLM (19%) suggests that other variables not sampled in this study could influence the CO_2 concentration in Peri Lake, as already reported by Fontes et al (2015). These likely include physical variables related to morphology and hydrology of the lake, as well described by other studies (Kosten et al., 2010; Jones et al., 2016).

A study on the importance of meteorological conditions on the CO_2 seasonality in Peri Lake was conducted by Fontes et al. (2015), but the authors did not explored the effects of rainfall in the water level.

They however found higher CO_2 levels occurring during the transition between seasons, which influences water column stability and could increase the influence of CO_2 fluxes from the bottom to the surface waters. The authors also reinforced the importance of meteorological events to CO_2 fluxes, regarding to El Niño and La Niña years. In El Niño year's higher rainfall is expected and it can carry allochthonous organic matter to the lake, supporting elevated respiration rates and CO_2 supersaturation (Marotta et al., 2010a). On the other hand, La Niña year's, where drier periods are expected also can contributed with the CO_2 supersaturation due to the benthic-pelagic coupling, as we observed in this study. Using a forecast model, we predicted that Peri Lake in the next years will present a persistent CO_2 supersaturation.

Historical data about rainfall in Santa Catarina Island shows that along 1992–2006 the annual average of rainfall was 1,674 mm (data from ICEA), a little higher than along 1961-1990, which was 1,518 mm. Thus, the recorded rainfall in 2012 (939 mm), and in the following years (around 1,200 mm) seems to be below the normal rainfall range to these area and therefore a climatic disturbance responsible for keeping the low level of Peri Lake. As the regional climate change scenario predicts rising air temperatures and reductions in rainfall in some areas (IPCC, 2014), reduction in water levels will likely occur affecting water column stability and chances of cyanobacterial blooms, which will affect the carbon cycling (Zohary & Ostrovsky, 2011). In subtropical regions the droughts have become more intense and widespread (Fauchereau et al., 2003) and similar physical changes have occurred in temperate lakes, causing major shifts in ecosystem functioning (Noges et al., 2010; Geraldes & George, 2012). In a recent study, Catalán et al. (2016) described the influence of hydrological variability on inland waters carbon cycle, in which wetter or drier regions will experience changes in organic carbon decay rates.

In summary, our studied lake experienced a pronounced water level reduction from changes in rainfall, which was also responsible for changes in organic carbon, nutrients and chlorophyll-a concentration, in turn enhancing CO_2 flux to the atmosphere. The unexpected positive relationship between chlorophyll-a and CO_2 suggests that lakes experiencing some level of eutrophication may continue to act as conduits of CO_2 to the atmosphere. Our analyses revealed that nutrients were important to CO_2 supersaturation when one month of lag time was considered and preditive analyses indicates persistent CO_2 supersaturation for the comming years. Our results highlight that absence of rainfall can induce significant physical and chemical changes in the systems, in turn affecting the biological processes and the rate of carbon cycling in the lake. Further studies about other CO_2 sources in Peri Lake and the importance of benthic-pelagic coupling with decreasing water levels are needed to better understand lake responses to droughts and to explain the observed decoupling between CO_2 and O_2.

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7.6 References

Abril, G., S. Bouillon, F. Darchambeau, C. R. Teodoru, T. R. Marwick, F. Tamooh, F. O. Omengo, N. Geeraert, L. Deirmendjian, P. Polsenaere & A. V. Borges, 2015. Technical Note: Large overestimation of pCO_2 calculated from pH and alkalinity in acidic, organic–rich freshwaters. Biogeosciences 12: 67–78.

Almeida, R. M., G. N. Nóbrega, P. C. Junger, A. V. Figueiredo, A. S. Andrade, C. G. B. Moura, D. Tonetta, E. S. Oliveira Jr, F. Araújo, F. Rust, J. M. Piñeiro-Guerra, J. R. Mendonça Jr, L. R. Medeiros, L. P. Silva, M. Miranda, M. R. A. Costa, M. L. Melo, R. Nobre, T. Benevides, F. Roland, J. de Klein, N. O. Barros, R. Mendonça, V. Becker, V. Huszar & S. Kosten, 2016. High primary production contrasts with intense carbon emission in a eutrophic tropical reservoir. Frontiers in Microbiology doi:10.3389/fmicb.2016.00717.

Amado, A. M., V. F. Farjalla, F. A. Esteves, R. L. Bozelli, F. Roland & A. Enrich-Prast, 2006. Complementary pathways of dissolved organic carbon removal pathways in clear-water Amazonian ecosystems: photochemical degradation and bacterial uptake. FEMS Microbiology Ecology 56: 8–17.

Amado, A. M., F. Meirelles-Pereira, L. O. Vidal, H. Sarmento, A. L. Suhett, V. F. Farjalla, J. B. Cotner & F. Roland, 2013. Tropical freshwater ecosystems have lower bacterial growth efficiency than temperate ones. Frontiers in Microbiology 4: 167.

Balmer, M. B. & J. A. Downing, 2011. Carbon dioxide concentrations in eutrophic lakes: undersaturation implies atmospheric uptake. Inland Waters 1: 125–132.

Bade, D. L. & J. J. Cole, 2006. Impact of chemically enhanced diffusion on dissolved inorganic carbon stable isotopes in a fertilized lake. Journal of Geophysical Research 111: C01014.

Bertilsson, S. & L. Tranvik, 2000. Photochemical transformation of dissolved organic matter in lakes. Limnology and Oceanography 45: 753–762.

Catalán, N., R. Marcé, D. N. Kothawala & L. J. Tranvik, 2016. Organic carbon decomposition rates controlled by water retention time across inland waters. Nature Geoscience doi: 10.1038/NGEO2720.

Cole, J. J. & N. F. Caraco, 1998. Atmospheric exchange of carbon dioxide in a low–wind oligotrophic lake measured by the addition of SF6. Limnology and Oceanography 43: 647–656.

Cole, J. J., Y. T. Prairie, N. F. Caraco, W. H. McDowell, L. J. Tranvik, R. G. Striegl, C. M. Duarte, P. Kortelainen, J. A. Downing, J. J. Middelburg & J. Melack, 2007. Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. Ecosystems 10: 171–184.

Crawley, M. J., 2012. The R Book. Wiley. 1076 pages

Duarte, C. M. & Y. T. Prairie, 2005. Prevalence of heterotrophy and atmospheric CO_2 emissions from aquatic ecosystems. Ecosystems 8: 862–870.

Dlugokencky, E. & P. Tans. 2016. National Oceanic and Atmospheric Administration – NOAA/ESRL. <URL:http://www.esrl.noaa.gov/gmd/ccgg/trends/>.

Farjalla, V. F., A. M. Amado, A. L. Suhett & F. Meirelles-Pereira, 2009. DOC removal paradigms in highly humic aquatic ecosystems. Environmental Science and Pollution Research 16: 531–538.

Fauchereau, N., S. Trzaska, M. Rouault & Y. Richard, 2003. Rainfall Variability and Changes in Southern Africa during the 20th Century in the Global Warming Context. Natural Hazards 29: 139–154.

Fontes, M. L. S., D. Tonetta, L. Dalpaz, R. V. Antônio & M. M. Petrucio, 2013. Dynamics of planktonic prokaryotes and dissolved carbon in a subtropical coastal lake. Frontiers in Microbiology 4: 71.

Fontes, M. L. S., H. Marotta, S. MacIntyre & M. M. Petrucio, 2015. Inter– and intra–annual variations of pCO_2 and pO_2 in a freshwater subtropical coastal lake. Inland waters 5: 107–116.

Garcia, H.E. & L. I. Gordon, 1992. Oxygen solubility in seawater – better fitting equations. Limnology and Oceanography 37: 1307–1312.

Geraldes, A. M. & C. George, 2012. Limnological variations of a deep reservoir in periods with distinct rainfall patterns. Acta Limnologica Brasiliensia 24: 417–426.

Granéli, W., M. Lindell & L. Tranvik, 1996. Photo-oxidative production of dissolved inorganic carbon in lakes of different humic content. Limnology and Oceanography 41: 698–706.

Gupta, G. V. M., S. D. Thottathil, K. K. Balachandran, N. V. Madhu, P. Madeswaran & S. Nair, 2009. CO_2 supersaturation and net heterotrophy in a tropical estuary (Cochin, India): influence of anthropogenic effect. Ecosystems 12: 1145–1157.

Hennemann, M. C. & M. M. Petrucio, 2011. Spatial and temporal dynamic of trophic relevant parameters in a subtropical coastal lagoon in Brazil. Environmental Monitoring and Assessment 181: 347–361.

Hennemann, M. C. & M. M. Petrucio, 2016. High chlorophyll a concentration in a low nutrient context: discussions in a subtropical lake dominated by Cyanobacteria. Journal of Limnology doi: 10.4081/jlimnol.2016.1347.

Hyndman, R. J., 2016. Forecast: Forecasting functions for time series and linear models. R package version 7.1, <URL:http://github.com/robjhyndman/forecast>.

IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change In R.K. Pachauri & L.A. Meyer (eds), Core Writing Team. IPCC, Geneva.

Jeppesen, E., S. Brucet, L. Naselli–Flores, E. Papastergiadou, K. Stefanidis, T. Nõges, P. Nõges, J. L. Attayde, T. Zohary, J. Coppens, T. Bucak, R. F. Menezes, F. R. S. Freitas, M. Kernan, M. Søndergaard & M. Beklioğlu, 2015. Ecological impacts of global warming and water abstraction on lakes and reservoirs due to changes in water level and related changes in salinity. Hydrobiologia 750: 201–227.

Jones, J. R., D. V. Obrecht, J. L. Graham, M. B. Balmer, C. T. Filstrup & J. A. Downing, 2016. Seasonal patterns in carbon dioxide in 15 mid-continent (USA) reservoirs. Inland Waters 6: 265–272.

Kirk, J. T. O., 1994. Light and Photosynthesis in Aquatic Ecosystems. Cambridge Univ. Press, New York.

Kortelainen, P., J. T. Huttunen, T. Väisänen, T. Mattsson, P. Karjalainen & J. Martikainen, 2000. CH_4, CO_2 and N_2O supersaturation in 12 Finnish lakes before the ice melt. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 27: 1410–1414.

Kosten, S., F. Roland, D. M. L. Motta Marques, E. H. Van Nes, N. Mazzeo, L. S. L. Sternberg, M. Scheffer & J. J. Cole, 2010. Climate-dependent CO_2 emissions from lakes. Global Biogeochemical Cycles 24: GB2007.

Lisboa, L. K., A. L. L. Silva, A. E. Siegloch, J. F. J. Gonçalves & M. M. Petrucio, 2014. Temporal dynamics of allochthonous coarse particulate organic matter in a subtropical Atlantic Rainforest Brazilian stream. Marine and Freshwater Research 66: 674–680.

Lorenzen, C. J., 1967. Determination of chlorophyll and pheopigments: Spectrophotometric equations. Limnology and Oceanography 12: 343–346.

Schiemerand, F. & K. T. Boland, 1996. Perpectives in Tropical Limnology. Academic Publishing, Amsterdan.

Maberly, S. C., P. A. Barker, A. W. Stott & M. M. De Ville, 2012. Catchment productivity controls CO_2 emissions from lakes. Nature Climate Change 3: 391–394.

Marcé, R., B. Obrador, J. A. Morguí, J. L. Riera, P. López & J. Armengol, 2015. Carbonate weathering as a driver of CO_2 supersaturation in lakes. Nature Geoscience 8: 107–111.

Marotta, H., C. M. Duarte, S. Sobek, A. Enrich-Prast, 2009. Large CO_2 disequilibria in tropical lakes. Global Biogeochemical Cycles 23: GB4022.

Marotta, H., C. M. Duarte, L. Pinho & A. Enrich–Prast, 2010a. Rainfall leads to increased $p\mathrm{CO}_2$ in Brazilian coastal lakes. Biogeosciences 7: 1607–1614.

Marotta, H., C. M. Duarte, F. Meirelles–Pereira, L. Bento, F. A. Esteves & A. Enrich–Prast, 2010b. Long–term CO_2 variability in two shallow tropical lakes experiencing episodic eutrophication and acidifications events. Ecosystems 13: 382–392.

Marotta, H., C. M. Duarte, B. A. Guimarães-Souza & A. Enrich–Prast, 2012. Synergistic control of CO_2 emissions by fish and nutrients in a humic tropical lake. Oecologia 168: 839–847.

Muduli, P. R., V. V. Kanuri, R. S. Robin, B. C. Kumar, S. Patra, A. V. Raman, G. N. Rao & B. R. Subramanian, 2012. Spatio–temporal variation of CO_2 emission from Chilika Lake, a tropical coastal lagoon, on the east coast of India. Estuarine, Coastal and Shelf Science 113: 305–313.

Noges, P., U. Mischke, R. Laugaste & A. G. Solimini, 2010. Analysis of changes over 44 years in the phytoplankton of Lake Võrtsjarv (Estonia): the effect of nutrients, climate and the investigator on phytoplankton–based water quality indices. Hydrobiologia. 646: 33–48.

Pacheco, F. S., F. Roland & J. A. Downing, 2013. Eutrophication reverses whole–lake carbon budgets. Inland Waters 4:41–48.

Pacheco, F. S., M. C. S. Soares, A. T. Assireu, M. P. Curtarelli, F. Roland, G. Abril, J. L. Stech, P. C. Alvalá & J. P. Ometto, 2015. The effects of river inflow and retention time on the spatial heterogeneity of chlorophyll and water–air CO_2 fluxes in a tropical hydropower reservoir. Biogeosciences 12: 147–162.

Peixoto, R. B., H. Marotta & A. Enrich–Prast, 2013. Experimental evidence of nitrogen control on $p\mathrm{CO}_2$ in phosphorus enriched humic and clear coastal lagoon waters. Frontiers in Microbiology, Aquatic Microbiology 4: 1–6.

Pinho, L., C. M. Duarte, H. Marotta & A. Enrich–Prast, 2016. Temperature–dependence of the relationship between $p\mathrm{CO}_2$ and dissolved organic carbon in lakes. Biogeosciences 13: 865–871.

R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL<:http://www.R-project.org/>.

Rantakari, M. & P. Kortelainen, 2005. Interannual variation and climate regulation of the CO_2 emission from large boreal lakes. Global Change Biology 11: 1368–1380.

Raymond, P. A., J. Hartmann, R. Lauerwald, S. Sobek, C. McDonald, M. Hoover, D. Butman, R. Striegl, E. Mayorga, C. Humborg, P. Kortelainen, H. Durr, M. Meybeck, P. Ciais & P. Guth, 2013. Global carbon dioxide emissions from inland waters. Nature 503: 355–359.

Roland, F., V. L. M. Huszar, V. F. Farjalla, A. Enrich–Prast, A. M. Amado & J. P. H. B Ometto, 2012. Climate change in Brazil: perspective in the biogeochemistry of inland waters. Brazilian Journal of Biology 72: 709–722.

Snoeyink, V. L. & D. Jenkins, 1980. Water Chemistry. Wiley, New York.

Sobek, S., L. J. Tranvik, Y. T. Prairie, P. Kortelainen & J. J. Cole, 2007. Patterns and regulation of dissolved organic carbon: An analysis of 7,500 widely distributed lakes. Limnology and Oceanography 52: 1208–1219.

Staehr, P. A., L. Baastrup-Spohr, K. Sand-Jensen & C. Stedmon, 2012. Lake metabolism scales with lake morphometry and catchment conditions. Aquatic Sciences 74: 155–169.

Stumm, W. & J. J. Morgan, 1996. Aquatic Chemistry: Chemical Equilibria and Rates in Natural Waters. Wiley–Interscience, New York.

Tonetta, D., R. Laudares-Silva & M. M. Petrucio, 2015. Planktonic production and respiration in a subtropical lake dominated by cyanobacteria. Brazilian Journal of Biology 75: 460–470.

Tonetta, D., P. A. Staehr, R. Schmitt & M. M. Petrucio, 2016. Physical conditions driving the spatial and temporal variability in aquatic metabolism of a subtropical coastal lake. Limnologica 58: 30–40.

Torgersen, T. & B. Branco, 2007. Carbon and oxygen dynamics of shallow aquatic systems: Process vectors and bacterial productivity. Journal of Geophysical Research 112: G03016.

Tranvik, L. J., *et al.,* 2009. Lakes and reservoirs as regulators of carbon cycling and climate. Limnology and Oceanography 54: 2298–2314.

Trolle, D., P. A. Staehr, T. A. Davidson, R. Bjerring, T. L. Lauridsen, M. Søndergaard & E. Jeppesen, 2012. Seasonal dynamics of CO_2 flux across the surface of shallow temperate lakes. Ecosystems 15: 336–347.

Tsai, J. W., T. K. Kratz, J. A. Rusak, W. Y. Shih, W. C. Liu, S. L. Tang & C. Y. Chiu, 2016. Absence of winter and spring monsoon changes water level and rapidly shifts metabolism in a subtropical lake. Inland Waters 6: 436–448.

Vachon, D. & Y. T. Prairie, 2013. The ecosystem size and shape dependence of gas transfer velocity versus wind speed relationships in lakes. Canadian Journal of Fisheries and Aquatic Sciences 70: 1757–1764.

Vadeboncoeur, Y., E. Jeppesen, M. J. V. Zanden, H. H. Schierup, K. Christoffersen & D. M. Lodge, 2003. From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. Limnology and Oceanography 4: 1408–1418.

Vadeboncoeur, Y., G. Peterson, M. J. V. Zanden & J. Kalff, 2008. Benthic algal production across lake size gradients: interactions among morphometry, nutrients, and light. Ecology 89: 2542–2552.

Valderrama, J. C., 1981. The simultaneous analysis of total nitrogen and phosphorous in natural waters. Marine Chemistry 10: 109–122.

Venables, W. N. & B. D. Ripley, 2002. Modern Applied Statistics with S. Springer, New York.

Weyhenmeyer, G. A., S. Kosten, M. B. Wallin, L. J. Tranvik, E. Jeppesen & F. Roland, 2015. Significant fraction of CO_2 emissions from boreal lakes derived from hydrologic inorganic carbon inputs. Nature Geoscience 8: 933–936.

Williamson, C. E., J. E. Saros, W. F. Vincent & J. P. Smol, 2009. Lakes and reservoirs as sentinels, integrators, and regulators of climate change. Limnology and Oceanography 54: 2273–2282.

Yvon-Durocher, G., J. I. Jones, M. Trimmer, G. Woodward & J. M. Montoya, 2010. Warming alters the metabolic balance of ecosystems. Philosophical Transactions of the Royal Society 365: 2117–2126.

Zohary, T. & I. Ostrovsky, 2011. Ecological impacts of excessive water level fluctuations in stratified freshwater lakes. Inland Waters 1: 47–59.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev & G. M. Smith, 2009. Mixed Effects Models and extensions in Ecology with R. Springer, US.

8 CAPÍTULO 4

Contrasting responses of CO_2 and O_2 fluxes to nutrients and organic matter additions in a mesocosm study in a tropical lake

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Lagoa Carioca e experimento em mesocosmo desenvolvido em janeiro de 2015
Foto: acervo pessoal

8.1 Abstract

Eutrophication and brownification are two conditions affecting the metabolic balance in aquatic ecosystems. To determine how the additions of inorganic nutrients (+NUTRI) and allochthonous organic matter (+OM) affected the air-water CO_2 and O_2 fluxes (*F*) we analyzed the daily dynamics in these gases over nine days in a mesocosm experiment. Additionally, we estimated the resistance and resilience of the gases to the different treatments. The control, representing the original state of the lake, showed low daily variability and a predominant FCO_2 to the atmosphere, but with mean values close to zero (0.1 ± 0.29 mmol m^{-2} d^{-1}). In +NUTRI and +NUTRI+OM treatments the FCO_2 and FO_2 showed similar response, where the FCO_2 was negative during all days (mean -1.7 mmol m^{-2} d^{-1}) and positive FO_2 which peaked around days 5 and 6. The +OM treatment intensified the FCO_2 to the atmosphere (0.5 ± 0.83 mmol m^{-2} d^{-1}) with highest values at day 7, decreasing after that. The +NUTRI and +NUTRI+OM treatments showed low resistance index values for CO_2, while high resistance was found for the control and +OM treatment. In general, nutrients promoted larger overall changes and higher daily variability in FCO_2 and FO_2 than organic matter additions. While nutrients were quickly consumed, levels of dissolved organic matter were more constant suggesting a greater resilience of the ecosystem, for OM additions. In conclusion, eutrophication (nutrients addition) and brownification (+OM) promoted contrasting effects in gas fluxes in a mesocosm experiment, where the lake was more responsive to nutrients, promoting negative FCO_2, while organic matter promoted positive FCO_2 to the atmosphere in a tropical lake.

Keywords: carbon cycling; daily dynamics; eutrophication; brownification resistance; resilience.

8.2 Introduction

Aquatic systems can be considered a sink or source of carbon dioxide (CO_2) to the atmosphere, using either dissolved inorganic carbon (e.g. Sobek et al. 2005; Trolle et al. 2012; Denfeld et al. 2016) or dissolved oxygen (O_2) as a tracer of carbon emission (e.g. Staehr et al. 2010; Laas et al. 2012; Brighenti et al. 2015). On daily scales the metabolic processes of photosynthesis and respiration often dominate gas fluxes in the pelagic zone, via simultaneous production and consumption of CO_2 and O_2, which enable us to use both gases as indicators of aquatic metabolism (Hanson et al. 2006). To determine the importance and the function of the lake in the carbon cycling, as well as the daily dynamics of the gases, is primordial to understand how the ecosystems respond to climatic changes affecting the limnological conditions of the lakes (Tranvik et al. 2009).

It is commonly assumed that CO_2 supersaturation derives from net heterotrophy, which means that aquatic respiration is higher than primary production (Dodds and Cole 2007). In general, this condition is supported in part by terrestrial organic matter (OM), despite other geochemical processes also contributing to the lake CO_2 supersaturation, such as catchment productivity and carbonate weathering (Marotta et al. 2010; Maberly et al. 2012; Marcé et al. 2015). Several studies have identified the factors related to the CO_2 supersaturation, such as the influence of temperature (Kosten et al. 2010), organic carbon (Hanson et al. 2003), geographical location (Lazzarino et al. 2009), weather (Kelly et al. 2001), and trophic status (Trolle et al. 2012). Temperature influences all the biological processes, where in warmer conditions the organisms typically exhibit higher primary production and respiration rates (Brown et al. 2004) mirrored by high rates of nutrient and carbon cycling. Usually the increase of nutrients (eutrophication) have strong effects on primary production in aquatic ecosystems (Palmer et al. 2013; Staehr et al. in press), where nitrogen and phosphorus inputs enhance primary production and may cause CO_2 depletion, changing the balance between primary production and respiration (Cole et al. 2000). On the other hand, inputs of OM (brownification) directly enhance the activity of the heterotrophic communities and indirectly reduces the autotrophic activity by reducing the light available (Ojala et al. 2011; Granéli 2012; Mormul et al. 2012; Thrane et al. 2014). In highly productive aquatic systems, rates of respiration are generally also elevated and a strong correlation between CO_2 and O_2 is expected (Zhai et al. 2009).

Precipitation events and human influence can impact the aquatic ecosystems through OM and nutrients inputs. In both cases, we can considered these inputs as disturbances or perturbations since they affect the stability of the communities and the ecosystems processes (Pimm 1984; Carpenter et al. 2001). Perturbations cause shifts in the ecosystems conditions which lead to alternative stable states before the system comes back to the original conditions previous the perturbation, or to be conducted to a new equilibrium status (Scheffer and Carpenter 2003). The degree to which an environmental variable changes following a perturbation is called resistance, and how fast a variable returns towards its equilibrium following a perturbation is the resilience (Pimm 1984). Addressing the resistance and resilience of the system can be important to understand how adaptive the ecosystems are in maintaining the ecosystem functions (Carpenter et al. 2001).

Eutrophication and brownification are two aquatic conditions that can lead to contrasting effects in the carbon cycling. The first promoting increases in O_2 and the second increases in CO_2. In this study, we tested the effects of inorganic nutrients and allochthonous OM additions on the daily variability of air-water fluxes of CO_2 and O_2 over nine days in a tropical lake. Additionally, we explore a new approach to estimate the resistance and resilience of the lake using CO_2 and O_2. We hypothesized that day-to-day variability in FCO_2 and FO_2 would increase with additions of inorganic nutrients and OM. These manipulations are however, expected to have contrasting effects, with more CO_2 for OM additions versus more O_2 for nutrients additions. Additionally, we expect that responses to OM and nutrient additions will change over time as nutrients become depleted and the pool of carbon changes in quantity and quality.

8.3 Material and Methods

Mesocosm setup

A mesocosm experiment was carried out at the tropical freshwater Carioca Lake (19°45’26.0’’S; 42°37’06.2"W), an environment protected from direct human impacts, located in the Rio Doce Park in the Atlantic Forest, south-east Brazil. The weather is well-defined with a dry season during May–September and rainy season during October–March. Carioca Lake is a warm monomictic lake, with a stable thermal stratification period beginning in September and lasting until May and a mixing period from June to August (Brighenti et al. 2015).

The mesocosms were deployed in the pelagic area of the lake (6 to 8 m) and were filled with water pumped from the lake with no sediment inside the mesocosms. Each treatment (control, +NUTRI, +OM and +NUTRI+OM) was replicated four times, totalizing 16 mesocosms (Figure 1). The mesocosms consisted of transparent plastic bags (low-density polyethylene 30 µm) with ~1.5 m depth, 1.30 m of diameter and around 2000 L of volume, were closed at the bottom, but opened at surface to allow gas exchange between water and atmosphere. We conducted the study during nine days starting on January 20, 2015, which we called day 0, where the additions of nutrients and OM were conducted.

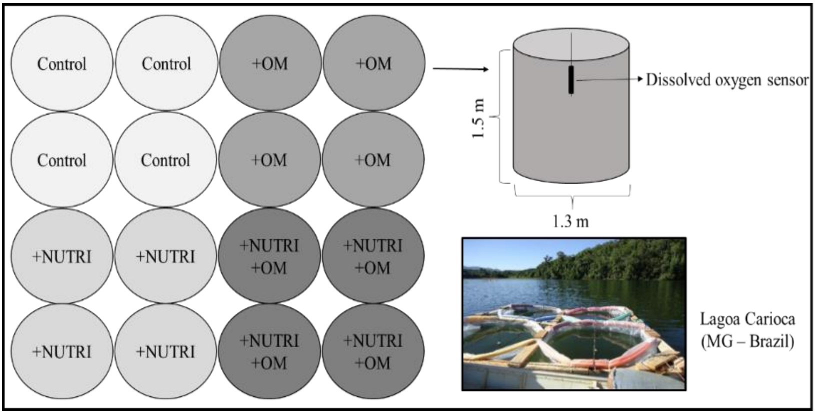

Figure 1: Design of the mesocosm study performed in Carioca Lake. Control represents the lake original state regarding nutrients and organic carbon. +NUTRI represents the additions of dissolved inorganic nitrogen and phosphate, +OM represents the additions of allochthonous organic matter and +NUTRI+OM represents the combined nutrients and organic matter additions.

The control mesocosms were conducted without any addition representing the original limnological condition of the lake (Table 1). Dissolved inorganic nitrogen (DIN = nitrate + nitrite + ammonia) at day 0 was 0.06 ± 0.02 mg L^{-1}, phosphate was 6.70 ± 3.48 µg L^{-1} and dissolved organic carbon (DOC) was 8.14 ± 0.37 mg L^{-1}. The control was considered nitrogen limited, with DIN:SRP ratio < 13 (Morris and Lewis 1988). The +NUTRI treatment consisted of single inorganic nutrients additions at day 0. To increase DIN and phosphate concentration we used $NaNO_3$, K_2HPO_4 and NH_4Cl. The nitrogen and phosphate additions intended to simulate eutrophication and the DIN:SRP ratio was around 17, indicating no nutrients limitation. The +OM treatment was conducted to simulate brownification, where OM was conducted to the lake. These mesocosms received OM extracted from the leaves collected from the watershed of Carioca Lake (Atlantic forest). We placed the leaves in water, left in darkness at 25ºC, for 7 days and then filtered through a 68 µm net. Finally, the +NUTRI+OM treatment received both inorganic nutrients and OM additions at day 0 and the DIN:SRP ratio was also around 17. The concentrations after the nutrients and OM additions in all treatments and in the control are shown in the Table 1.

Water samplings

Dissolved oxygen (O_{2sat}) was estimated daily from MiniDOT loggers as the average recorded between 10:00 to 12:00 h. For daily $p\mathrm{CO_2}$ we used the headspace equilibrium according to Cole and Caraco (1998), collecting water sampled between 10:00 and 12:00 h. One 30 mL glass bottle was filled with 20 mL of mesocosm surface water and immediately capped and sealed. Ten mL of the atmospheric air were introduced to each bottle and we shook them vigorously for 60 seconds to allow the CO_2 equilibrium between air and water. Headspace air was collected with a syringe and injected in an infrared gas analyzer (IRGA – environmental gas monitor EDS EGM4) for $p\mathrm{CO_2}$ measurements (accuracy < 1% of span concentration over the calibrated range).

Table 1: Mean and standard deviation of nutrients and organic matter from the day 0 (after the additions) in the control and treatments. DIN: dissolved inorganic nitrogen = nitrate + nitrite + ammonia; DOC: dissolved organic carbon.

	DIN (mg L^{-1})	Phosphate (µg L^{-1})	DOC (mg L^{-1})
Control	0.06 ± 0.02	6.70 ± 3.48	8.14 ± 0.37
+NUTRI	2.62 ± 0.17	156.38 ± 25.76	7.81 ± 0.20
+OM	0.06 ± 0.01	12.22 ± 0.92	8.59 ± 0.10
+OM+NUTRI	2.57 ± 0.12	149.79 ± 36.90	8.60 ± 0.09

From $p\mathrm{CO_2}$ and O_{2sat} measurements we estimated net $F\mathrm{CO_2}$ and $F\mathrm{O_2}$ across the air–water interface. We calculated the gas flux from the difference in surface gas concentration $[\mathrm{gas}_{(aq\ meas)}]$ from gas saturation $[\mathrm{gas}_{(aq\ sat)}]$ multiplied by the transport coefficient of gas exchange (k): gas flux = k ($[\mathrm{gas}_{(aq\ meas)}] - [\mathrm{gas}_{(aq\ sat)}]$). The gas concentration at atmospheric equilibrium was calculated from water temperature for O_2 (Weiss 1974) and for CO_2 solubility as a function of temperature and salinity (Likens 2009). The transport coefficient k was calculated from the estimated k_{600} and the ratio of Schmidt numbers as $k = k_{600}\,((Sc/600)^{-0.5})$, according to Jähne et al. (1987). We calculated k_{600} (k for a Schmidt number (Sc) of 600) from 1.5 m s^{-1} wind speed (mean wind speed during the experiment).

To measure chlorophyll-a, phosphate, DOC and DIN water samples were collected every three days at 0.5 m depth of each mesocosm following gentle stirring, between 10:00 and 12:00 h. Chlorophyll-a was determined on 0.47 µm glass-fiber filters after extraction in 90% acetone (Lorenzen 1967). DOC was determined through high temperature combustion (TOC analyzer Shimadzu 5000A) from samples filtered in 0.22 µm glass-fiber filters and stored in the dark at 4ºC. Samples for ammonia, nitrate, nitrite (DIN) and phosphate were pre-filtered (0.47 µm filter) and stored in plastic containers at 4ºC. Samples were unfrozen and re-filtered in Millex-HV Syringe Filter Unit (0.45 µm, Millipore) and analyzed in an ion chromatography (Metrohm 883 Basic IC). Additionally daily measurements of water temperature, turbidity, pH and conductivity were conducted in situ using a probe Hydrolab DS5 (Hach Inc.)

Statistical analysis

We used a two-way analysis of variance to determine if control and treatments were different in relation to gases and limnological variables. We fitted geometric mean linear regression to each treatment and to the control to describe the relationship between $F\mathrm{CO_2}$ and $F\mathrm{O_2}$. Additionally, we used the analysis of covariance (ANCOVA) to test differences in slopes among regression lines. All statistical tests were performed using the R Development Core Team (2011). We calculated the resistance index of $p\mathrm{CO_2}$ and $\mathrm{O_{2sat}}$ for control and treatments to compare how variable they were. We considered the day 0 as the day before the disturbance, which for the control, the disturbance was considered the deployment of the mesocosms, and for treatments the nutrients and OM additions. The index was calculated according to Uehlinger (2000) where: $resistance = 1 - \frac{x_{before} - x_{after}}{x_{before}}$. The highest dimensionless value represents the highest resistance. The resilience of the gas was considered as the gas recovery to the initial conditions or similar to observed in the control.

8.4 Results

General conditions

All mesocosms showed the same water temperature daily variation along the days sampled (Figure 2) and mesocosms with organic matter additions (+OM and +NUTRI+OM) showed higher temperatures, indicating elevated light absorption by OM. The control and +OM treatment showed similar conductivity and pH along the days with lower values than +NUTRI and +NUTRI+OM treatments (Table 2). Turbidity was highly variable along the days, and the highest values were recorded for +OM+NUTRI treatment. Along the days turbidity picked in all mesocosms around days 4 and 5 (Figure 2).

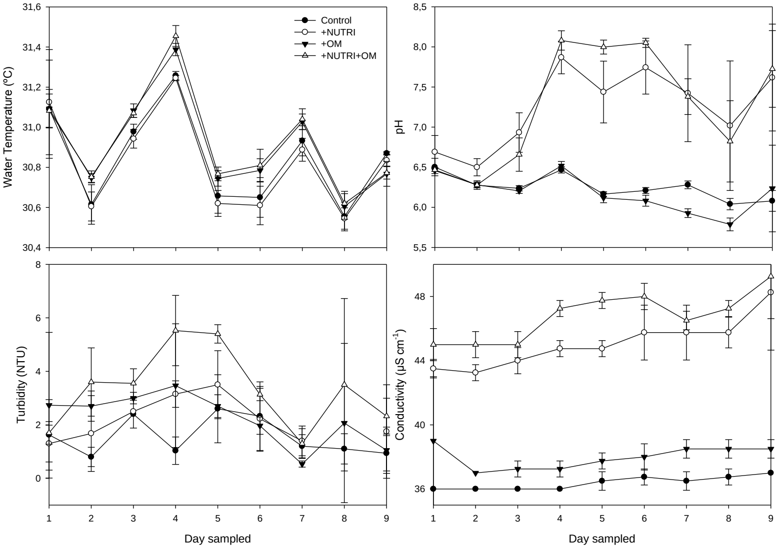

Figure 2: Mean and standard deviation from daily measurements of limnological variables along nine days in the control and treatments.

Table 2: Mean and standard deviation from limnological variables during nine days for the control and treatments.

Variables	Control	+NUTRI	+OM	+OM+NUTRI
O_{2sat} (%)	92.0 ± 1.95	98.2 ± 7.66	84.2 ± 5.22	97.0 ± 11.71
FO_2 (mmol m^{-2} d^{-1})	-0.3 ± 0.05	-0.1 ± 0.19	-0.4 ± 0.15	-0.1 ± 0.31
pCO_2 (µatm)	400.0 ± 12.54	322.7 ± 43.93	416.6 ± 35.72	323.6 ± 51.07
FCO_2 (mmol m^{-2} d^{-1})	0.1 ± 0.29	-1.7 ± 1.03	0.5 ± 0.83	-1.7 ± 1.19
Temperature (ºC)	30.8 ± 0.25	30.8 ± 0.26	30.9 ± 0.24	30.9 ± 0.25
Turbidity (NTU)	1.5 ± 0.98	2.1 ± 1.30	2.2 ± 1.58	3.4 ± 1.76
pH	6.3 ± 0.16	7.2 ± 0.61	6.2 ± 0.28	7.3 ± 0.73
Conductivity (µS cm^{-1})	36.4 ± 0.49	45.1 ± 1.99	38.0 ± 1.42	46.8 ± 1.74
Chlorophyll-a (µg L^{-1})	2.5 ± 0.92	10.1 ± 2.43	6.6 ± 3.50	14.2 ± 1.41
DIN (mg L^{-1})	0.02 ± 0.01	1.70 ± 0.45	0.02 ± 0.01	1.58 ± 0.52
Phosphate (µg L^{-1})	1.9 ± 3.41	82.2 ± 31.28	7.4 ± 3.15	100.2 ± 26.46
DOC (mg L^{-1})	7.8 ± 0.24	8.2 ± 0.38	8.6 ± 0.25	8.8 ± 0.43

Nutrients additions promoted higher chlorophyll-a in both +NUTRI and +NUTRI+OM treatments, while low chlorophyll-a was recorded in the control (Figure 3; Table 2). The high chlorophyll-a variability in +OM treatment occurred at the end of the experiment, suggesting that gradual degradation of organic matter released inorganic nutrients which were assimilated by autotrophic organisms. DIN and phosphate were also different between treatments and along the days DIN decreased in both +NUTRI and +NUTRI+OM treatments (Figure 3). DOC increases along the days in all treatments showing that organic matter is from autotrophic activity. All the variables were significantly different among the treatments, and along the days, except for chlorophyll-a and phosphate that were different among treatments but not along the days (Table 3).

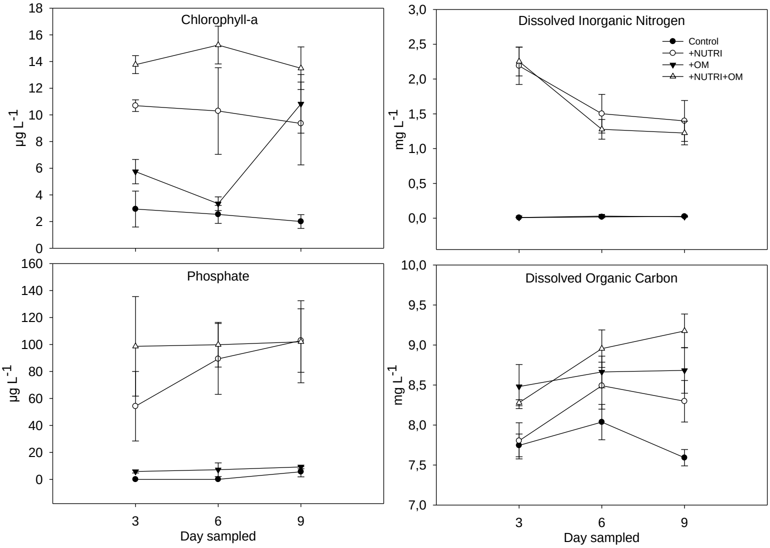

Figure 3: Mean and standard deviation from chlorophyll-a, dissolved inorganic nitrogen, phosphate and dissolved organic carbon during three samplings in the control and treatments mesocosms.

Gas dynamics

The control and +OM treatment showed predominantly positive FCO_2 to the atmosphere, with higher day-to-day variability in +OM than in the control. The highest variability, however, was recorded in +NUTRI and +NUTRI+OM treatments, with predominant negative FCO_2 (Figure 4). In the control the FO_2 was negative during all days, similar to +OM treatment (Table 2). In +NUTRI treatment the $F\mathrm{O_2}$ was slightly positive only around day 6. In +NUTRI+OM treatment, initially the $F\mathrm{O_2}$ was negative but became positive around day 4 until day 6. $F\mathrm{CO_2}$ was highly variable compared to $F\mathrm{O_2}$, and both gases were significant different among days and treatments (Table 3).

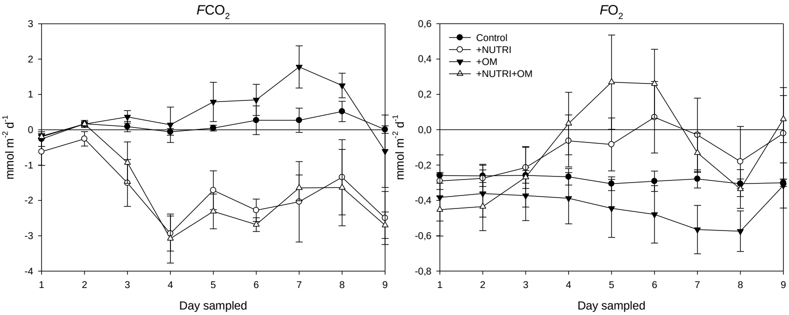

Figure 4: Mean and standard deviation from daily measurements of $F\mathrm{CO_2}$ and $F\mathrm{O_2}$ along nine days in the control and treatments.

Table 3: *p* values from ANOVA two-way comparing the day sampled, the treatment (Control, +NUTRI, +OM, +OM+NUTRI), and the interaction treatment x day. Significant values at $p<0.05$. $^{¥}$ represents the variables sampled in three days. All the remaining variables were sampled during nine days.

Variables	Day	Treatment	Treatment x Day
$\mathrm{O_{2sat}}$	0.000	0.000	0.000
$F\mathrm{O_2}$	0.000	0.000	0.000
$p\mathrm{CO_2}$	0.000	0.000	0.000
$F\mathrm{CO_2}$	0.000	0.000	0.000
Temperature	0.000	0.000	0.62
Turbidity	0.000	0.000	0.389
pH	0.000	0.000	0.000
Conductivity	0.000	0.000	0.22
Chla$^{¥}$	0.208	0.000	0.000
DIN$^{¥}$	0.000	0.000	0.000
Phosphate$^{¥}$	0.094	0.000	0.222
DOC$^{¥}$	0.000	0.000	0.001

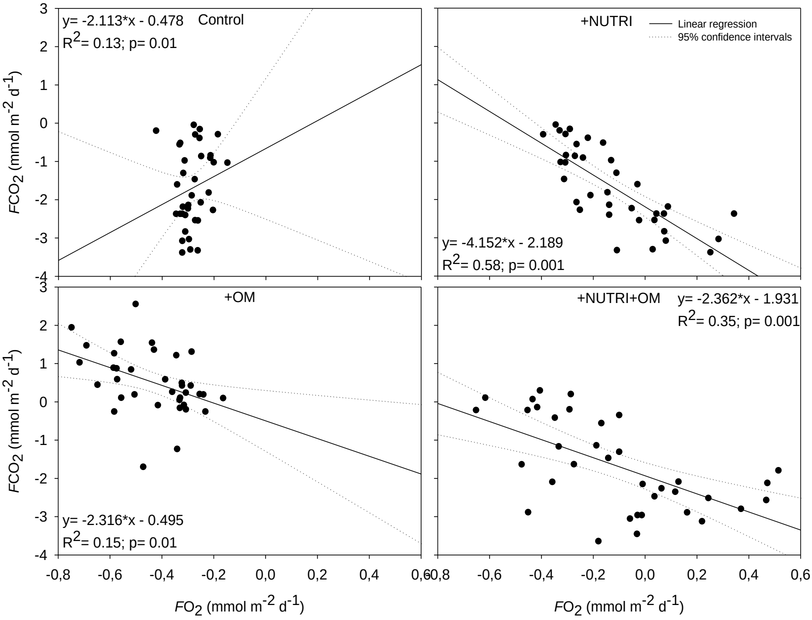

Figure 5: Linear regression between $F\text{CO}_2$ and $F\text{O}_2$ sampled daily along nine days, for the control and treatments.

The coupling between $F\text{CO}_2$ and $F\text{O}_2$ through a linear regression (Figure 5) showed similar slopes between +NUTRI and +NUTRI+OM treatments (ANCOVA; p=0.17), while +OM and +NUTRI treatments were significantly different from the control (ANCOVA; p<0.001).

Applying the resistance index to evaluate disturbance effects of OM and nutrient additions, showed opposite effects for CO_2 and O_2 (Figure 6). In +NUTRI and +NUTRI+OM treatments showed higher resistance for O_2 and the lower for CO_2. In the control and +OM, however, higher resistance was observed for CO_2 and the lower for O_2. Observing the gas behavior during the experiment (Figure 4) suggest a higher resilience of the mesocosms for +OM, since around day 8 the O_2 concentration tended to reach similar values than in the control (Figure 4). For +NUTRI and +NUTRI+OM treatments similar O_2 values were observed around day 8.

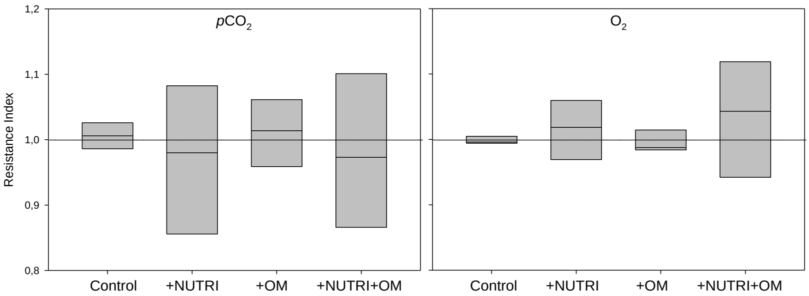

Figure 6: Median and percentiles of Resistance Index for pCO_2 and O_{2sat} from daily measurements, considering the day 0 as the day of the disturbance.

8.5 Discussion

Control mesocosms and those with only organic matter additions were characterized by CO_2 flux to the atmosphere, as well as similar conductivity, pH, chlorophyll-a and nutrients. The +OM treatment featured higher CO_2 fluxes to the atmosphere which is an evidence of higher respiration than primary production, typical condition of lakes in the Atlantic Forest (Marotta et al. 2009; Marotta et al. 2012). In contrast, nutrients additions in +NUTRI and +NUTRI+OM treatments raised the day-to-day variability resulting in negative CO_2 flux, as expected from increases in chlorophyll-a and pelagic primary production (Pacheco et al. 2013; Peixoto et al. 2013).

The low day-to-day variability in both CO_2 and O_2 and the predominantly CO_2 supersaturation in the control mesocosms corroborated previous findings in Carioca Lake (Reis and Barbosa 2014; Brighenti et al. 2015). Efflux of CO_2 is a typical condition from pristine Brazilian tropical lakes as well as many temperate lakes (eg. Trolle et al. 2012), and has previously been explained by relatively high levels of organic carbon and high temperatures (Sobek et al. 2005; Kosten et al. 2010; Pinho et al. 2016). The higher concentration of allochthonous DOC in +OM treatment than in the control supported CO_2 production through organic degradation, which has been also experimentally confirmed by Lennon (2004) and observed in both tropical and temperate lakes, where terrestrial organic matter significantly stimulates ecosystem respiration (Marotta et al. 2010; Brothers et al. 2014). Influx of oxygen in the +OM treatment furthermore signifies that respiration exceeded primary production, as high concentrations of DOC subsidizes the heterotrophic food web. In addition to this, removal of oxygen by photo-oxidation is known to be significant in tropical areas under high light incidence (Bertilsson and Tranvik 2000).

Apart from changes in the DOC concentration during the experiment, alteration in DOC quality, such as molecular weight and structure may affect the biological activity directly and indirectly. For instance trough changes in water colour, as we observed the turbidity variability along the days. In +NUTRI and +NUTRI+OM treatments the observed DOC increases at day 3 and 6 were consistent with chlorophyll-a increases, suggesting autochthonous DOC which has different quality than allochthonous carbon. Autochthonous DOC can also be inferred in +OM treatment, where chlorophyll-a concentrations increased through days 6 to 9, suggesting that nutrients released from the OM degradation supported the phytoplankton growth. DOC from algae is more available to bacteria compared to DOC originating from the forest, which is more sensitive to photochemical reactions (Amado et al. 2006). On a daily scale, this labile DOC released by photoautotrophs during the daylight could result in increase in CO_2 at night (Sadro et al. 2011). Although, we did follow the diel cycle of the gases, we could infer that the drop in O_2 after day 6 together with the slightly increase in CO_2 in both +NUTRI and +NUTRI+OM treatments could be the result of bacterial degradation of DOC of autochthonous origin.

The decline in CO_2 in both +NUTRI and +NUTRI+OM treatments relative to the control is consistent with observations from previous studies where nutrients enrichment favor the primary production and consequently the net autotrophy (Spivak et al. 2011; Peixoto et al. 2013). Additionally, elevated pH was observed in +NUTRI and +NUTRI+OM treatments denoting high photosynthetic activity (Jakobsen et al. 2015). Along the days the increase in phytoplankton biomass (chlorophyll-a) in both +NUTRI and +NUTRI+OM treatments favors growth of zooplankton which with some time lag likely grazed and decrease chlorophyll-a, as observed towards day 6 to day 9. In line with this, the community dynamics affected the gases concentration, where after day 6 we observed a drop in O_2 and slight increase in CO_2 indicating that zooplankton growth not only affect directly the aquatic respiration, but also depress primary production through their grazing activity (Schindler et al. 1997; Polis 1999).

We observed that around days 8 and 9 the gas concentrations in the treatments were similar to the control and to the first day of the experiment, indicating a faster recovery, even though nutrients and chlorophyll-a were different compared to day 0. The relative faster nutrient and carbon cycling observed in the mesocosms with additions of nutrients and OM was favored by the high temperature occurring during the experiment (~30ºC) which accelerates the biological processes (Brown et al. 2004; Ometto et al. 2005). Gallardo et al. (2012) recorded in floodplain lakes that the water chemistry took 4 days to recover from a flood event, while Lennon (2004) also observed a reduce in CO_2 flux six days after organic matter additions. In general, recovery rates will depend on the inputs intensity and frequency, as well as the lake chemical and physical conditions (Reynolds 2002; Borics et al. 2013; Hipsey et al. 2015).

The resistance levels determined for the control mesocosms were similar to those previously determined for rivers in a study by Uehlinger (2000), where respiration showed higher resistance than primary production. Comparing to our gas measurements, from all treatments we observed the opposite, where CO_2 presented higher resistance than O_2. Usually, weather disturbances have a lasting impact in lakes with a longer recovery time, which in turn depends on the severity of the disturbance and the lake features (Jennings et al. 2012). Addressing the resistance and resilience of the system can be important to understand how disturbances can affect the ecosystems and how adjustable the communities are to absorb current and future pressures.

Additions of nutrients strengthened the coupling between CO_2 and O_2. However, an imbalance between gases fluxes was observed in +NUTRI treatment, which could be related to processes consuming more CO_2 in relation to amount of O_2 produced (Torgersen and Branco 2007; 2008). In the control, for instance the amount of CO_2 released was higher than the O_2 uptake. The same was observed in the beginning of the +OM treatment probably because of the photo-oxidation, which could increase the CO_2 but not affect the O_2 concentration. The slope and strength between CO_2 and O_2 varied among treatments, and the strongest was observed under nutrients additions, which presented total phosphorus concentrations above 40 µg L^{-1}.

In a scenario of global changes the mesocosms experiments can provide important knowledge about the biological complexity of natural systems and can contribute to test, at close to ecosystem level, responses to different environmental conditions (Stewart et al. 2013). As climate changes is expected to modify the precipitation patterns, for example in El Niño year's higher rainfall is expected. The high precipitation carries allochthonous organic matter to the lake and can promote brownification in aquatic systems. From the results obtained from this experiment we can infer that not only eutrophication, but also brownification affect the carbon cycling, in this sense as a potential driver of O_2 depletion, as well as increase in CO_2 emissions.

In conclusion, eutrophication and brownification promoted contrasting effects in gas fluxes from a mesocosm experiment in a tropical lake, where the lake was more responsive to nutrients, promoting negative FCO_2, while organic matter promoted positive FCO_2 to the atmosphere. The high variability in CO_2 confirms the high sensitive of this gas to changes in limnological conditions, where CO_2 showed lower resistance for nutrients additions than for OM additions. Nutrients and organic matter clearly promoted contrasting effects in CO_2 and O_2 with important changes along the days regarding the nutrients absorption and organic matter degradation.

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8.6 References

Amado AM, Farjalla VF, Esteves FA, Bozelli RL, Roland F, Enrich-Prast A (2006) Complementary pathways of dissolved organic carbon removal pathways in clear-water Amazonian ecosystems: photochemical degradation and bacterial uptake. FEMS Microbiology Ecology 56:8-17.

Bertilsson S, Tranvik L (2000) Photochemical transformation of dissolved organic matter in lakes. Limnology and Oceanography 45:753-762.

Borics G, Várbíró G, Pádisak J (2013) Disturbance and stress: different meanings in ecological dynamics? Hydrobiologia 711:1-7.

Brighenti LS, Staehr PA, Gagliardi LM, Brandão LPM, Elias EC, Mello NAST, Barbosa FAR, Bezerra-Neto JF (2015) Seasonal changes in metabolic rates of two tropical lakes in the Atlantic Forest of Brazil. Ecosystems 18:589-604.

Brothers S, Kohler J, Attermeyer K, Grossart HP, Mehner T, Meyer N, Scharnweber K, Hilt S (2014) A feedback loop links brownification and anoxia in a temperate, shallow lake. Limnology and Oceanography 59:1388-1398.

Brown JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85:1771-1789.

Carpenter SR, Walker B, Anderies JM, Abel N (2001) From metaphor to measurement: resilience of what to what? Ecosystems 4:765-781.

Cole JJ, Caraco NF (1998) Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF6. Limnology and Oceanography 43:647-656.

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

Denfeld BA, Kortelainen P, Rantakari M, Sobek S, Weyhenmeyer GA (2016) Regional Variability and Drivers of Below Ice CO2 in Boreal and Subarctic Lakes. Ecosystems 19:461-476.

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.

Gallardo B, Español C, Comin FA (2012) Aquatic metabolism short-term response to the flood pulse in a Mediterranean floodplain. Hydrobiologia 693:251-264.

Granéli W (2012) Brownification of Lakes. In: Bengtsson L, Herschy RW, Fairbridge RW (ed) Encyclopedia of Lakes and Reservoirs. doi:10.1007/978-1-4020-4410-6, Springer Science and Business Media B.V

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

Hanson PC, Carpenter SR, Armstrong DE, Stanley EH, Kratz TK (2006) Lake dissolved inorganic carbon and dissolved oxygen: changing drivers from days to decades. Ecological Monographs 76:343-363.

Hipsey MR, Hamilton DP, Hanson PC, Carey CC, Coletti JZ, Read JS, Ibelings BW, Valesini FJ, Brookes JD (2015) Predicting the resilience and recovery of aquatic systems: A framework for model evolution within environmental observatories. Water Resources Research 51:7023-7043.

Jakobsen HH, Blanda E, Staehr PA, Højgård JK, Rayner TA, Pedersen MF, Jepsen PM, Hansen BW (2015) Development of phytoplankton communities: Implications of nutrient injections on phytoplankton composition, pH and ecosystem production. Journal of Experimental Marine Biology and Ecology 473:81-89.

Jähne B, Munnich KO, Bosinger R, Dutzi A, Huber W, Libner P (1987) On parameters influencing air-water gas exchange. Journal of Geophysical Research 92:1937-1949.

Jennings E, Jones E, Arvola L, Staehr PA, Gaiser E, Jones ID, Weathers KC, Weyhenmeyer GA, Chiu CY, Eyto E (2012) Effects of weather-related episodic events in lakes: an analysis based on high-frequency data. Freshwater Biology 57:589-601.

Kelly CA, Fee E, Ramlal PS, Rudd JWM, Hesslein RH, Anema C, Schindler EU (2001) Natural variability of carbon dioxide and net epilimnetic production in the surface waters of boreal lakes of different sizes. Limnology and Oceanography 46:1054-1064.

Kosten S, Roland F, Motta-Marques DML, Van Nes EH, Mazzeo N, Sternberg LSL, Scheffer M, Cole JJ (2010) Climate-dependent CO_2 emissions from lakes. Global Biogeochemical Cycles 24:GB2007.

Laas A, Nõges P, Kõiv T, Nõges T (2012) High-frequency metabolism study in a large and shallow temperate lake reveals seasonal switching between net autotrophy and net heterotrophy. Hydrobiologia 694:57-74.

Lazzarino JK, Bachmann RW, Hoyer MV, Canfield J (2009) Carbon dioxide supersaturation in Florida lakes. Hydrobiologia 627:169-180.

Likens GE (2009) Encyclopedia of Inland Water. Elsevier Academic Press, New York.

Lennon JT (2004) Experimental evidence that terrestrial carbon subsidies increase CO_2 flux from lake ecosystems. Oecologia 138:584-591.

Lorenzen CJ (1967) Determination of chlorophyll and pheopigments: Spectrophotometric equations. Limnology and Oceanography 12:343-346

Maberly SC, Barker PA, Stott AW, Ville MM (2012) Catchment productivity controls CO_2 emissions from lakes. Nature Climate Change 3:391-394.

Marcé R, Obrador B, Morguí JA, Riera JL, López P, Armengol J (2015) Carbonate weathering as a driver of CO_2 supersaturation in lakes. Nature Geoscience 8:107-111.

Marotta H, Paiva LP, Petrucio MM (2009) Changes in thermal and oxygen stratification pattern coupled to CO_2 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_2 in Brazilian coastal lakes. Biogeosciences 7:1607-1614.

Marotta H, Fontes MLS, Petrucio MM (2012) Natural events of anoxia and low respiration index in oligotrophic lakes of the Atlantic Tropical Forest. Biogeosciences Discussion 9:4225-4244

Mormul RP, Ahlgren J, Ekvall MK, Hansson LA, Bronmark C (2012) Water brownification may increase the invisibility of a submerged non-native macrophyte. Biological Invasions 14:2091-2099.

Morris DP, Lewis WM (1988) Phytoplankton nutrient limitation in Colorado mountain lakes. Freshwater Biology 20:315-327.

Ojala A, Bellido JL, Tulonen T, Kankaala P, Huotari J (2011) Carbon gas fluxes from a brown-water and a clear-water lake in the boreal zone during a summer with extreme rain events. Limnology and Oceanography 56:61-76.

Ometto JPHB, Nobre A, Rocha H, Artaxo P, Martinelli L (2005) Amazonia and the modern carbon cycle: lessons learned. Oecologia 143:483-500.

Pacheco FS, Roland F, Downing JA (2013) Eutrophication reverses whole-lake carbon budgets. Inland Waters 4:41-48.

Palmer MA, van Dijken GL, Mitchell BG, Seegers BJ, Lowry KE, Mills MM, Arrigo KR (2013) Light and nutrient control of photosynthesis in natural phytoplankton populations from the Chukchi and Beaufort seas, Artic Ocean. Limnology and Oceanography 58:2185-2205.

Peixoto RB, Marotta H, Enrich-Prast A (2013) Experimental evidence of nitrogen control on $p\mathrm{CO}_2$ in phosphorus enriched humic and clear coastal lagoon waters. Frontiers in Microbiology, Aquatic Microbiology 4:1-6.

Pimm SL (1984) The complexity and stability of ecosystems. Nature 5949:321-326.

Pinho L, Duarte CM, Marotta H, Enrich-Prast A (2016) Temperature-dependence of the relationship between $p\mathrm{CO}_2$ and dissolved organic carbon in lakes. Biogeosciences 13:865-871.

Polis GA (1999) Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos 86:3-15.

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Reis PCJ, Barbosa FAR (2014) Diurnal sampling reveals significant variation in CO_2 emission from a tropical productive lake. Brazilian Journal of Biology 74:113-119.

Reynolds CS (2002) Resilience in aquatic ecosystems-hysteresis, homeostasis, and health. Aquatic Ecosystem Health & Management 5: 3-17.

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

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution 18:648-656.

Schindler DE, Carpenter SR, Cole JJ, JF Kitchell, Pace ML (2007) Influence of Food Web Structure on Carbon Exchange Between Lakes and the Atmosphere. Science 277:248-251.

Spivak AC, Vanni MJ, Mette EM (2011) Moving on up: can results from simple aquatic mesocosm experiments be applied across broad spatial scales? Freshwater Biology 56:279-291.

Sobek S, Tranvik LJ, Cole JJ (2005) Temperature Independence of carbon dioxide supersaturation in global lakes. Global Biogeochemical cycles 19:GB2003.

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. Limnology and Oceanography Methods 8:628-644.

Staehr PA, Brighenti LS, Honti M, Christensen J, Rose KC (in press) Global patterns of light saturation and photo-inhibition of lake primary production. Inland waters.

Stewart RIA, Dossena M, Bohan DA, Jeppesen E, Kordas RL, Ledger ME, Meerhoff M, Moss B, Mulder C, Shurin JB, Suttle B, Thompson R, Trimmer M, Woodward G (2013) Mesocosm Experiments as a Tool for Ecological Climate-Change Research. Advances in Ecological Research 48:71-181.

Thrane JE, Hessen DO, Andersen T (2014) The absorption of light in lakes: negative impact of dissolved organic carbon on primary productivity. Ecosystems 17:1040-1052.

Torgersen T, Branco B (2007) Carbon and oxygen dynamics of shallow aquatic systems: Process vectors and bacterial productivity. Journal of Geophysical Research 112:G03016.

Torgersen T, Branco B (2008) Carbon and oxygen fluxes from a small pond to the atmosphere: Temporal variability and the CO_2/O_2 imbalance. Water resources research 44:W02417.

Tranvik LJ, et al. 2009. Lakes and reservoirs as regulators of carbon cycling and climate. Limnology and Oceanography 54:2298-2314.

Trolle D, Staehr PA, Davidson TA, Bjerring R, Lauridsen TL, Søndergaard M, Jeppesen E (2012) Seasonal dynamics of CO_2 flux across the surface of shallow temperate lakes. Ecosystems 15:336-347.

Uehlinger U (2000) Resistance and resilience of ecosystem metabolism in a flood-prone river system. Freshwater Biology 45:319-332.

Weiss RF (1974) Carbon dioxide in water and seawater: the solubility of a non-ideal gas. Marine Chemistry 2:203-215.

Zhai WD, Dai M, Cai WJ (2009) Coupling of surface $p\mathrm{CO}_2$ and dissolved oxygen in the northern South China Sea: impacts of contrasting coastal processes. Biogeosciences 6:2589-2598.

9 CONSIDERAÇÕES FINAIS

Esta tese investigou o metabolismo aquático de lagos inseridos no bioma Mata Atlântica e como diferentes variáveis limnológicas e meteorológicas estão relacionadas à dinâmica espaço-temporal das taxas de produção primária e respiração desses ambientes. Observando a escala diária nas concentrações de CO_2 na Lagoa do Peri foram registradas menores fluxos entre a água e a atmosfera durante o dia e maiores fluxos à noite. Além disso, durante períodos de alta temperatura e intensidade luminosa, típicas de verão, ocorreu influxo de CO_2 na Lagoa do Peri. Nas demais estações do ano houve predomínio do fluxo de CO_2 para a atmosfera, condição relacionada com a alta concentração de carbono orgânico e densidade de bactérias heterotróficas. Entretanto, essas variáveis tiveram baixo poder de explicação para a variação do CO_2, sugerindo a influência de outras variáveis não consideradas nesta abordagem.

Em um estudo mais detalhado sobre a variação diária das taxas de produção primária e respiração, foram utilizadas medidas de oxigênio dissolvido a cada 15 minutos e em duas áreas do lago, na região pelágica e na litorânea. A predominante condição heterotrófica da Lagoa do Peri foi confirmada, no qual a autotrofia líquida foi registrada apenas na superfície da coluna d’água. O padrão vertical de maior produção primária na superfície diminuindo em direção ao fundo da lagoa, e menor respiração na superfície aumentando em direção ao fundo, aliado à distribuição homogênea dos nutrientes e clorofila-a na coluna d’água corrobora com a importância da luz na variação vertical do metabolismo aquático, bem como a influência do sedimento para as maiores taxas de respiração nas camadas mais profundas. Temporalmente, quando a estabilidade da coluna d’água aumentou em função da maior temperatura e menor velocidade do vento, as taxas de produção primária foram maiores. Por outro lado, a região litorânea apresentou maior variabilidade que a região pelágica, possivelmente relacionada à influência do ambiente terrestre e da coluna d’água mais rasa. Esses resultados sugerem que neste ambiente as variáveis físicas como a estabilidade da coluna d’água, o vento e a profundidade do ambiente são determinantes para a dinâmica espaço-temporal das taxas metabólicas.

A importância das variáveis físicas também foi explorada no terceiro capítulo, no qual foram analizados oito anos consecutivos de coletas mensais na Lagoa do Peri. Ao longo desse período importantes alterações foram observadas no nível d’água em decorrência da reduzida precipitação. Foi possível observar que o aumento da $p\mathrm{CO}_2$ e do fluxo de CO_2 foi concomitante ao aumento da clorofila-a e do carbono orgânico. O aumento na concentração de nutrientes e clorofila-a também foi devido à diminuição do nível d'água da Lagoa do Peri, como resultado da precipitação abaixo da média para a região, registrada entre 2012 e 2014. Isso indica que o aumento da clorofila-a ao invés de promover o aumento da produção primária, tem favorecido indiretamente a respiração por aumentar a limitação da luz e a concentração de carbono orgânico autóctone na coluna d'água. Além disso, a falta de relação direta entre CO_2 e O_2 sugere que a bacia de drenagem pode estar contribuindo para a supersaturação de CO_2 na Lagoa do Peri.

Quando adições experimentais de matéria orgânica e nutrientes inorgânicos foram conduzidas em mesocosmos na Lagoa Carioca, foi observado que a dinâmica dos gases foi alterada, uma vez que a matéria orgânica favoreceu o aumento do CO_2 com consumo do O_2, enquanto que os nutrientes inorgânicos favoreceram o aumento do O_2 e o consumo do CO_2. A adição de nutrientes promoveu maior variabilidade no ecossistema que a adição de matéria orgânica, embora o sistema rapidamente tendeu a retornar às condições iniciais.

Em síntese, com a realização desta tese foi possível observar que os lagos inseridos no bioma Mata Atlântica tendem a ser heterotróficos e altamente dinâmicos. Essa dinamicidade está relacionada à interação das variáveis meteorológicas e limnológicas, que determinam as dinâmicas espacial e temporal da produção primária e da respiração. Com isso, mudanças no clima global podem alterar ou intensificar a função dos lagos como fontes ou sumidouros de carbono.

Por fim, esta tese mostra que mesmo esses lagos estando inseridos em locais de proteção ambiental, impedindo que as atividades antrópicas impactem diretamente esses ambientes, as mudanças climáticas globais podem afetar esses ecossistemas, principalmente através de alterações no padrão de precipitação. Assim, observando que as variáveis físicas podem ser determinantes na variação espaço-temporal do metabolismo aquático, é importante que elas sejam consideradas nas estratégias de gerenciamento e restauração dos ambientes aquáticos, bem como do seu entorno.

10 PERSPECTIVAS

Juntamente com os resultados obtidos por esta tese, alguns tópicos emergem e merecem ser explorados futuramente, tais como:

- Determinar qual é a contribuição do sedimento para a concentração de CO_2 e O_2 na coluna d’água, através da degradação aeróbica e anaeróbica;
- Identificar a contribuição da bacia de drenagem para a supersaturação em CO_2, através de medições diretas de CO_2;
- Avaliar o papel do vento na quebra de estabilidade da coluna d’água e como isso pode afetar as taxas de produção primária e respiração;
- Estimar a resiliência e resistência dos ambientes aquáticos frente às mudanças climáticas globais que alteram a estabilidade desses ecossistemas.

Diante disso, é nítido que os estudos sobre metabolismo aquático nos ambientes tropicais e subtropicais merecem atenção e dedicação por parte de limnólogos e ecólogos. Devido à sua posição geográfica e as condições ambientais, esses ambientes podem apresentar diferentes dinâmicas no processamento da matéria orgânica e dos nutrientes. Por fim, a compreensão de como as diversas variáveis limnológicas e meteorológicas controlam as taxas de produção primária e respiração aquática dos ecossistemas é essencial para descrever o ciclo do carbono em ambientes tropicais e subtropicais e prever sua resposta às mudanças climáticas e ambientais em andamento, bem como as previstas a ocorrer.