

UNIVERSIDADE FEDERAL DE MINAS GERAIS
Instituto de Ciências Biológicas
Programa de Pós-graduação em Ecologia, Conservação e Manejo da Vida Silvestre

Elisa Aguiar Porto Viana

**A REDUÇÃO DE VOLUME LEVA A UM AUMENTO NAS TAXAS DE PRODUÇÃO
PRIMÁRIA E RESPIRAÇÃO EM UM LAGO TROPICAL NATURAL**

Belo Horizonte

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PRIMÁRIA E RESPIRAÇÃO EM UM LAGO TROPICAL NATURAL**

Dissertação apresentada ao Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre da Universidade Federal de Minas Gerais como requisito parcial para obtenção do título de Mestre em Ecologia, Conservação e Manejo da Vida Silvestre.

Orientador: José Fernandes Bezerra-Neto

Coorientadora: Ludmila Silva Brighenti

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Elisa Aguiar Porto Viana

No dia 30 de agosto de 2021, às 14:30 horas, por videoconferência, teve lugar a defesa de dissertação de mestrado no Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, de autoria do(a) mestrando(a) Elisa Aguiar Porto Viana, intitulada: **“A redução de volume leva a um aumento nas taxas de produção primária e respiração em um lago tropical natural”**. Abrindo a sessão, o(a) orientador(a) e Presidente da Comissão, Doutor(a) José Fernandes Bezerra Neto, após dar a conhecer aos presentes o teor das normas regulamentares do trabalho final, passou a palavra para o(a) candidato(a) para apresentação de seu trabalho. Estiveram presentes a Banca Examinadora composta pelos Doutores: Paula Campos Junqueira Reis (Université du Québec à Montréal), André Megali Amado (UFJF) e demais convidados. Seguiu-se a arguição pelos examinadores, com a respectiva defesa do(a) candidato(a). Após a arguição, apenas os senhores examinadores permaneceram no recinto para avaliação e deliberação acerca do resultado final, sendo a decisão da banca pela:

- (X) Aprovação da dissertação, com eventuais correções mínimas e entrega de versão final pelo orientador diretamente à Secretaria do Programa, no prazo máximo de 30 dias;
- () Reavaliação da dissertação com avaliação pelos membros da banca do documento revisado, sem nova defesa, no prazo máximo de 30 dias, sob possibilidade de reprovação;
- () Reformulação da dissertação com indicação de nova defesa em data estabelecida a critério do Colegiado em observância às Normas Gerais da Pós-graduação na UFMG a ao Regimento do PPG-ECMVS;
- () Reprovação

Nada mais havendo a tratar, o Presidente da Comissão encerrou a reunião e lavrou a presente ata, que será assinada por todos os membros participantes da Comissão Examinadora.

Belo Horizonte, 30 de agosto de 2021.

Assinaturas dos Membros da Banca Examinadora



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Resumo

Lagos são importantes centros de transformação de carbono e devido a isso, estão sujeitos aos efeitos das mudanças climáticas enquanto também são capazes de regulá-las. O metabolismo aquático é amplamente utilizado para monitorar os efeitos do clima nesses ecossistemas, uma vez que responde rapidamente a diversas alterações induzidas ou provocadas pelo clima. Sabendo disso, identificar e compreender as alterações na dinâmica da produção primária bruta (PPB), da respiração (R) e da produção líquida ecossistêmica (PLE) é crucial para melhor caracterizar as vulnerabilidades desses ambientes frente a diferentes distúrbios. O objetivo deste estudo foi comparar as mudanças físico-químicas, e nas taxas metabólicas de um lago tropical que perdeu cerca de 60% de volume nos últimos 10 anos. Acredita-se que a diminuição de volume pode levar a um aumento nas concentrações de nutrientes e de carbono, reduzindo a transparência e a disponibilidade de luz, influenciando as taxas metabólicas direta e indiretamente. Sendo assim, foram testadas as previsões de que: i) as taxas de PPB e de R epilimnéticas aumentariam; e ii) o papel da sazonalidade no metabolismo epilimnético enfraqueceria devido as alterações físico-químicas induzidas pela perda de volume. Dois períodos distintos e duas estações (seca e chuva) foram utilizadas. O primeiro compreendeu os anos de 2011 e 2012 (P1) e o segundo compreendeu os anos entre 2017-2019 (P2), quando o lago apresentou um volume 60% menor que durante o P1. As taxas metabólicas foram estimadas utilizando dados de alta frequência e a técnica da modelagem inversa. Além disso, o fluxo atmosférico foi estimado utilizando 10 equações para entender o papel dos processos físicos nas estimativas do metabolismo. De uma forma geral, no P2 as concentrações de nitrogênio e fósforo total, clorofila-a, carbono orgânico dissolvido, sólidos totais em suspensão aumentaram e houve uma redução da disponibilidade de luz na camada de mistura. Tanto a PPB quanto a R aumentaram durante o P2 (40% e 38%, respectivamente). Enquanto a R variou sazonalmente e registrou os maiores valores na estação seca, a PPB foi semelhante na seca e na chuva, em contraste com o P1, onde ambas as taxas variaram de acordo com a estação, sendo maiores na estação seca. Com relação a PLE, enquanto durante o P1 o lago esteve próximo ao equilíbrio com a atmosfera ($-0.18 \pm 0.29 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$; média \pm erro padrão), no P2 houve uma troca entre autotrofia na chuva e heterotrofia na seca ($6.44 \pm 0.51 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ e $-18.98 \pm 1.81 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$, respectivamente). Além disso, a diminuição do volume do lago no P2 tornou o tamanho da camada de mistura mais variável durante todo o período. Uma vez que processos físicos também afetam a oscilação do OD na água, a mudança na estabilidade da estratificação também contribuiu para as mudanças observadas nas taxas metabólicas. O

metabolismo ecossistêmico mudou durante o período de seca hidrológica persistente e é provável que continue mudando em resposta às variações atuais e futuras no padrão pluviométrico e de temperatura.

Palavras-chave: Mudanças climáticas, Oxigênio dissolvido, Carbono, Metabolismo ecossistêmico, Modelagem inversa, Dados de alta frequência.

Abstract

Lakes are important centers of carbon transformation, and due to that, are subjected to the effects of climate change, while they are also capable of regulating these changes. Aquatic metabolism is considered a good sentinel of climate, once the metabolic rates respond quickly to a series of alterations induced or caused by climate change. Therefore, identifying and understanding the alterations in lake gross primary production (GPP), respiration (R), and net ecosystem production (NEP) dynamics is vital to better characterize the vulnerabilities of these environments to natural and to human-induced disturbances. The study aimed at comparing the changes in physical, chemical, and, especially, in the dynamic and in the magnitude of metabolic rates of a tropical lake that lost about 60% of its volume in the last 10 years. It is believed that the decrease in volume can lead to an overall increase in nutrient and dissolved organic matter concentrations, reducing water transparency and light availability. These changes may influence metabolic rates directly and indirectly. Therefore, two predictions were assessed: i) epilimnetic PPB and R would increase; and ii) the role of seasonality in epilimnetic metabolism would diminish due to the physicochemical changes induced by water loss. Two distinct periods were sampled, the first one, between 2011-2012 (P1), and the second one, between 2017-2019 (P2), when the lake volume was ca. 60% lower than during P1. Each period was also evaluated between seasons (rainy and dry season). The metabolic rates were estimated using high-frequency measurements and the inverting modeling approach. Moreover, the atmospheric flux was calculated using 10 different equations to understand the role of physical processes in metabolic rates estimates. In general, during P2 there was an increase in concentrations of total nitrogen, total phosphorus, chlorophyll-a, dissolved organic carbon, total suspended solids, and a decrease in light availability in the upper mixed layer. Both GPP and R increased during P2 (40% and 38%, respectively). While R rates were different between seasons, with the highest rates registered during the dry season, GPP was similar in both dry and rainy seasons, contrasting with P1, when both rates responded to seasonality. In relation with NEP, during P1 the lake was close to atmosphere equilibrium ($-0.18 \pm 0.29 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$; mean \pm standard error), however, in P2 there was a switching between autotrophy during the rainy season and heterotrophy in the dry season ($6.44 \pm 0.51 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ e $-18.98 \pm 1.81 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$, respectively). Moreover, the decrease in lake volume during P2 turned the mixed layer depth more variable during the entire period. Since the physical processes also affect the DO oscillation in the water column, the change in the stability of stratification also contributed to the changes observed in metabolic rates. The results of this study showed that

ecosystem metabolism changed during the period of persistent hydrological drought, and it may continue to change in response to the ongoing variation in rainfall and temperature patterns.

Keywords: Climate change, Dissolved oxygen, Carbon, Ecosystem metabolism, Inverting modeling approach, High-frequency data.

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1. INTRODUÇÃO GERAL

Quando falamos em metabolismo, automaticamente pensamos nos processos fisiológicos que nos mantêm vivos. Em ambientes aquáticos, o metabolismo do ecossistema pode ser definido como um conjunto de processos biogeoquímicos que envolvem a formação e a degradação de matéria orgânica por todos os organismos vivos que compõem aquele sistema. Os produtores primários (também chamado de autotróficos) são aqueles responsáveis pela formação da matéria orgânica nesses ambientes, mas como todo ser vivo, também degradam a matéria no processo chamado de respiração, juntamente com os organismos heterotróficos (e.g. peixes, zooplâncton e bactérias). O balanço entre esses dois processos completa o conjunto denominado de metabolismo ecossistêmico (Staeher et al., 2012a). Devido a esses processos, e, juntamente com a capacidade de emitir e estocar carbono em seu sistema, lagos desempenham um papel central no ciclo global desse elemento (Cole et al., 2007) apesar de cobrirem apenas uma pequena fração do globo (2,8%; Downing e Duarte, 2009).

De forma geral, os produtores primários utilizam a radiação solar como fonte de energia para transformação de CO_2 e H_2O em glicose ($\text{C}_6\text{H}_{12}\text{O}_6$) e O_2 que é liberado na água. Por sua vez, tanto os seres autotróficos quanto os heterotróficos utilizam o O_2 disponível no processo de respiração (quebra de moléculas orgânicas como a glicose para a utilização da energia armazenada), liberando CO_2 e água para o sistema novamente. O processo de formação de matéria pelos produtores primários é comumente chamado de Produção Primária Bruta (PPB ou GPP, do inglês *Gross Primary Production*), e é a soma de toda fotossíntese. Já o processo de degradação dessa matéria para a manutenção de todos os organismos é chamado de Respiração (R). Quando subtraímos a quantidade de matéria que foi degradada (R) de toda a fotossíntese realizada (GPP), obtemos outro índice metabólico muito importante e muito útil na avaliação de um ecossistema aquático, esse processo é chamado de Produção Líquida Ecossistêmica, e é toda a fotossíntese que resulta na formação de biomassa (PLE ou NEP, do inglês *Net Ecosystem Production*; $\text{PLE} = \text{PPB} - \text{R}$) (Esteves e Gonçalves Júnior, 2011; Staeher et al., 2012a).

A PLE é um processo que quando quantificado é extremamente útil e informativo (Staeher et al., 2012a). Na literatura especializada, é comum utilizar a PLE como um indicativo do status trófico daquele ambiente (Odum, 1956; Staeher e Sand-Jensen, 2007). Um corpo aquático considerado ou um determinado período de tempo, pode ser classificado como autotrófico quando PLE é maior que 0. Ambientes autotróficos ou períodos de autotrofia indicam que o ambiente pode exportar matéria orgânica para ambientes adjacentes ou estocar

essa matéria no sistema, funcionando, também, como sumidouro de CO₂ atmosférico. Quando a PLE é menor que 0, considera-se que o ambiente é heterotrófico ou tem períodos de heterotrofia. Nesses casos, o ambiente importa matéria orgânica (ou degrada o estoque do sistema) e os organismos dependem dessa importação de matéria para desempenhar suas funções no sistema (del Giorgio e Duarte, 2002). Segundo Cole et al. (2000) a maior parte dos ambientes aquáticos continentais ao redor do globo são heterotróficos, o que significa, em prática, que são emissores de CO₂ para a atmosfera.

As pesquisas com metabolismo aquático tiveram início em 1927 com o estudo de Gaarder e Gran. Esse estudo envolveu o plâncton costeiro e o metabolismo foi mensurado a partir de incubações de uma pequena quantidade de água dentro de frascos com e sem exposição à luz solar, com o propósito de estimar as taxas de produção primária e respiração, respectivamente. Embora esse método tenha sido desenvolvido há mais de 90 anos, ele ainda é empregado (Murrell et al., 2017; Guimarães-Bermejo et al., 2018), uma vez que oferece a possibilidade de obter medidas precisas, altamente controladas, e de mensurar diretamente os processos de interesse. Ainda assim, o emprego desse método requer um trabalho intensivo, é difícil extrapolar os resultados para o ecossistema como um todo, além das dificuldades de se obter medidas com alta resolução temporal. Sendo assim, outros métodos são preferidos atualmente no estudo do metabolismo aquático (Staeher et al., 2012a).

Esses métodos estão incluídos na categoria que ficou conhecida como métodos de água livre (do inglês *Free-water* ou *Open-water*). Esses métodos se baseiam na mudança diária das concentrações de oxigênio dissolvido (ou gás carbônico) no corpo aquático, e essencialmente refletem o balanço entre fotossíntese, respiração e as trocas gasosas na interface ar-água (Staeher et al., 2010; Staeher et al., 2012a). Embora Sargent e Austin (1949) tenham sido os pioneiros no uso dessa técnica, a popularização dessa aplicação se deu através dos estudos dos irmãos Odum na década de 1950 (Odum e Odum, 1955; Odum, 1956, 1957). As estimativas de metabolismo (baseadas no ciclo diário do oxigênio dissolvido) são calculadas a partir da seguinte equação:

$$\frac{\Delta O_2}{\Delta t} = PPB - R - F - A \quad (1)$$

onde, $\Delta O_2 / \Delta t$ é a mudança na concentração do oxigênio dissolvido no intervalo de tempo definido pelo pesquisador; PPB é a produção primária bruta; R é a respiração; F é a troca gasosa na interface ar-água; A é o termo que inclui outros processos que são responsáveis pela mudança na concentração de oxigênio (ex: mistura de camadas de água induzidas pelo vento, mistura de camadas devido ao movimento das massas de água, fluxo horizontal).

A imagem a seguir demonstra alguns dos processos físicos, químicos e biológicos que podem gerar variabilidade no OD em lagos.

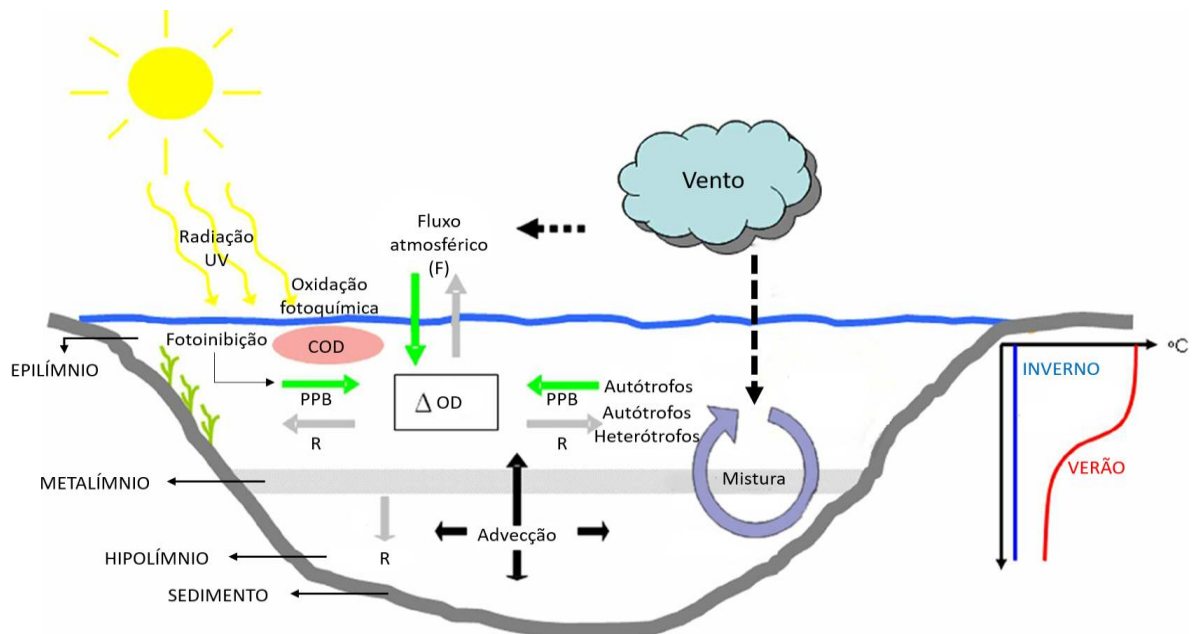


Fig. 1 - Modelo conceitual dos processos que podem gerar variabilidade na concentração de oxigênio dissolvido (OD) em um lago. Adaptado de Staehr et al., 2010. A produção primária bruta (PPB) e a respiração (R) são geralmente as principais fontes de variação no OD em um lago. Enquanto a PPB é realizada pelos autótrofos - fitoplâncton, macrófitas e algas benthicas - principalmente no epilímnio dos lagos, a R é realizada por todos os organismos presentes no sistema e em toda a coluna d'água. Um dos principais fatores físicos que contribuem para a variabilidade no OD é o fluxo atmosférico (F) na interface ar-água, devido ao gradiente de concentração e induzido pela ação do vento. Além disso, a oxidação fotoquímica do carbono orgânico dissolvido e a fotoinibição da PPB induzida principalmente pela radiação UV podem gerar variações nos dados de OD mensurados. Outros fatores como a mistura da coluna d'água, correntes de advecção e trocas de oxigênio com massas de água se movendo horizontalmente podem causar ruído nas leituras de OD (A - Eq. 1) feito por sensores ou sondas.

Utilizando a equação 1 é possível calcular as taxas metabólicas assumindo que: (1) A respiração é estimada através das mudanças no oxigênio dissolvido durante a noite; (2) a respiração durante o dia é igual a respiração durante a noite; (3) a PPB é estimada através das mudanças no oxigênio dissolvido durante o dia somado ao valor da respiração; (4) a PLE é estimada subtraindo a PPB pela R. Além disso, o fluxo (F) é geralmente calculado utilizando um coeficiente de troca gasosa baseado na velocidade do vento (Cole e Caraco, 1998); a mudança na concentração de oxigênio dissolvido é medida de forma direta; e o termo A é geralmente considerado como negligível (Staehr et al., 2010).

O método descrito acima é conhecido como *bookkeeping*, e apresenta a vantagem de poder oferecer medidas precisas em alta frequência com grande resolução espacial. Com o avanço da tecnologia, sensores que mensuram oxigênio dissolvido na água se tornaram bastante populares, oferecendo robustez e medidas confiáveis a um custo relativamente baixo. Apesar disso, esse método possui algumas desvantagens, como as dificuldades de incluir nas estimativas processos físicos que podem sobrepor os biológicos (e.g. mistura induzida pelo

vento, advecção etc.) em alguns ambientes ou causar ruído nas medidas captadas pelo sensor (ou seja, desconsiderar o termo A da equação 1 ao fazer as estimativas das taxas metabólicas). Além disso, existem implicações ao considerar que a respiração durante o dia é igual a noite, uma vez que algas podem continuar a fixar carbono utilizando a energia restante após o pôr do sol e que há evidências de que a respiração durante o dia é maior do que durante a noite, causando uma subestimação dessa taxa (Hanson et al., 2008; Staehr et al., 2012a; Staehr et al., 2012b).

Outros métodos também se baseiam na técnica de água livre, como por exemplo o método envolvendo isótopos de oxigênio e balanço de massa. Entretanto, esses métodos são menos comuns, uma vez que são mais difíceis de se obter as amostragens, como no caso dos isótopos, ou possuem requisitos difíceis de mensurar, como o fluxo ar-água no caso do método de balanço de massa (Staehr et al., 2012a).

Com o avanço e a expansão do uso da tecnologia e o aumento do poder de processamento de computadores domésticos, outros métodos começaram a ser desenvolvidos ou aprimorados. É o caso da aplicação da abordagem da modelagem inversa (IMA, do inglês *Inverse Modeling Approach*) utilizando dados de sensores que operam em alta frequência de amostragem. Com essa técnica, é possível estimar determinados parâmetros e processos que em outros casos só seria possível através de experimentação. No caso do metabolismo ecossistêmico, especificamente em lagos, a técnica se baseia na utilização de algoritmos de otimização que irão gerar valores para os parâmetros de interesse que melhor aproximam o valor de oxigênio que foi observado com o que foi estimado pelo modelo. Além da vantagem citada anteriormente, o uso da modelagem inversa também oferece flexibilidade para que o pesquisador utilize equações que melhor se adaptam ao ambiente de estudo. Essa possibilidade elimina, por exemplo, a incerteza da estimativa da respiração pelo método de *bookkeeping*, ao utilizar equações que relacionam a respiração à temperatura (Hanson et al., 2008; Solomon et al., 2013; Brighenti et al., 2015, 2018).

Apesar disso, a modelagem do metabolismo também possui incertezas associadas. Adicionar dados de oxigênio dissolvido com ruídos pode, por exemplo, sub- ou superestimar as taxas metabólicas. Fenômenos físicos que não são comumente incorporados no modelo podem gerar valores de parâmetros que não são biologicamente plausíveis. Por fim, a utilização de equações de fluxo ar-água que não são adequadas ao ambiente também pode ser um fator gerador de incerteza nas taxas metabólicas estimadas (Hanson et al., 2008).

O conhecimento gerado sobre o metabolismo em ecossistemas aquáticos provém, em sua maioria, de estudos em ambientes temperados. De acordo com Staehr e colaboradores

(2012a) apenas 8% dos estudos com metabolismo aquático são conduzidos em ambientes tropicais. Essa má distribuição de áreas investigadas ou sob investigação fomentam os *gaps* no conhecimento a respeito dos possíveis *drivers* e efeitos de diversas variáveis sobre o metabolismo ecossistêmico, uma vez que ambientes tropicais e temperados diferem em diversos aspectos, como clima, relevo, vegetação, dentre outros.

A grande maioria dos estudos pioneiros em limnologia tropical foram conduzidos nos sistemas aquáticos africanos (Beadle, 1932; Talling, 2008). No Brasil, mais especificamente no sistema lacustre do médio Rio Doce (sudeste brasileiro), estudos com metabolismo aquático vêm sendo realizados desde a década de 1980, acompanhando a evolução de métodos, técnicas e abordagens. Além disso, em 1998 foi implantado nessa região um sítio do Programa de Pesquisas Ecológicas de Longa Duração (PELD), mais especificamente no Parque Estadual do Rio Doce (PERD), que abriga o maior remanescente florestal de Mata Atlântica do estado de Minas Gerais. Com o estabelecimento do sítio PELD no PERD, 4 lagoas (Carioca, Jacaré, Gambazinho e Dom Helvécio) foram amostradas mensalmente do período de 1999-2010 para diversos parâmetros que caracterizam as condições físico-químicas e biológicas desses ambientes. Apesar da diminuição da frequência, as amostragens foram realizadas de forma periódica até o início de 2020, quando os trabalhos de campo foram suspensos devido a pandemia da Covid-19.

Os estudos pioneiros em metabolismo aquático nessa região foram conduzidos principalmente nas Lagoas Carioca e Dom Helvécio, e abordaram a produtividade primária do fitoplâncton, além da variação diária do oxigênio dissolvido e a influência da estrutura térmica do lago na distribuição de nutrientes (Barbosa e Tundisi, 1980; 1989). Posteriormente, em 1995 pesquisadores enfatizaram a importância de compostos nitrogenados regenerados como fonte nutricional para o fitoplâncton e para produção primária, como consequência (Mitamura et al., 1995). Em 2002, Rahaingomanana e colaboradores demonstraram a importância do pico e do nanoplâncton para a produção primária total em diferentes lagos do médio Rio Doce. Além disso, esse estudo também evidenciou diferenças entre a produção fitoplanctônica em lagos impactados e não impactados pela plantação de eucalipto na área de bacia. Em 2004, outro estudo conduzido na região demonstrou a importância da produção bacteriana para o metabolismo dos lagos, especialmente aqueles que são ricos em matéria orgânica e nutrientes. Este estudo também reforçou os resultados dos estudos pioneiros da região, os quais demonstraram que os maiores valores de produção primária na lagoa Carioca foram encontrados na estação seca, principalmente durante o período da manhã (Petrucio e Barbosa, 2004). Em outro estudo publicado em 2006 foi possível evidenciar a variação inter- e intra-

anual do metabolismo aquático, nos quais os autores também demonstraram que a produção primária aumentou cerca de 3 vezes nos lagos estudados quando comparados aos valores registrados na década anterior (Petruccio et al., 2006). Em 2010, outro estudo veio a corroborar os resultados descritos anteriormente para a lagoa Carioca acrescentando, porém, a mudança na comunidade fitoplanctônica provavelmente devido a introdução de espécies exóticas de peixes (Carvalhais Júnior, 2010).

Até esse momento a técnica utilizada para quantificar a produtividade primária nos lagos do médio Rio Doce envolviam incubações de um determinado volume de água em frascos que eram distribuídos em diferentes profundidades, correspondendo a 100%, 10% e 1% da irradiância de luz na subsuperfície e na zona afótica. A produção primária era determinada *in situ* utilizando o método de incorporação de ^{14}C (Steemann-Nielsen, 1952). No ano de 2011, foram instalados na lagoa Carioca e Dom Helvécio os primeiros sensores capazes de obter dados de diferentes parâmetros com altíssima resolução temporal. Ao longo de 2011 e 2012, as boias que mantinham os diferentes sensores coletando dados a cada 15 minutos contavam com: sensor de oxigênio, sensores de radiação subaquática, temperatura, pressão atmosférica, velocidade do vento e um sensor de radiação solar. Além disso, foram instalados também placas solares e registradores de dados (do inglês *Data logger*) (Fig. 2)



Fig. 2 - Estrutura e sensores utilizados no período de 2011 a 2013 nos lagos do PERD.

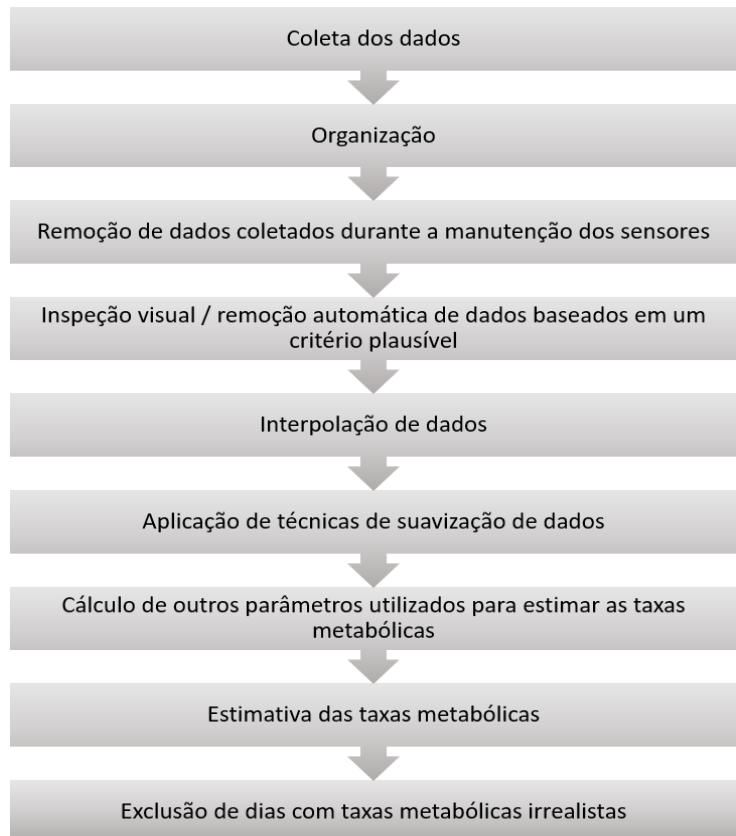
A implementação e utilização de novas tecnologias para o estudo do metabolismo ecossistêmico, traz novos desafios juntamente com as vantagens da sua utilização. De uma forma geral, os sensores requerem limpeza e manutenção de forma regular a fim de se manter

a confiabilidade dos dados gerados (Fig. 3). Além disso, o aprendizado do processo de utilização desses dados requer tempo e dedicação dos pesquisadores envolvidos, sendo muitas as etapas até que de fato seja possível estimar as taxas metabólicas (Fig. 4).



Fig. 3 - Acúmulo de biofilme em cordas e sensores. A limpeza e a manutenção deve ser periódica e regular a fim de garantir a qualidade dos dados coletados. Recomenda-se a limpeza das cordas com escova ou esponja. Os sensores devem ser limpos apenas com o auxílio de um tecido macio.

Fig. 4 - Processos e etapas para estimativa das taxas metabólicas utilizando dados de sensores de alta frequência. De forma geral, as etapas que precedem as estimativas do metabolismo podem ser aplicadas a uma variedade de parâmetros, mas são cruciais aos dados de temperatura da água, oxigênio dissolvido e radiação subaquática. A remoção automática de dados refere-se a exclusão de dados que claramente não representam o ambiente estudado (ex: temperatura da água acima de 50°C). É possível que em alguns ambientes e a depender da qualidade geral dos dados, as etapas de interpolação e o uso de técnicas de suavização de dados não sejam necessários.



De 2011 até a presente data foram publicados 3 estudos sobre metabolismo aquático nos lagos do PERD utilizando os sensores de alta frequência instalados no período de 2011 ao início de 2013. Dois deles utilizando a abordagem da modelagem inversa e o mais recente, bookkeeping. Em 2015, Brighenti e colaboradores demonstraram a importância da sazonalidade e do regime térmico das Lagoas Carioca e Dom Helvécio para as taxas metabólicas. Durante o verão, os lagos estão estratificados durante a maior parte do tempo devido às altas temperaturas da região. A estratificação térmica isola os nutrientes e a matéria orgânica no hipolímnio, fazendo com que a camada luminosa seja deplecionada dos substratos essenciais para ocorrência da produção primária. A combinação da depleção nutricional aliada a alta disponibilidade de luz aumenta o grau de fotoinibição experimentado pelos produtores primários, fazendo com que as taxas metabólicas nesse período sejam as mais baixas registradas durante o ano. No período do inverno, no entanto, as temperaturas mais baixas induzem a mistura dos lagos durante a maior parte desse período, o que, por sua vez, faz com que os nutrientes sejam disponibilizados para toda a coluna de água. Além disso, a mistura das camadas também promove a ressuspensão do sedimento e a distribuição dos sólidos suspensos e da matéria orgânica no epilímnio. Dada a capacidade desses parâmetros em atenuar e absorver a radiação solar, a disponibilidade de luz durante esse período diminui juntamente com o grau de fotoinibição, aumentando significativamente as taxas metabólicas nos lagos estudados.

Em 2018, um experimento de mesocosmos evidenciou o aumento da PPB e da R devido a adição de nutrientes e carbono. Ambos os parâmetros influenciaram direta e indiretamente no aumento das taxas metabólicas. Enquanto os nutrientes são utilizados diretamente pelos produtores primários e seu aumento subsidia maiores taxas de produção, o carbono pode estimular a PPB ao ser degradado e liberar nutrientes dissolvidos na coluna d'água. Ademais, ambos os parâmetros tiveram papel na redução da disponibilidade média de luz e do grau de ocorrência de fotoinibição, refletindo, então, no aumento das taxas metabólicas (Brighenti et al., 2018). Já em 2019, Gagliardi e colaboradores demonstraram que a influência da variação na precipitação sobre as taxas metabólicas depende de características morfométricas do corpo hídrico, bem como da área de bacia. Em suma, os efeitos da redução da precipitação (diminuição do volume dos lagos, aumento da concentração de nutrientes e redução na disponibilidade de luz) foram mais proeminentes em lagos com menor volume em relação a área da bacia. Além disso, lagos com maior porcentagem de floresta nativa na área de drenagem se mostraram mais transparentes, tendo uma menor PPB como consequência.

Dada a finalização dos projetos em andamento, em 2013 os sensores foram recolhidos dos respectivos lagos. Uma nova instalação de um conjunto de sensores foi feita na metade de

2017, durante a nova fase do projeto PELD que se estendeu formalmente até 2020. Nesse período, foi possível instalar uma plataforma de monitoramento de diversos parâmetros físico-químicos na lagoa Carioca, que recebeu novos sensores quando comparados ao período de 2011-2013. Em adição ao conjunto anterior de sensores, foram instalados na plataforma: 8 sensores de oxigênio e temperatura, 8 sensores de radiação subaquática, linígrafo, sensor de temperatura e umidade relativa do ar, sensor de direção do vento e um pluviômetro (Fig. 5).



Fig. 5 - Plataforma e sensores instalados na lagoa Carioca (PERD) desde 2017.

Segundo dados do Instituto Nacional de Meteorologia (INMET), entre 2012 e 2016 a região em que se localiza o PERD passou por diversos eventos de seca severa. Além disso, o déficit hídrico se estendeu, também, durante 2018 e 2019. Além da seca, a região também experimentou grandes volumes de chuva concentrados em um ou poucos dias, seguido de muitos dias de seca (Fig. 6).

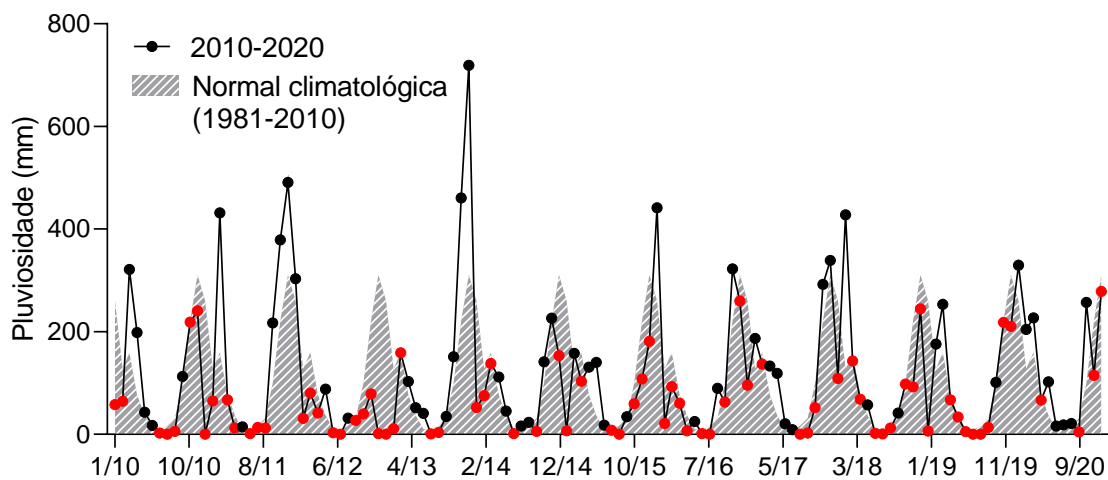


Fig. 6 – Pluviosidade acumulada mensal entre 2010 e 2020. Áreas em cinza indicam a normal climatológica (1981-2010) para a região. Linhas e pontos em preto indicam a precipitação acumulada mensal entre 2010 e 2020 que ultrapassaram a normal climatológica. Pontos em vermelho indicam os meses que a precipitação acumulada esteve abaixo da normal.

Tal variabilidade na dinâmica pluviométrica resultou em uma perda de volume em diversos lagos do PERD, sendo mais pronunciada em lagos pequenos, como a lagoa Carioca, que perdeu 4 metros de coluna de água (representando aproximadamente 60% do volume e 30% da área; Fig. 7). O capítulo que se segue é resultado da urgência em identificar e avaliar os efeitos da crise climática sobre os corpos hídricos tropicais, trazendo uma visão integrada sobre os diversos processos que são alterados pela variabilidade climatológica e que podem, como consequência, reforçar os efeitos da crise climática via *feedback* positivo.



Fig. 7 - Imagens de satélite da Lagoa Carioca (PERD) obtidas pelo Google Earth. O traçado em vermelho demonstra a redução da área da lagoa em um período de 10 anos (2009 e 2019 respectivamente).

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3. Reduced water level leads to a high increase in gross primary production and respiration in a natural tropical lake

Shortened version: Increase in metabolic rates due to water loss

*Manuscrito submetido na revista *Ecosystems*

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HIGHLIGHTS

- A 60% lake volume decrease increased ca. 50% nutrients and carbon concentrations;
- There was a negative relation between light availability and GPP;
- Net Ecosystem Production switched from autotrophy to heterotrophy between seasons.

Viana contributed to the study design, field work, data analyses and modelling, and wrote the paper. Brighenti contributed to the study design, field work, data analyses and modelling, and revised the manuscript. Pujoni contributed to data analyses and modelling and revised the manuscript. Barbosa and Bezerra-Neto conceived the study, were responsible for funding acquisition, contributed to the methods, and revised the manuscript.

3.1.ABSTRACT

As hotspots of the global carbon cycle, lakes can regulate climate change while being regulated by it, via a feedback loop. As ecosystem metabolism is considered to be a good sentinel to these changes, we used high frequency measurements and the inverting modeling approach to study the temporal dynamic of gross primary production (GPP), respiration (R), and net ecosystem production (NEP) of a tropical lake, which lost about 60% of its volume in ten years. We show that this water loss led to an increased concentration of nitrogen, phosphorus, and carbon, and decreased water transparency and light availability. During the low volume period, GPP increased 40% in comparison with a full lake volume period, and R surpassed GPP during the mixing period of the lake. We discuss that this modification is a result of higher carbon and nutrients concentrations, lower light availability, and a change in the lake thermal stability. Ecosystem metabolism changed due to meteorological and hydrological drought, and it may continue to change under the ongoing variation in rainfall pattern, and temperature.

Key words: ecosystem metabolism; water loss; lake volume; trophic status; climate change; high frequency data; inverting modeling approach.

3.2.INTRODUCTION

The carbon transformation in the aquatic environment involves the formation (i.e. gross primary production - GPP) and degradation (i.e. respiration - R) of organic matter (OM) by the organisms, as well as physical processes. The balance of these two processes is usually described as net primary production ($NEP = GPP - R$) which stands for the total biomass formation of primary producers, and these processes are known as the metabolism of the ecosystem (Staehr and others, 2012a). NEP is useful to describe and evaluate the trophic state of lakes and also help to define the role of the ecosystem in the carbon cycle as a sink ($NEP > 0$; net autotrophic systems or periods) or a source ($NEP < 0$; net heterotrophic systems or periods) of atmospheric CO_2 (del Giorgio and Duarte, 2002).

The effects of nutrients, organic matter, and light availability on lake metabolism is an active research topic. There is a general agreement that an increase in nutrients concentrations and light availability will stimulate algal growth, increasing both GPP and R rates (Hanson and others, 2003; Staehr and others 2012b; Hoellein and others, 2013). However, because these drivers are not independent from each other, the specific result may not be directly predicted due to complex interactions and feedback loops. Some studies have shown that dissolved organic matter (DOM), especially its colored fraction (colored DOM - CDOM), can reduce water transparency, thus decreasing primary production and increasing respiration rates (Jones, 1992; Thrane and others, 2014). On the other hand, DOM degradation releases dissolved nutrients, stimulating algal growth, thus enhancing GPP more than ecosystem respiration (Solomon and others, 2015; Feuchtmayr and others, 2019). In addition, DOM reduces the mixed layer depth, retaining primary producers to an upper and illuminated zone, thus increasing epilimnetic GPP rates (Jones, 1992).

Even more complex outcomes can be described when we consider tropical lakes, that receive a lot more solar radiation throughout the entire year than its temperate counterparts. For this reason, light availability by itself is not commonly the limiting factor for primary producers in this region

77 (Staeher and others, 2016). Indeed, this elevated amount of irradiation in combination with nutrient
78 privation was evidenced to decrease GPP (Brighenti and others, 2015; 2018). Despite that, it is known
79 that allochthonous DOM reduced light availability (Karlsson and others, 2009) and the penetration
80 of harmful ultraviolet light into the water column (Arts and others, 2000; Brandão and others, 2018),
81 thus preventing light-induced damages to the photosystem II with no net loss of production (Keren
82 and Liskay, 2011).

83 One of the most visible effects of climate change in aquatic ecosystems is the reduction of
84 water volume in response to changes in rainfall patterns and increased evapotranspiration
85 (Williamson and others, 2009). With a lower water level, the concentrations of nutrients and organic
86 matter might increase, affecting directly GPP and R rates (Jeppensen and others, 2015; Brasil and
87 others, 2016). Gagliardi and others (2019) showed that the response of ecosystem metabolism to
88 changes in rainfall pattern depends on morphometric and catchment characteristics and suggested that
89 their results could be also associated with a reduction in lake volume. Moreover, Mendonça Júnior
90 and others (2018) and Junger and others (2019) demonstrated that prolonged droughts in Northeast
91 Brazil reduced lakes and reservoirs water volume, favoring primary production through a higher
92 concentration of nutrients and, therefore, leading to the reduction of CO₂ in the water column.
93 However, as demonstrated by Tsai and others (2016), despite the initial increase in ecosystem
94 metabolism following the reduction in lake volume, metabolic rates might decline due to a shallower
95 mixed layer depth and a strong thermal stratification (i.e. reducing the internal load), and also due to
96 a decline in nutrient levels during the dry years, following the decrease in terrestrial runoff (Chiu and
97 others, 2020). This indicates that the influence of drought and the changes in rainfall patterns are
98 complex and might extend in the subsequent years, as demonstrated in previous studies (Fenner and
99 others, 2001; Jennings and others, 2009; Chiu and others, 2020).

100 Loss of water volume may also impact the seasonal pattern of a lake. A two-year study in two
101 monomictic tropical lakes demonstrated that the combination of high light conditions and nutrient

102 depletion during stratification (rainy season - summer) raised the levels of photosynthetic
103 photoinhibition and thus decreased the metabolic rates. GPP and R raised again during the mixing
104 period (dry season - winter), when nutrients and DOM are resuspended, decreasing photoinhibition
105 and promoting primary production and respiration (Brighenti and others, 2015). In this sense, with a
106 lower water volume, the general increase in nutrients and DOM could diminish or neutralize the role
107 of seasonality in ecosystem metabolism. Moreover, shallower lakes may decrease water column
108 stability, becoming more prone to occasional mixing events (Fee and others, 1996), reinforcing its
109 effects in metabolic rates (Staehr and Jensen, 2007).

110 Herein, we aim to discuss that a complex range of lake parameters acts simultaneously (i.e.
111 influencing each other) to modulate the response of ecosystem metabolism to climatic variations. To
112 accomplish this, we compared two distinct periods (2011-2012 and 2017-2019) of the epilimnetic
113 metabolism of a tropical lake that lost about 60% of its volume and c. 30% of its surface area
114 compared to the last decade (Bezerra-Neto and others, *unpubl.*). We evaluated whether a persistent
115 lower water level changed lake physical and chemical characteristics, thus altering the magnitude and
116 the dynamics of GPP, R, and NEP rates. We predict a general increase in nutrients and dissolved
117 organic matter, which will reduce water transparency and light availability, (i) enhancing both
118 epilimnetic GPP and R (ii) and weakening the role of seasonality on epilimnetic metabolism (the
119 metabolic rates will be similar between rainy and dry seasons).

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125 3.3.METHODS

126 3.3.1. *Study Area*

127 This study was performed in Carioca Lake (19.75°S; 42.6°W), a tropical, small (perimeter:
128 1718 m, area: 0.14 km², maximum depth: 11.8 m, mean depth: 4.8 m; Bezerra-Neto and others, 2010),
129 and monomictic lake surrounded by preserved Tropical Atlantic Forest. This lake is subjected to two
130 distinct seasons, the dry season (Winter - May to August) when total mixing of the water column
131 occurs, and the rainy season (September to March/April) when the water column is stratified most of
132 the time. Carioca lake has been monitored since 1999 as part of a long-term ecological research
133 project (LTER project site #4 - Atlantic Forest and Lacustrine System of the middle Rio Doce - Brazil;
134 www2.icb.ufmg.br/limneapeld/site/index.php). Previous studies described Carioca Lake as
135 mesotrophic (Petruccio and others, 2006; Brighenti and others, 2015), however, recently data evidence
136 a shift to a eutrophic state (see Table S1). This lake is located inside a conservation unit (Parque
137 Estadual do Rio Doce - PERD), being part of the middle Rio Doce lacustrine system that is recognized
138 as a wetland of international importance by the Ramsar Convention (Ramsar 2010—
139 www.ramsar.org).

140 3.3.2. *Environmental variables*

141 Environmental variables were collected in two distinct periods. The first one (P1), from May
142 2011 to December 2012, comprised two dry (mixing) and two rainy (stratified) seasons. While the
143 second one (P2), from July 2017 to December 2019, covered three dry and three rainy seasons. During
144 P2 lake volume was ca. 60% lower than during P1 (Bezerra-Neto and others, 2010; Bezerra-Neto,
145 *unpub.*).

146 Water samples for nutrients, DOM, Chlorophyll-a (Chl-a), and Total suspended solids (TSS)
147 were collected monthly during P1 (n = 20) and at irregular intervals during P2 (n = 19). In both
148 periods, the samples covered the dry and the rainy season and were collected at 0.5m for different

149 analyses. Unfiltered samples were used to determine total phosphorus (TP; Mackereth, 1978) and
150 total nitrogen (TN; TOC analyzer Shimadzu TOC-5000A). Samples for dissolved organic carbon
151 (DOC) and colored dissolved organic matter (CDOM) were filtered (0.22 μ m Millipore filter) after
152 collection. DOC concentrations were determined with a TOC analyzer. CDOM were determined at
153 three absorbance coefficients to characterize different sources of carbon: allochthonous (at 254nm),
154 autochthonous (at 440nm), and at 272nm as a measure of CDOM concentration/ watercolor (Loiselle
155 and others, 2008; Brandão and others, 2018). Chl-a concentration was estimated according to
156 Lorenzen (1967) after extraction in 90% acetone. TSS were determined using the gravimetric method
157 (Millipore AP40 filter).

158 In both P1 and P2 campaigns, high-frequency data were sampled every 15 minutes from
159 instrumentation deployed at the central deep region. In the P1 campaign the buoy was equipped with
160 1 dissolved oxygen (DO) and temperature sensor at 0.5m (D-OptoLogger, Zebra Tech Ltda.) and 1
161 thermistor chain with 5 sensors (WQ101, Global Water). For a complete description about the
162 equipment used see Brighenti and others (2015). In the P2 campaign the instrumentation in the buoy
163 was the following: 8 DO and temperature sensors at the depths (0.5m, 1.0m, 1.5m, 2.0m, 3.0m, 4.0m,
164 5.0m, and 6.5m) (miniDOT Logger, PME; D-OptoLogger, Zebra Tech Ltda.); 1 PAR radiation sensor
165 at 1.6m height (Sq214, Apogee); 1 wind speed sensor at 1m above the surface (RK100-02, Rika
166 Electronic Technology); 1 barometric pressure sensor (WE100, Global Water); 1 rainfall sensor at
167 0.5m above the surface (RainEW111, RainWiseInc); 1 air temperature and humidity sensor at 1m
168 height (RK330-01, Rika Electronic Technology); and light profiles were measured using four light
169 sensors (UA-002, HOBO).

170 To make a general comparison of the meteorological data between P1 and P2 (e.g. air
171 temperature and rainfall) we used data from a meteorological station located at 30 km of distance
172 from the lake for both periods (<https://tempo.inmet.gov.br/>). We also used wind speed values from

173 this station when the data from lake instrumentation were missing (from July 2017 to February 2018
174 and from September 2018 to November 2018).

175 The daily diffuse photosynthetically active radiation attenuation coefficient (K_{dPAR}) was
176 mainly determined using the data collected between 10 am to 2 pm by HOBO sensors and converted
177 to PAR according to Long and others, 2012. We also used a BIC radiometer to evaluate K_{dPAR} in
178 periods that HOBO information was not available. Mean available light at the upper mixed layer
179 (E_{mean} ; $\text{mmol photons m}^{-2} \text{ s}^{-1}$) was estimated using the PAR radiation sensor. HOBO sensor (0.25m)
180 was used when PAR values were not available or missing (from July 2017 to January 2018, from
181 September 2018 to November 2018 and in September 2019), and calculated according to equation 1
182 (Staehr and Sand-Jensen, 2007).

$$183 \quad E_{mean} = 0.9 * I_0(1 - e^{-K_{dPAR}Z_{mix}})/(K_{dPAR}Z_{mix})(1)$$

184 Where I_0 is the radiation measured in the atmosphere and 0.9 is a coefficient for backscattering and
185 surface reflection (when radiation is measured inside the water, this term is removed from the
186 equation); K_{dPAR} is the diffuse photosynthetically active radiation attenuation coefficient and Z_{mix} is
187 the mixing depth (calculated using the package rLakeAnalyzer). See Brighenti and others, 2015 for
188 more specific details about K_{dPAR} , E_{mean} and Z_{mix} calculation for 2011-2012 period.

189 We use Brunt–Väisälä (BV) frequency to characterize the stability of stratification and Z_{mix}
190 to identify major changes in the mixing pattern in Carioca Lake. BV frequency was calculated using
191 the package rLakeAnalyzer in R software (R Core Team, 2020).

192 3.3.3. *Metabolic rates estimative*

193 The metabolism rates were estimated using the inverse modeling approach (IMA; Brighenti
194 and others, 2015; Hanson and others, 2008; Solomon and others, 2013). In this technique, we used a
195 nonlinear calibration procedure to estimate the best parameter values combination to obtain the best
196 correlation between estimated and observed DO concentrations. We use DO concentrations measured

197 at 0.5m for P1 and 1.0m for P2, this difference does not affect our results because our long term data
 198 has shown that the DO concentrations of this two depths are highly correlated ($R^2 = 0.91$) along the
 199 1:1 line (supplemental material – Fig. S1).

200 The DO concentrations obtained for every 15 min were averaged to obtain 30 min intervals.
 201 All temperature and DO measurements pass through visual inspection to remove erroneous values
 202 obtained by sensor errors, low battery, sampling days, and biofilm accumulation. Data also went by
 203 the moving averages technique (1:30 hour interval) to remove erratic variation and noise. DO
 204 fluctuations were described using the equation 2 adapted from Odum (1956):

$$205 \quad DO_{t+1} = DO_t + GPP_t - R_t + F_t \quad (2)$$

206 where DO_{t+1} and DO_t are DO concentrations (mg/L) at times $t + 1$ and t ; GPP_t is the gross primary
 207 production; R is the ecosystem respiration; F is the flux of O_2 at the interface lake-atmosphere.

208 Gross primary production (GPP) was calculated using the double exponential model of Platt
 209 and others, (1980). This model was chosen as it can evidence the occurrence of photoinhibition and
 210 saturation. Moreover, this light intensity relationship proved to be the best model to evaluate GPP on
 211 Carioca lake, as described in Brighenti and others, (2015; 2018).

$$212 \quad GPP_t = P_{max} \left(1 - e^{\left(-\frac{\alpha I_t}{P_{max}}\right)} \right) e^{\left(-\frac{\beta I_t}{P_{max}}\right)} \quad (3)$$

213 where P_{max} is a free parameter describing the maximum potential photosynthetic rate; α (mg O_2 /L
 214 mmol photons $m^{-2} s^{-1}$) is a free parameter representing the initial linear slope of the relationship
 215 between photosynthesis and light; I_t is the mean available light in the upper mixed layer (E_{mean} ; mmol
 216 photons $m^{-2} s^{-1}$) measured at time t ; β is a free parameter describing the degree of photoinhibition in
 217 the same unit as α .

218 Ecosystem respiration (R) was calculated according to Jørgensen (1979), considering R
 219 dependent on temperature. We use a thermal dependence coefficient of 1.07 and a temperature
 220 reference point of 30°C:

$$221 \quad R_{(t)} = R_{max} \times 1.07^{(T_{(t)}-30)} \quad (4)$$

222 where R_{max} is a free parameter describing the respiration rate at 30°C and T_t is the water temperature
 223 (°C) at time t measured at the same depth of the DO sensor.

224 The atmospheric flux ($m\ h^{-1}$) was calculated according to Staehr and others, (2010a) as
 225 follows:

$$226 \quad F_{(t)} = \frac{k_{(t)}[DO_{sat(t)}-DO_t]/Z_{mix}}{2} \quad (5)$$

227 where $DO_{sat(t)}$ is the concentration in water at equilibrium with atmosphere at ambient temperature
 228 and pressure calculated according to Weiss (1970) at time t ; DO_t is the concentration measured in
 229 the water at time t ; Z_{mix} is the mixed layer depth (m); $k_{(t)}$ is the coefficient of gas exchange and was
 230 calculated considering the relationship between Schmidt numbers (Sc) and temperature (Jahne and
 231 others, 1987): $k = k_{600} \times (Sc/600)^{-0.5}$. k_{600} ($m\ h^{-1}$; k for a Sc of 600) simulate the piston velocity.

232 There has been much discussion in the literature about the accuracy of predicting k from wind
 233 measurements and the influence of the k models on metabolism estimates (Dugan and others, 2016;
 234 Klaus and Vachon, 2020). In this work, we used ten different approaches to estimate k_{600} and further,
 235 the metabolic rates. We aimed to understand if and how the models can affect the major results (i.e.
 236 the mean seasonal results) of this work, and we also evaluated the strengths and vulnerabilities about
 237 the application of these models for metabolism estimates. We separate the models into two groups:
 238 1) wind-based models and 2) models that consider other processes that generate turbulence close to
 239 the air-water interface besides the wind. We tested the follow approaches: 1.1) Cole and Caraco
 240 (1998); 1.2) Cole and others, (2010); 1.3) linear model of Crusius and Wanninkhof (2003); 1.4)

241 bilinear model of Crusius and Wanninkhof (2003); 1.5) power function of Crusius and Wanninkhof
242 (2003); 2.1) the Vachon and Prairie (2013) model that considerate the lake area; 2.2) the buoyancy
243 flux model of MacIntyre and others, (2010); 2.3) the combination of the surface renewal model from
244 Read and others, (2012) and the breaking wave component of Soloviev and others, (2007); 2.4) the
245 buoyancy flux model from Heiskanen and others (2014). Lastly, we also used k_{600} as a free parameter
246 simulating the piston velocity. We used the LakeMetabolizer package (Winslow and others, 2016) to
247 obtain the models 2.3 and 2.4. Refer to supplemental material for the equations used and the
248 abbreviations names of the models (Table S2).

249 We used the free parameters (P_{max} , α , β , R_{max} , k_{600}) and the equations above (Eq. 3-5) to
250 estimate DO concentrations at 30 min intervals and, thus, calculated daily metabolic rates. NEP was
251 calculated as the difference between the daily GPP and R ($NEP = GPP - R$).

252 To evaluate the adequacy of the model for each day, we performed a linear regression between
253 the estimated and observed DO to obtain the p and R^2 values. Only model fits of $R^2 \geq 0.7$ and $p <$
254 0.05 were considered good. In this way, we assume that in days with a good model fit, the biological
255 processes and air-water flux are the main factors acting on DO fluctuations. On the other hand, in
256 days with a poor model fit, other physical processes as internal waves, periodic mixing, and water
257 movements from the littoral zone might be controlling the DO patterns, and thus, the model is not
258 proper to represent these processes (Hanson and others, 2008; Brighenti and others, 2015).

259 For the two sampling periods, 58% (8.000 data points including all k_{600} models) of the data
260 achieved our model requirements and were used in the data analysis. Days with poor model fit were
261 more frequent in P2 (2017-2019; 46% of the days), and mainly in the dry season of the same period
262 (59% of the days), however the unbalancing was not strong.

263 We also evaluated the occurrence of apparent light saturation (i.e. light intensity point at which
264 an additional increase do not increase photosynthesis rates) and photoinhibition process (i.e. light

265 intensity point at which an additional increase decreases photosynthesis rates). We used the adapted
 266 approach from Fahnenstiel and others (1989) to estimate the onset of light saturation (I_k) and the
 267 Harrison and Platt (1986) to calculate the onset of photoinhibition (I_{critic}).

$$268 \quad I_k = P_m/\alpha \quad (6)$$

$$269 \quad I_{critic} = (P_{max}/\alpha) \times \ln((\alpha + \beta)/\beta) \quad (7)$$

270 where P_m is the maximum photosynthetic rate at light saturation (Fahnenstiel and others, 1989). P_{max} ,
 271 α and β are as described as in Equation 3.

272 For each data point, we assessed whether the mean light availability in the upper mixed layer
 273 (E_{mean}) exceeded the I_k and the I_{critic} values. We consider that light saturation occurred when E_{mean}
 274 was greater than I_k , and that photoinhibition occurred when E_{mean} was greater than I_{critic} . If the
 275 opposite occurred (i.e. E_{mean} lower than I_k and I_{critic}), then we consider that none of the processes
 276 affected primary production.

277 3.3.4. Data analysis

278 Non-parametric Kruskal-Wallis test was used to verify differences in environmental variables
 279 between the combination of the periods and seasons (P1-rainy vs P1-dry vs P2-rainy vs P2-dry) of
 280 this work. We used the Dunn's test with Bonferroni p-adjustment method to compare the groups.
 281 Spearman correlation analysis was also used to assess the relationship between the carbon indices
 282 and concentration, nutrients, light availability, and metabolic rates. We used linear model to assess
 283 the main factors and interactions effects of periods, seasons, and models (i.e. the ten different
 284 approaches to calculate k_{600}) in the metabolic rates (e.g. GPP, R, NEP). All statistical analysis were
 285 performed in software R (R Core Team, 2020). The graphics were made in GraphPad Prism 8.

286 3.4.RESULTS

287 Maximum depth ranged between 9.4 and 11.25 m in P1 and 6.9 - 8.8 m in P2 (Table S3). The
288 mean water level in P2 (7.6 m) represents a total decrease of 4.2 m in comparison with the last
289 bathymetry data and a 2.6 m decrease in comparison to mean water level in P1. According to the
290 hypsographic curves, 65.4% of the total lake volume corresponds to depths less than 4.0 m and, thus,
291 the total lake volume in P2 ranged around 50 and 35% of the volume registered in the last decade
292 (Bezerra-Neto and others, 2010).

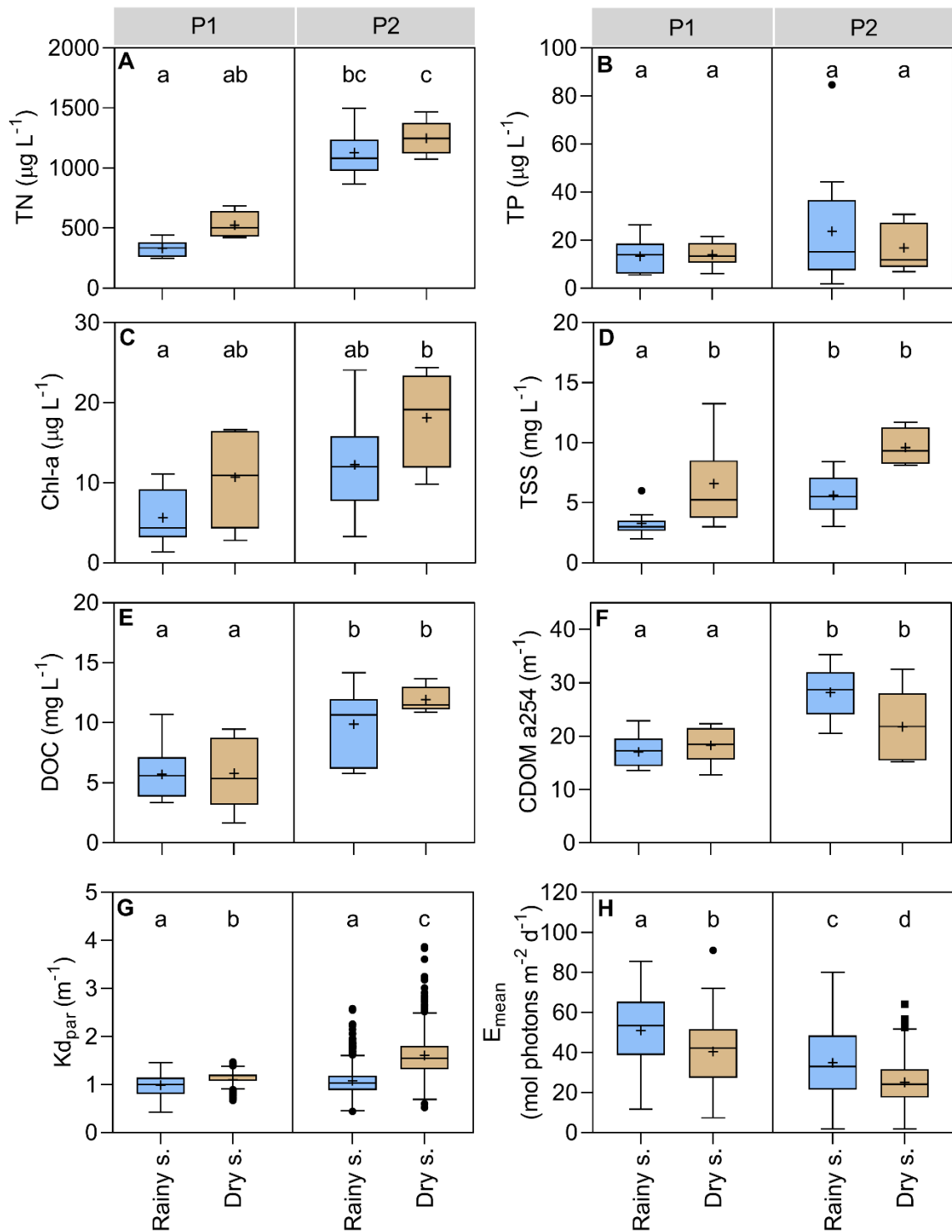
293 3.4.1. *Water chemistry and environmental variables*

294 The mean concentration of all the environmental variables varied between the periods and
295 seasons with exception of TP and CDOM a440. However, the variation between periods was higher
296 than between seasons. Besides this, the mean parameters concentrations were higher in P2 than in P1.
297 Period P2 presented higher mean concentration of TN (2.8 times), Chl-a (1.7 times), DOC (1.8 times),
298 CDOM a272 and CDOM a254 (1.5 times), TSS (1.4 times) than P1. Although not statistically
299 significant, the TP mean concentration was also higher in P2 (1.6 times). The mean parameters
300 concentrations were also higher in the dry season than in the rainy season for both periods, except for
301 TP, CDOM a254, a272, a440, and E_{mean} , which were higher in the rainy season of P2 than in the dry
302 season of the same period (Table S3; Fig. 1).

303 The PAR attenuation coefficient (K_{dpar}) was higher and the E_{mean} was reduced in P2 when
304 compared to P1. Thus, the average E_{mean} value in the rainy season of P2 was much lower than the one
305 found in the same season of P1 and it was also similar to the value recorded in the dry season of P1.
306 The average E_{mean} value in the dry season of P2 was the lowest recorded for both periods and seasons,
307 reflecting the higher concentrations of DOC, TSS, TN, and Chl-a in this season (Table S3; Fig. 1 –
308 G, H).

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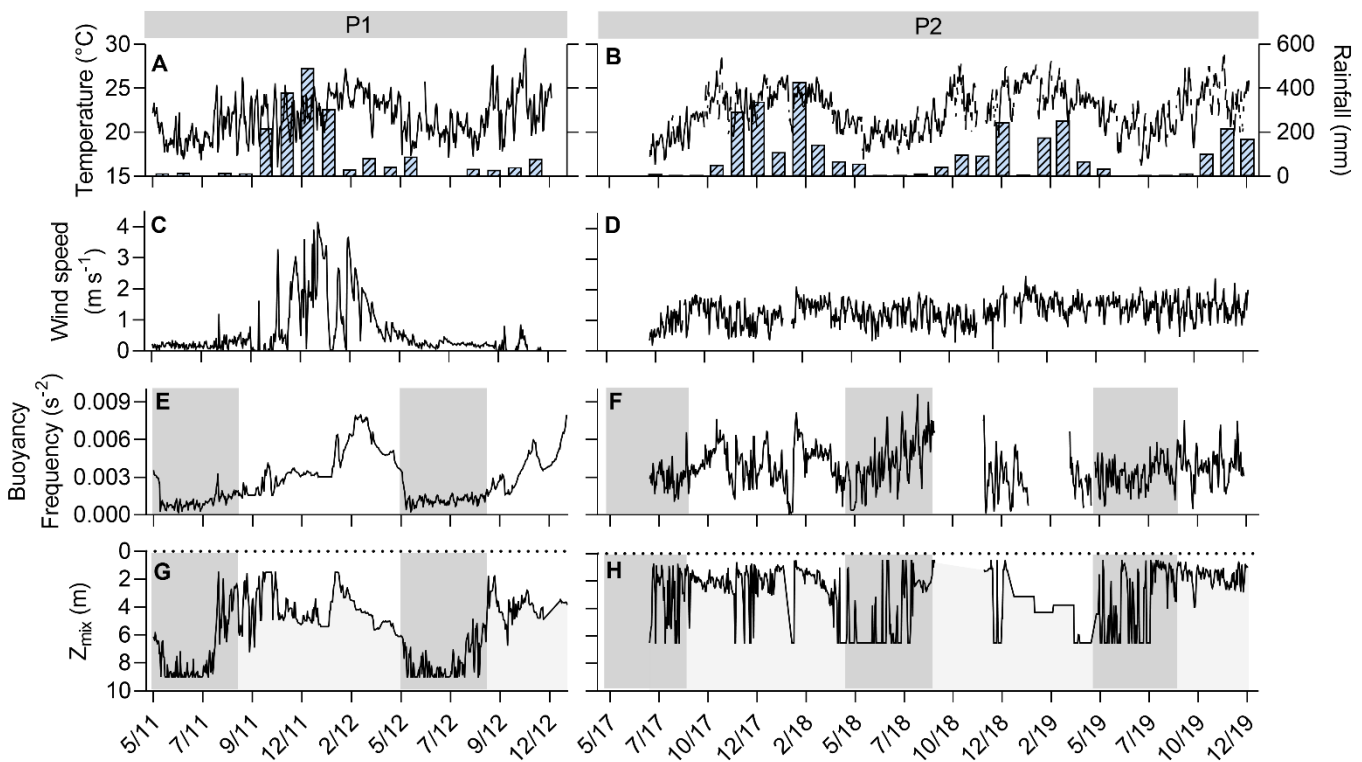


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Figure 1: Variation of environmental variables in Lake Carioca between periods and seasons. All box plots show the third and first quartiles, the center line is the median and the "+" symbol indicates the mean value. Error bars represent the minimum and maximum values. Black circles indicate outliers. Different letters represent significant differences between seasons and periods ($p < 0.05$), and equal letters represent no significant differences between the groups ($p > 0.05$). P1 column indicates the 2011-2012 period. P2 column indicates the 2017-2019 period. Blue bars represent the data collected in the rainy season and the light brown bars represent the data collected in the dry season for (A) total nitrogen; (B) total phosphorus; (C) chlorophyll-a; (D) total suspended solids; (E) dissolved organic carbon; (F) absorbance coefficient at 254nm; (G) light attenuation coefficient; and (H) mean available light at the upper mixed layer.

321 It was observed a higher seasonal amplitude in water temperature for P2, which showed an
322 average 1.1°C higher and 0.7°C lower than P1 for the rainy and dry seasons, respectively, following
323 the pattern observed in air temperature (P1 $21.9 \pm 3.6^\circ\text{C}$; P2 $22.5 \pm 3.8^\circ\text{C}$; mean \pm standard deviation
324 (Table S3). The accumulated rainfall was 1866mm in P1 and 3034.8mm in P2, however, the rainfall
325 pattern was quite dissimilar between the years for both periods (Fig. 2 – A, B). The years 2012, 2018,
326 and 2019 registered the lowest rainfall values (726.2 mm, 1296.4 mm, and 1084 mm respectively),
327 and were below the historical mean for the region (1981-2010: 1359.5 mm). We call the reader
328 attention to the years 2014 and 2015 (Fig. S2), where accumulated rainfall was also below the
329 historical mean (990.6mm and 947.2mm, respectively), in contrast to the mean air temperature, which
330 was 0.5°C above the historical mean in the rainy season of 2015 (1981-2010: 24.6°C; see
331 supplemental material Fig. S2). The region also registered extremely higher values of maximum air
332 temperature in the period ranging from 2011 to 2019, being in average 2.6°C above the historical
333 mean for the region (1981-2010: 28.8°C; details not shown).

334



335 Figure 2: Intra and inter-annual changes in daily (A-B) mean air temperature (line) and monthly accumulated rainfall
 336 (bars); (C-D) wind speed at 10m; (E-F) stratification stability (BV frequency); (G-H) mixed layer depth (Z_{mix}; in P2,
 337 maximum depth ranged between 6.9 to 8.8m). Because of that, the deepest sensor measured the temperature at 6.5m). The
 338 grey area represents the typical dry season for both periods. High-frequency data for Z_{mix} and BV frequency is missing
 339 from September 2018 to November 2018 and from January 2019 to March 2019 (monthly data are shown for Z_{mix}).
 340 Dates in the x axis are represented in the format MM/YY.
 341

342 The BV frequency in P1 showed a clear seasonal pattern, where the stratification stability
 343 decreased in the dry season and raised again in the rainy season. The mixed layer depth followed the
 344 same tendency and indicated two full mixing periods, both at the dry seasons of 2011 and 2012 (Fig.
 345 2 – E-G). However, in P2 the stratification stability was quite variable during the entire period and
 346 did not show the same clear seasonal pattern exhibited in P1 (Fig. 2 - F). This instability in P2 might
 347 indicate a higher susceptibility to occasional mixing events during the entire year and higher variation
 348 in the mixed layer depth. This is supported by the greatest coefficient of variation of daily Z_{mix} in P2
 349 in comparison to P1 (64.8% and 40.3%, respectively; CV= SD/mean X 100%). We also noticed the
 350 occurrence of occasional mixing events in the P2 rainy season in contrast to the same season of P1
 351 (Fig. 2 – G-H).

352 3.4.2. *Metabolic rates*

353 All metabolic rates (GPP, R, NEP) varied according to the interaction between periods and
354 seasons. Furthermore, R and NEP also varied with the different k_{600} models (Table 1; refer to
355 supplemental material for the number of data points for each period, season, and model - Table S4).

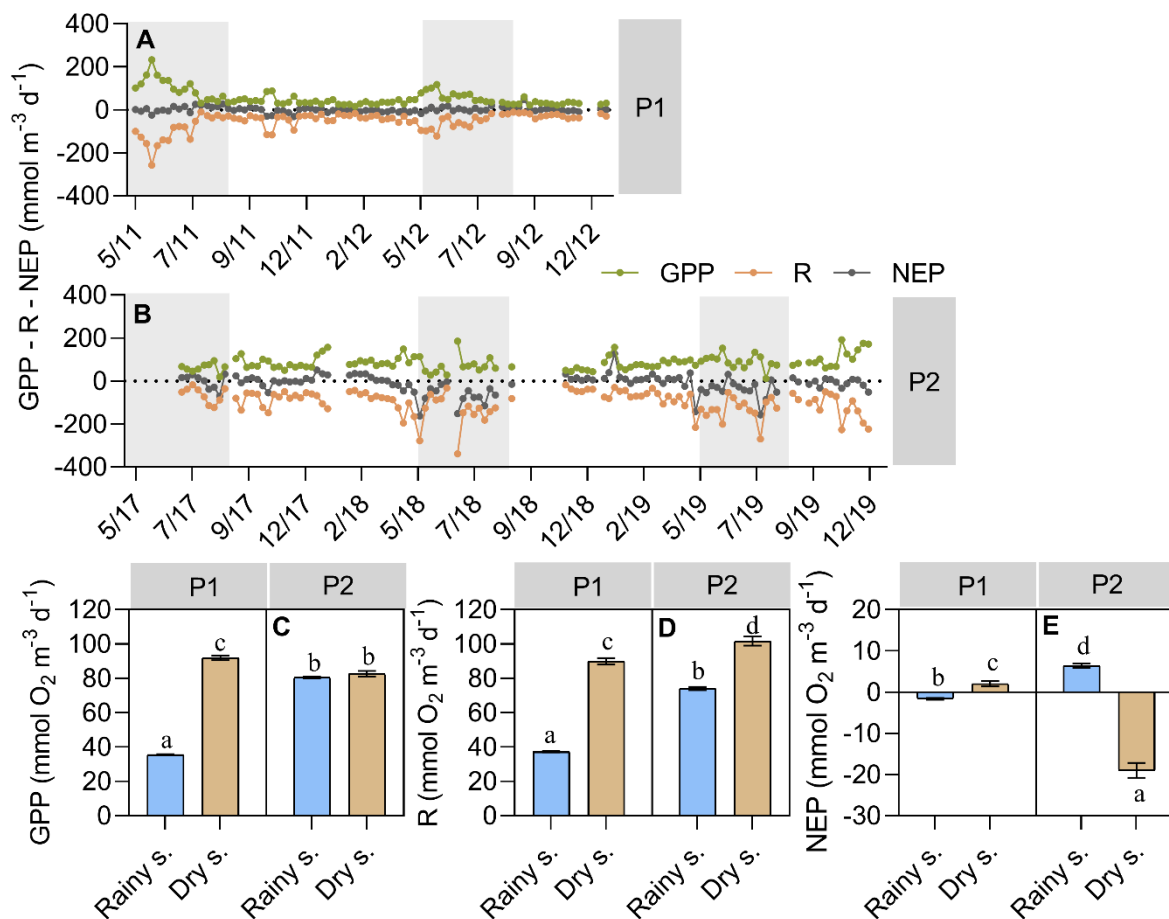
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357 Table 1. Variance analyses in the linear model testing the effects of periods, seasons, and models (i.e.
 358 the different k_{600} models), and their interactions on the metabolic rates.

	Source of variation	Sum Sq	Degrees of freedom	F value	p value
GPP	season	1669344	1	1159.4	<0.001
	period	1523269	1	1057.9	<0.001
	model	16780	9	1.3	0.23
	season:period	1215119	1	843.9	<0.001
	season:model	8256	9	0.6	0.77
	period:model	12995	9	1.0	0.44
	season:period:model	2724	9	0.2	0.99
	Residuals	11461398	7960		
R	season	2848773	1	976.3	<0.001
	period	1647904	1	564.8	<0.001
	model	57886	9	2.2	0.02
	season:period	252008	1	86.4	<0.001
	season:model	35049	9	1.3	0.21
	period:model	30372	9	1.2	0.32
	season:period:model	56224	9	2.1	0.02
	Residuals	23226176	7960		
NEP	season	156658	1	175.2	<0.001
	period	2450	1	2.7	0.10
	model	12647	9	1.6	0.12
	season:period	360385	1	403.1	<0.001
	season:model	30700	9	3.8	<0.001
	period:model	6651	9	0.8	0.59
	season:period:model	45669	9	5.7	<0.001
	Residuals	7116116	7960		

359 GPP = gross primary production; R = respiration; NEP = net ecosystem production.

360 Following the increase in nutrients, organic matter, algal biomass, and the decrease in water
 361 transparency and light availability, mean GPP was 40% higher in P2 than in P1 (81.03 ± 0.60 mmol
 362 $\text{O}_2 \text{ m}^{-3} \text{ d}^{-1}$ and 58.08 ± 0.74 mmol $\text{O}_2 \text{ m}^{-3} \text{ d}^{-1}$, respectively; mean \pm standard error). In P1, GPP rates
 363 were higher in the dry season than in the rainy season (91.97 ± 1.41 mmol $\text{O}_2 \text{ m}^{-3} \text{ d}^{-1}$ and 35.58 ± 0.31
 364 mmol $\text{O}_2 \text{ m}^{-3} \text{ d}^{-1}$, respectively). In P2, there was no difference in GPP rates between the seasons (82.70
 365 ± 1.54 mmol $\text{O}_2 \text{ m}^{-3} \text{ d}^{-1}$ in the dry season and 80.5 ± 0.63 mmol $\text{O}_2 \text{ m}^{-3} \text{ d}^{-1}$ in the rainy season).
 366 Therefore, GPP value in P2 rainy season was quite similar to the P1 dry season (80.5 ± 0.63 mmol
 367 $\text{O}_2 \text{ m}^{-3} \text{ d}^{-1}$ and 91.97 ± 1.41 mmol $\text{O}_2 \text{ m}^{-3} \text{ d}^{-1}$, respectively) (Table 1; Fig. 3 – A, B, C).



368

369 Figure 3: Variation in metabolism estimates of (A) weekly interval of P1 (2011-2012) and (B) P2 (2017-2019); and
 370 between periods and seasons for (C) GPP – gross primary production; (D) R – respiration; (E) NEP – net ecosystem
 371 production. Grey areas indicate the typical dry season. Bars represent the mean value and error bars represent standard
 372 error. Blue bars indicate the rainy season and light brown bars indicate the dry season. Different letters represent
 373 significant differences between seasons and periods ($p < 0.05$), and equal letters represent no significant differences
 374 between the groups ($p > 0.05$).

375 Mean R also increased in P2 in comparison to P1 ($80.71 \pm 0.94 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ and $58.26 \pm$
376 $0.87 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$, respectively). There was a difference between the seasons for both periods,
377 where the highest rates were found in the dry season ($89.93 \pm 1.79 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ in P1 and 101.68
378 $\pm 2.62 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ in P2; Fig. 3 – D). The mean R registered in the P2 rainy season was almost
379 two times higher than in the same season of P1 ($74.07 \pm 0.89 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ and $37.23 \pm 0.42 \text{ mmol}$
380 $\text{O}_2 \text{ m}^{-3} \text{ d}^{-1}$; Table 1; Fig. 3 – A, B, D).

381 In consequence, NEP shifted from a state near of equilibrium with atmosphere ($\text{NEP} \approx 0$) in
382 P1 (mean NEP -0.18 ± 0.29) to an autotrophy state in the P2 rainy season and a heterotrophy state in
383 the P2 dry season ($6.44 \pm 0.51 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ and $-18.98 \pm 1.81 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$, respectively;
384 Table 1; Fig. 3 – A, B, E), following the higher concentrations of DOC observed in this season.

385 Although the different k_{600} models were sources of variation for R and NEP, the main results
386 (i.e. seasonal differences in the Fig. 3) remained almost the same regardless of the model used. Two
387 exceptions were the bilinear and the power function of Crusius and Wanninkhof (2003) in which R
388 rates were equal between the rainy and dry season of P2. Regarding NEP, we noticed that k_{600} as a
389 free parameter was the model responsible for the statistical difference found between the seasons of
390 P1. For the other 9 models tested, no statistical difference between the rainy and dry seasons of P1
391 was observed. Moreover, R and NEP absolute values were higher than expected in some of the
392 models, especially those that consider other turbulence generating processes besides the wind, mainly
393 during the P2 for both seasons (see supplemental material; Fig. S3).

394 Regarding light saturation and photoinhibition process, in P2 E_{mean} was greater than I_k (light
395 saturation) for 65% of the days, 5% less than in P1 (2,775 and 2,930 data points considering all k
396 models tested, respectively). This decrease was pronounced during the P2 dry season, which
397 registered 40% less days with light saturation in comparison with the same season from P1 (623 and

398 1,036 data points, respectively). In addition, during the P2 rainy season the frequency of occurrence
399 of light saturation increased 14% (P1 1,894; P2 2,152).

400 Following the decrease in mean light availability, the frequency of occurrence of apparent
401 photoinhibition decreased 22% in P2 in relation to P1 (1,411 and 1,817, respectively). For both
402 periods, E_{mean} was greater than I_{critic} mainly during the rainy season, when P2 registered 16% less
403 days with apparent photoinhibition than P1 (P1 1,215; P2 1,016). This decrease was even more
404 pronounced during the P2 dry season, which registered 34% less days with occurrence of
405 photosynthetic photoinhibition (P1 602; P2 395).

406 3.5.DISCUSSION

407 3.5.1. *Water loss, water chemistry, and metabolic rates*

408 According to our expectations, the mean metabolic rates were higher during the P2 than in P1
409 (Fig. 3), coinciding with the increase in concentrations of nutrients, carbon, light attenuation, and the
410 consequential decrease in light availability in the mixed layer (Fig. 1). Furthermore, the effect of
411 seasonality in GPP and R rates during the P2 was lower than in P1, except for NEP. During the P1
412 rainy season, the nutrient depletion in combination with the higher light availability and greater levels
413 of photoinhibition, driven by higher stratification stability, reduced primary production as previously
414 shown by Brighenti and others (2015). However, in P2, higher gross primary production was
415 associated with higher concentration of nutrients (TN; $r = 0.62$, $p < 0.001$; details not shown) observed
416 during the entire period, with the overall decrease in light availability in the mixed layer ($r = -0.66$, p
417 < 0.001), and also with the consequential reduction in the degree of apparent photoinhibition, which
418 together weakened the effect of seasonality on primary production.

419 During 2014 and 2015 the accumulated rainfall was 29% lower than expected for the region
420 and the dry season extended through the rainy season of these years, when the meteorological drought
421 led to a hydrological drought (Fig. S2; Lake, 2011). This fact in combination with the higher air

422 temperature resulted in a process known as evapoconcentration, increasing lake nutrients and DOM
423 due to less dilution (Waiser and others, 2006; Brasil and others, 2016; Mendonça Júnior and others,
424 2018; Junger and others, 2019). Furthermore, during the P2 the precipitation returned to normal
425 values (2017), carrying terrestrial loads of nutrients and DOM to the lake, but not refilling the system
426 to its previous volume (Schindler and others, 1997; Chiu and others, 2020). As a result, higher DOC
427 concentrations in P2 were accompanied by higher allochthonous DOM (a254) in the rainy season (r
428 = 0.52, $p < 0.001$). Drought-induced water level reduction was reported before by Brasil and others
429 (2016), Jeppensen and others (2015) and by Tsai and others (2016), and its overall effects on lake
430 ecosystem (e.g. elevated concentration of nutrients, phytoplankton biomass, and lower water
431 transparency) were similar to those described in this study.

432 The effects of DOM in the water column are usually expected to decrease GPP by reducing
433 light availability, while stimulates R, resulting in negative NEP values (i.e. heterotrophy) (Staeher and
434 others, 2010b; Bogard and others, 2020). However, in Carioca lake, the higher DOC concentration in
435 P2 most likely stimulated both GPP and R. Higher DOM concentration in the water column might
436 have influenced primary producers not only through decreasing photoinhibition due to lower light
437 availability (DOC: $r = -0.68$, $p < 0.001$; CDOM: $r = -0.52$, $p < 0.001$), but also through increasing
438 nutrients levels in the lake (TN; $r = 0.65$, $p < 0.001$; Feuchtmayr and others, 2019). Allochthonous
439 DOM reaches the lake as relatively recalcitrant molecules, however, through biological and/or light-
440 induced mineralization the organic fraction of DOM can become available for the aquatic microbial
441 community (Vähätalo and Wetzel, 2008) releasing nutrients and CO₂ to the water column (Jansson
442 and others, 2012), thus enhancing primary production. Furthermore, previous studies show that
443 allochthonous DOM can also increase nutrients concentration by co-exporting and releasing bound
444 nutrients (Kissman and others, 2013; Solomon and others, 2015; Zwart and others, 2016). In fact, the
445 higher a254 index (i.e. proxy of allochthonous DOM content) found during the P2 rainy season was
446 accompanied by elevated and more variable concentration of TP (Fig. 1 – B, F).

447 Despite this, as light is a bottom-up control for algal growth (Reynolds, 2006), the change in
448 light availability pattern conducted by the greater content of optically active substances in P2
449 probably drove the lack of seasonal variation in GPP rates. The 30% reduction in mean light available
450 in the mixed layer during the P2 rainy season (when compared to the same season of P1) makes the
451 light conditions and the GPP rates very similar to the P1 dry season, the most productive season of
452 the first period of the study (Fig. 1 – H; Fig. 3 – C). The even higher light reduction in the P2 dry
453 season triggered by the higher TSS and DOC concentration did not have the same effect of increasing
454 the GPP rates, even with the 48% increase in algal biomass in this season (Fig. 1 – C). This result
455 contrasts with the experiments of Graham and Vinebrooke (2009) and Feuchtmayr and others (2019),
456 during which phytoplankton growth decreased with DOC concentrations above 10 mg L⁻¹. Here, algal
457 biomass peaked at higher carbon concentrations (11.9 mg L⁻¹; $r = 0.42$, $p = 0.008$), in agreement with
458 the unimodal curve relationship described by Bergstrom and Karlsson (2019), where algal biomass
459 showed the maximum values at DOC levels around 11 mg L⁻¹ but beyond that threshold starts to
460 decline due to poorer light conditions even under higher concentration of nutrients.

461 Despite the positive effect of DOC on primary production, the fact that GPP rates during P2
462 dry season did not follow the increase in phytoplankton biomass might indicate a threshold for light
463 limitation and a decrease of light saturation even under conditions of high nutrient. In fact, higher
464 GPP during P2 concurred with less days of occurrence of light saturation and photoinhibition,
465 especially during the dry season, which had 40% less days of light saturation in comparison with the
466 same season from P1. Moreover, at days which light saturation occurred, algal growth might have
467 benefited from the 34% less days with occurrence of photosynthetic photoinhibition during the P2
468 dry season, and thus maintaining the same high levels of primary production observed during the P2
469 rainy season (Brighenti and others, 2018).

470 Regarding ecosystem respiration rates, our results showed that the R values increased with
471 GPP rates in the P2 rainy season and surpassed primary production in the P2 dry season (Fig. 3 – D).

472 Regardless of the greater variation of daily mixed layer depth found during P2, most of the lake
473 mixing events continue to occur during the dry season (Fig. 2 – H). Mixing events not only provides
474 inorganic material to DOM production by primary producers but also releases organic substrates from
475 the sediment which is used by bacteria as energy source in the respiration process (Staehr and Jensen,
476 2007; Brighenti and others, 2015). Even though most of the organic carbon trapped in the
477 hypolimnion is comprised of allochthonous material, the elevated amount of autochthonous
478 production in Carioca Lake during the P2 can facilitate the degradation and utilization of the
479 recalcitrant DOM pool by the heterotrophic community, enhancing respiration rates (i.e. priming
480 effect; Guenet and others, 2010; Townsend and others, 2011). Therefore, with the increase in DOC,
481 greater bacterial biomass and respiration levels is likely to occur (Tranvik, 1988). In fact, the highest
482 concentrations of DOC were found during the P2 dry season, which, along with autotrophic
483 production, might explain the seasonal variation in the R rates (Fig. 1 – E).

484 In relation to the changes in lake mixing pattern, the effect of the decrease in water level and
485 lake volume can produce two antagonistic results. Water loss can reduce the temperature gradient
486 between surface and deep layers, deepening Z_{mix} (Landkildehus and others, 2014) and also increase
487 the susceptibility to wind-induced mixing events (Fee and others, 1996). However, water loss also
488 increases the concentration of nutrients and carbon due to less dilution, reducing the water
489 transparency and increasing the absorption of solar radiation in the surface waters, thus, shortening
490 the mixed layer depth (Read and Rose, 2013; Tsai and others, 2016; Bezerra-Neto and others, 2019).
491 Both processes seem to occur simultaneously in Carioca lake but at different moments, with the
492 occurrence of occasional mixing events prevailing in the P2 rainy season and the shortening of Z_{mix}
493 occurring during many days in the P2 dry season, when the highest concentrations of DOC and TSS
494 were found. The same processes were not registered during P1 (Fig. 2 – G, H).

495 In P2, although most of the mixing events continue to occur in the dry season, the observed
496 lack of a clear stratification stability pattern as in P1 (Fig. 2 – E, F), the occasional mixing events

497 occurring during the rainy season, and the greater variation in Z_{mix} means that nutrient and carbon
498 rich bottom waters are constantly re-entering the surface optical zone. Thus, these reinforce their
499 direct (e.g. algal growth stimulation) and indirect (e.g. lower light availability) effects in metabolic
500 rates (Staehr and Jensen, 2007).

501 Finally, the combination of all these changes in lake physical and chemical characteristics
502 influenced the shift in the metabolic balance of Carioca lake. While during P1 NEP rates were near
503 to equilibrium state with a slight tendency for heterotrophy ($\text{NEP} = -0.18 \pm 0.29$; mean \pm standard
504 error), during the P2 the lake trophic status switched from a significant autotrophy state in the rainy
505 season to a highly heterotrophic state in the dry season (Fig. 3 – E). Dodds and Cole (2007),
506 demonstrated that many factors can control and influence the switching between autotrophy and
507 heterotrophy in lakes, including the concentrations of TN, TP, carbon, and light availability. In our
508 study, the elevated GPP found during the P2 rainy season drove the autotrophy in this season,
509 benefiting from the low light conditions due to higher DOC concentration and water color and also
510 by the higher concentration of nutrients (del Giorgio and Peters, 1994; Brighenti and others, 2015;
511 Junger and others, 2019). Moreover, the remarkable R rate that was fueled by higher DOC content
512 during the dry season drove NEP towards a more heterotrophic state (Staehr and others, 2010b;
513 Tonetta and Petruccio, 2020). Changes in CO_2 flux and alternation of autotrophy and heterotrophy
514 periods were previously recorded for Carioca lake by Reis & Barbosa (2014) through diurnal scale
515 measurements. Furthermore, our results confirm the findings of the mesocosm study by Brighenti and
516 others (2018), conducted at the same lake of this work, where nutrients and carbon additions strongly
517 enhanced the metabolic rates through a combination of stimulation of algal growth and the decrease
518 of likelihood of apparent photoinhibition. Here, the effect of water loss and the variation in the
519 precipitation pattern turned the DOC levels ~ 2 times higher than the concentration used to simulate
520 carbon addition in the experiment ($8.6 \pm 0.1 \mu\text{g L}^{-1}$; mean \pm standard deviation), explaining the shift
521 in lake trophic status seen in this study, contrary to the NEP results of the mesocosms study.

522 The complex mechanisms of the ongoing climate change also imply in a complex range of
523 consequences in aquatic ecosystems. The lake metabolism and its role in the global carbon cycle
524 changed due to prolonged drought and will probably continue to change, hence the climate variability
525 will continue to act.

526 3.5.2. *Modeling process and its influence on metabolic rates*

527 Although the free water technique and the inverse modeling approach have advantages for
528 estimating ecosystem metabolism (Staeher and others, 2012a), processes as convective and advective
529 mixing, horizontal flows, and internal waves, that are not commonly included in the modeling
530 equations may cause uncertainties in the estimated metabolic rates (Hanson and others, 2008; Staeher
531 and others, 2010a). Moreover, the different approaches to estimate a single component of the
532 modeling process may significantly influence the GPP, R and NEP estimations and the interpretation
533 of the results.

534 The influence of air-water exchange term in metabolic estimates is an issue of frequent
535 concern (Staeher and others, 2010a; Dugan and others, 2016). Our study used 10 different equations
536 to estimate the air-water flux exchange component (Table S2). Most of these approaches are wind-
537 based models, but some of them consider heat loss and gain by the water masses, breaking waves
538 component, and also wind shear and convection as controls on dissolved oxygen exchange. Although
539 these models did not influence the GPP variability (Table 1) and did not change the general seasonal
540 pattern of R and NEP rates, their magnitude varied among the different k models, mainly during the
541 P2 dry season (Fig. S3).

542 In general, we noticed that higher R and lower NEP rates during P2 occurs mostly among the
543 models from MacIntyre and others (2010), Heiskanen and others (2014), the combination of the
544 models from Read and others (2012) and Soloviev and others (2007), Vachon and Prairie (2013), and
545 also by the k_{600} estimated as a free parameter. All these approaches have in common the fact that they

546 do not consider wind speed as the only factor influencing the air-water exchange. As a tropical, small,
547 shallow, and wind sheltered lake, diel heating and cooling can be the primary mechanism that drives
548 surface gas exchange, explaining the lack of variability between the wind-based models and the
549 higher absolute values of R and NEP found for the surface renewal models, in agreement with the
550 results of Dugan and others (2016) for small lakes. Furthermore, these higher values occurred only in
551 a few days, mainly in the dry season, where most of the lake full-mixing events occurred.

552 Besides the influence of the models, these higher values could also be a result of oscillations
553 in the DO measured that was captured by them. As cited previously, we found a greater day-to-day
554 variation in the mixed layer depth during the P2 dry season which could be a result of the cooling and
555 heating dynamics (Stæhr and others, 2012c). These abrupt and constant deepening of Z_{mix} could bring
556 oxygen depleted bottom waters to surface, causing oscillations in the signal captured by the sensor,
557 which further might result in an overestimation of R and NEP rates. Despite this, it is unlikely that
558 these noise in the DO measurements affect the daily, weekly, and seasonal metabolic means, being
559 more important at sub daily timescales (Stæhr and Jensen, 2007; Stæhr and others, 2010a) that are
560 beyond the scope of this work. To deal with this source of uncertainty: i) we applied smoothing
561 solutions to our dissolved oxygen data (Coloso and others, 2008); ii) the number of days under
562 investigation was elevated (Stæhr and others, 2010a); and iii) most of the days with noise in the
563 oxygen measurements, which in fact occurred mostly during the P2 dry season, had a poor model fit
564 ($R^2 < 0.7$) and were not included in the results shown here.

565 Regarding the use of k_{600} as a free parameter, this approach had the highest R and NEP rates
566 between all the models (Fig. S3). As the function of an optimization algorithm is to find a parameter
567 value that best fits the data, k_{600} as a free parameter can result in a better fit than other models but
568 could not represent properly the internal processes of the system. Thus, if noise DO data was
569 incorporated in the modeling process, those few days with higher R and NEP rates could represent an
570 overestimation of these rates, despite our efforts to maintain conservative results.

571 Future studies should investigate more carefully the influence of physical processes in
572 metabolic rates, even in meso and eutrophic systems. Although most of the large daily DO oscillation
573 found in productive systems is driven by biological processes (Richardson and others, 2017), the
574 physical ones could help to understand underlying variation in the DO data and improve metabolic
575 estimates.

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586 3.7.REFERENCES

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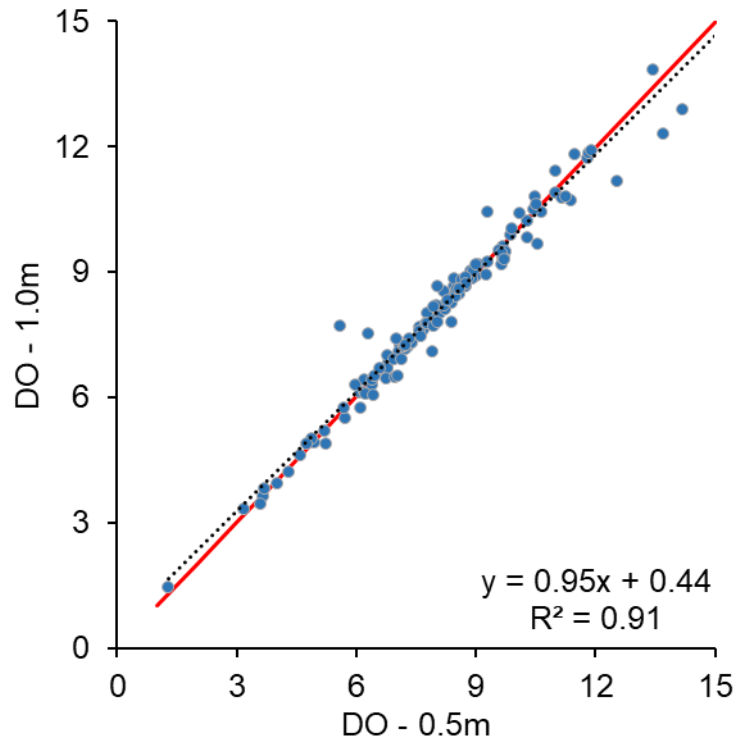
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787 4. SUPPLEMENTAL MATERIAL

788 4.1. Supplemental material 1:

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791 Fig S1 – Linear regression between the concentration of dissolved oxygen (mg L^{-1}) at 1.0m and 0.5m

792 depth. The red line represents the 1:1 line and the dotted black line indicates the tendency line of data.

793 The data used ranged from 1999 to 2019.

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801 4.2.Supplemental material 2

802 Table S1 – Concentration of nutrients and algal biomass in Carioca Lake between 1999-2009 and
 803 2017-2019.

	1999 - 2009	2017-2019
	Mean ± standard deviation	
<i>Total nitrogen – TN ($\mu\text{g L}^{-1}$)</i>	500.8 ± 346.9	1309.2 ± 534.9
<i>Total phosphorus – TP ($\mu\text{g L}^{-1}$)</i>	28.6 ± 15.9	33.2 ± 43.8
<i>Chlorophyll-a – Chl-a ($\mu\text{g L}^{-1}$)</i>	27.6 ± 18.1	13.6 ± 6.2

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809 4.3.Supplemental material 3

810 Table S2 – List of the models used and its respective equations.

Model abbreviation	Equation (k_{600})	Unit	Reference	Obs
CC98	$2.07 + 0.215 \times U_{10}^{1.7}$	cm h ⁻¹	Cole and Caraco, 1998	U_{10} = wind speed at 10m height
CO10	$0.497 + 0.0064 \times U_{10}^{1.8}$	m d ⁻¹	Cole and others, 2010	U_{10} = wind speed at 10m height
CWBL03	$4.33 \times U_{10} - 13.3$ if $U_{10} \geq 3.7$ $0.72 \times U_{10}$ if $U_{10} < 3.7$	cm h ⁻¹	Crusius and Whanninkhof, 2003	U_{10} = wind speed at 10m height
CWL03	$5.14 \times U_{10} - 17.9$ if $U_{10} \geq 3.7$ 1 if $U_{10} < 3.7$	cm h ⁻¹	Crusius and Whanninkhof, 2003	U_{10} = wind speed at 10m height
CWPF03	$0.228 \times U_{10}^{2.2} + 0.168$	cm h ⁻¹	Crusius and Whanninkhof, 2003	U_{10} = wind speed at 10m height
MI10	$(1.74 \times U_{10} - 0.15)$ if $T_{t+1} > T_t$ $(2.04 \times U_{10} + 2.0)$ if $T_{t+1} < T_t$	cm h ⁻¹	MacIntyre and others, 2010	T = water temperature at same depth of dissolved oxygen sensor
VP13	$2.51 + (1.48 \times U_{10})$ $+ (0.39 \times U_{10} \times \log_{10} LA)$	cm h ⁻¹	Vachon and Prairie, 2013	LA = lake area in km ²

811 The models from Heiskanen and others (2014) and the combination of the models from Read and others (2012) and Soloviev and others (2007) were not

812 included as we used the LakeMetabolizer R package to generate the k_{600} values.

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814 4.4.Supplemental material 4:

815 Table S3 - Variation of environmental variables in Lake Carioca between periods and seasons

Period	Season		Max depth	Tw*	K _d **	E _{mean} **	Chl-a	TSS	TP	TN	DOC	a254	a272	a440
			(m)	(°C)	(m ⁻¹)	(mol photons m ⁻² d ⁻¹)	(µg l ⁻¹)	(mg l ⁻¹)	(µg l ⁻¹)	(µg l ⁻¹)	(mg l ⁻¹)	(m ⁻¹)	(m ⁻¹)	(m ⁻¹)
P1 2011-2012	Dry season (n=8)	Avg	10.4	24.3	1.1	40.4	10.7	6.6	13.9	525.3	5.8	18.3	14.8	1.0
		Med	10.4	24.0	1.1	42.1	10.9	5.3	13.4	501.0	5.4	18.4	14.8	0.9
		Q1	10.2	23.2	1.1	27.6	7.4	4.4	10.7	432.5	4.3	16.8	13.8	0.7
		Q3	10.5	25.1	1.2	51.5	16.1	8.0	17.2	592.6	8.3	20.4	16.3	1.2
	Rainy season (n=12)	Avg	10.1	28.0	1.0	51.1	5.6	3.3	13.3	331.6	5.7	17.0	13.6	0.7
		Med	10.2	28.0	1.0	53.4	4.4	3.0	14.0	334.9	5.6	17.2	13.7	0.6
		Q1	10	26.3	0.8	38.9	3.7	3.3	13.3	331.6	3.9	15.1	12.0	0.6
		Q3	10.4	29.7	1.1	65.3	8.5	2.7	7.5	265.2	6.8	18.5	14.9	0.7
P2 2017-2019	Dry season (n=5)	Avg	7.4	23.6	1.6	25.1	18.1	9.6	16.8	1248.2	11.9	21.8	17.2	0.6
		Med	7.3	23.3	1.6	24.2	19.2	9.3	11.7	1247.0	11.5	21.8	17.0	0.6
		Q1	7.0	22.5	1.3	17.8	16.0	8.5	11.2	1171.0	11.4	15.8	12.2	0.4
		Q3	7.6	24.3	1.8	31.5	21.3	10.4	23.6	1278.0	12.3	23.6	18.6	0.7
	Rainy season (n=14)	Avg	7.9	29.1	1.1	34.8	12.2	5.6	23.7	1128.7	9.9	28.2	22.7	0.8
		Med	8.0	29.4	1.0	33.0	12.0	5.5	15.1	1081.5	10.7	28.7	22.9	0.8
		Q1	7.8	27.7	0.9	21.6	8.5	4.8	8.0	988.0	6.7	24.4	18.9	0.6
		Q3	8.1	30.7	1.2	48.5	14.9	6.9	33.4	1167.5	11.5	31.5	26.3	1.0
Kruskal – Wallis test		H			344.12	317.93	12.37	18.58	1.26	31.97	19.94	21.78	22.04	3.93
		p value			< 0.001	< 0.001	0.006	< 0.001	0.739	< 0.001	< 0.001	< 0.001	< 0.001	0.270

816 Water samples in P1 were collected monthly at 0.5m from May 2011 to December 2012. For P2 the samples were collected at irregular intervals at 0.5m

817 from July 2017 to December 2019.

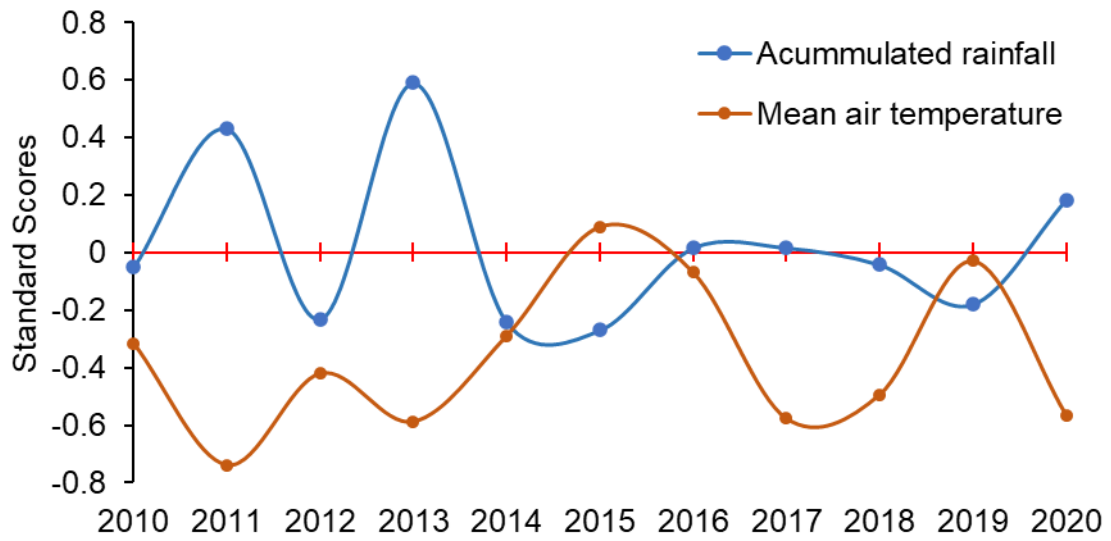
818 Avg = Average; Med = Median; Q1 = First quartile; Q3 = Third quartile; Max depth = Maximum depth; Tw = water temperature; K_d = light attenuation
819 coefficient; E_{mean} = mean available light at the upper mixed layer; Chl-a = concentrations of chlorophyll-a; TSS = total suspended solids; TP = total
820 phosphorus; TN = total nitrogen; DOC = dissolved organic carbon; a_{254} = absorbance coefficient at 254nm; a_{272} = absorbance coefficient at 272nm;
821 a_{440} = absorbance coefficient at 272nm, respectively.

822 *Tw is high frequency data collected at the same depth of dissolved oxygen (0.5m for P1 and 1m for P2) at 30min interval (P1 dry season: n = 11,808;
823 P1 rainy season: n = 16,416; P2 dry season: n = 14,256; P2 rainy season: n = 23,568).

824 ** K_d and E_{mean} are high frequency data averaged to a daily interval (P1 dry season: n = 246; P1 rainy season: n = 342; P2 dry season: n = 297; P2 rainy
825 season: n = 491).

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827 4.5.Supplemental material 5:



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829 Figure S2 – Standard scores of accumulated rainfall (blue line) and mean air temperature (orange
830 line) for 2010 to 2020 period. The red line at 0 represents a threshold where values higher than 0
831 indicate rainfall and/or temperature above the historical mean. Values lower than 0 indicate rainfall
832 and/or temperature below the historical mean for the region.

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848 4.6.Supplemental material 6:

849 Table S4 – Number of data points with good model fit (i.e. $R^2 \geq 0.7$ e $p < 0.05$) for each model, period, and season.

Period	Season	CC98	CO10	CWB03	CWL03	CWPF03	HE14	K600F	MI10	RS712	VP13	Total
P1 (2011-2012)	Dry season	148	148	149	148	150	149	172	147	149	150	1510
	Rainy season	225	224	221	225	219	219	272	223	223	223	2274
	Total	373	372	370	373	369	368	444	370	372	373	3784
P2 (2017-2019)	Dry season	98	102	109	106	110	76	131	97	90	95	1014
	Rainy season	316	325	326	328	324	267	378	315	311	312	3202
	Total	414	427	435	434	434	343	509	412	401	407	4216

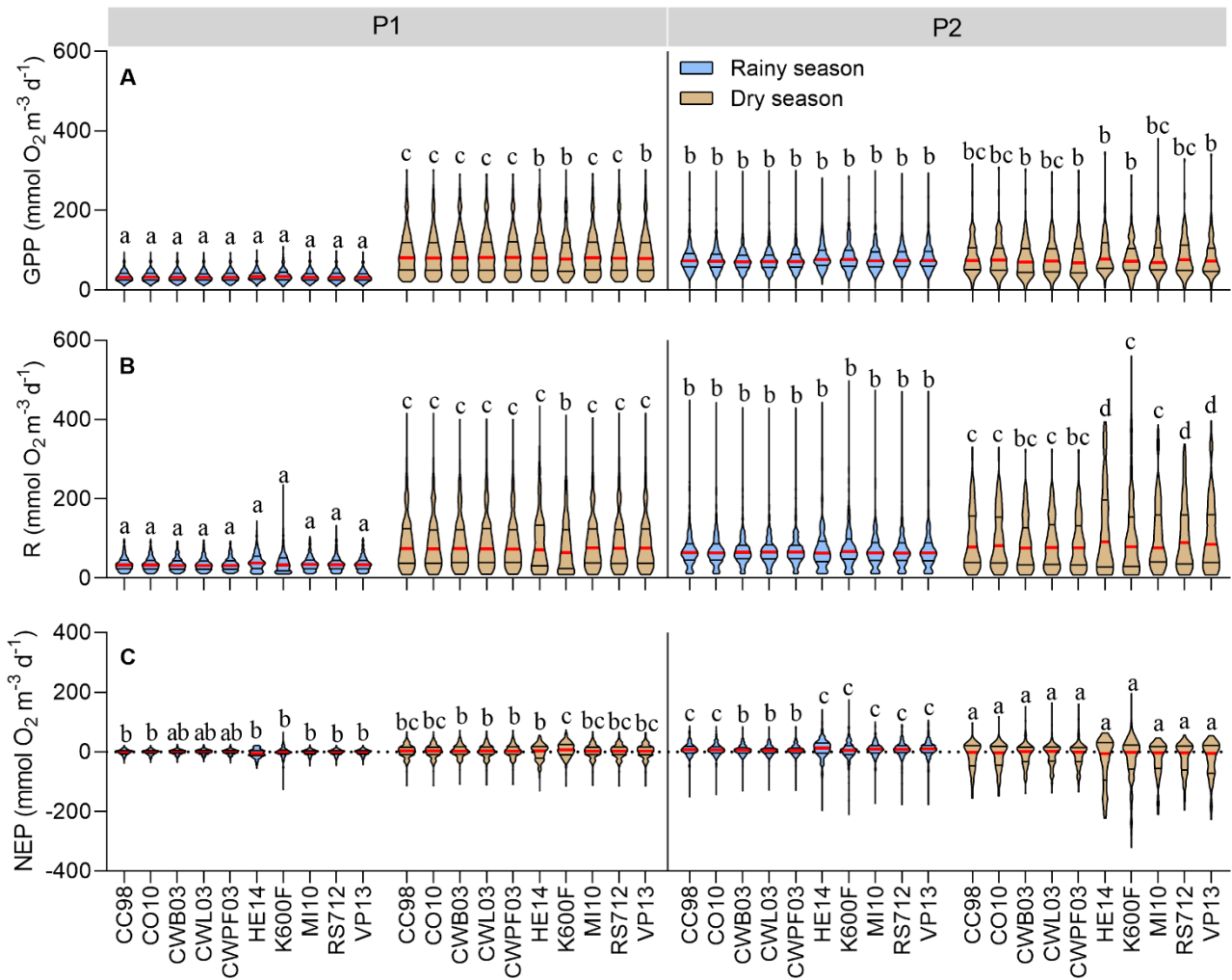
850 CC98 is the Cole and Caraco (1998) model; CO10 – Cole and others (2010); CWB03 – Crusius and Whanninkhof (2003) bilinear function; CWL03 -

851 Crusius and Whanninkhof (2003) linear function; CWPF03 - Crusius and Whanninkhof (2003) power function; HE14 – Heiskanen and others (2014);

852 K600F – k_{600} used as free parameter; (MI10) MacIntyre and others (2010); RS712 – the combination of the models from Read and others (2012) and

853 Soloviev and others (2007); VP13 – Vachon and Prairie (2013).

854 4.7. Supplemental material 7:



855 Figure S3 – Violin plots for (A) gross primary production; (B) respiration; (C) net ecosystem
 856 production, for the different models for P1 (2011-2012) and P2 (2017-2019). Blue plots are values in
 857 rainy season and light brown are values in dry season. Red center line is the median and black lines
 858 are the first and third quartiles. The violin graphs show the complete distribution of the data, so the
 859 narrowest areas have the least concentration of data. Different letters represent significant differences
 860 between seasons and periods ($p < 0.05$), and equal letters represent no significant differences between
 861 the groups ($p > 0.05$).

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5. CONCLUSÃO

Esse estudo demonstrou que a redução de volume atuou como um *driver* para diversas mudanças nas características físicas, químicas e biológicas de um lago tropical. Com a diminuição do nível da água na lagoa Carioca, as concentrações de nitrogênio total, fósforo total e de carbono orgânico dissolvido aumentaram. Os resultados apontaram que tais elevações influenciaram direta e indiretamente no aumento das taxas metabólicas. Diretamente, devido a sua importância para o metabolismo dos organismos e indiretamente devido a capacidade desses elementos em regular a disponibilidade de luz na camada de mistura. Durante o período de 2011-2012 as taxas de produção primária e de respiração demonstraram uma marcada sazonalidade, isso devido à baixa disponibilidade de nutrientes e alta disponibilidade de luz na estação chuvosa que aumentam a ocorrência de dias em que ocorre fotoinibição da produção primária. Durante a estação seca, porém, os eventos de mistura ressuspendem o sedimento, havendo então um aumento na disponibilidade de nutrientes, carbono e sólidos em suspensão na coluna de água, garantindo a essa estação uma menor disponibilidade de luz e as maiores taxas metabólicas registradas durante o ano. Já no período de 2017-2019, essa sazonalidade nas taxas metabólicas não foi tão pronunciada, uma vez que houve uma redução significativa na disponibilidade de luz e na ocorrência de fotoinibição tanto na estação seca quanto na chuvosa. Além disso, a diminuição do volume do lago também fez com que a estabilidade da estratificação diminuísse, e eventos de mistura aleatórios foram observados durante o segundo período de estudo. Esses eventos de mistura também podem ter contribuído para uma maior disponibilidade de nutrientes, carbono e sólidos em suspensão em ambas as estações amostradas, e, portanto, nas altas taxas metabólicas registradas. Por fim, através do uso de 10 equações de fluxo gasoso na interface ar-água, esse estudo também destacou a importância dos fatores físicos para a variabilidade nos dados de oxigênio, que afetam diretamente a modelagem das taxas metabólicas, podendo sub- ou superestimá-las. Ressalta-se que o metabolismo do ecossistema mudou devido a um período de seca hidrológica persistente, e, é possível que diversas funções ecossistêmicas continuem a mudar devido as variações na temperatura e na pluviosidade.