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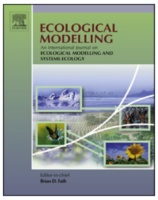

Process-based modeling of shallow lake metabolism: Spatio-temporal variability and relative importance of individual processes

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ABSTRACT

A process-based model was used to evaluate distributed estimates of aquatic metabolism and the importance of different individual processes related to dissolved-oxygen dynamics in a large shallow subtropical lake, Lake Mangueira, on the southern coast of Brazil. In order to assess spatial differences in metabolism estimates, the lake was divided into three geographical areas (North, Central, and South) and each area was subdivided into two biological zones (littoral and pelagic). A well-marked littoral to pelagic gradient was observed, with significant differences in the metabolism estimates between the biological zones of each compartment. In addition, a significant longitudinal difference in metabolism between the North and other lake areas was also apparent. Temporal dynamics featured continuous switching between net autotrophic and net heterotrophic conditions. Phytoplankton primary production and respiration were the main individual processes controlling gross primary production and ecosystem respiration, respectively, for the entire lake. Our findings indicated that spatially distributed estimates of lake metabolism led to different conclusions than did overall metabolism estimates based on single points. Also, individual processes must be taken into account in order to fully understand their relative importance on different spatial and temporal scales for the overall metabolism of aquatic ecosystems.

1. Introduction

The aquatic metabolism is an important parameter integrating the biological activity of an aquatic ecosystem. Several factors acting on different temporal and spatial scales, such as carbon inputs and air-water-sediment fluxes, can control lake metabolism (e.g., Hanson et al., 2006; Staehr and Sand-Jensen, 2007; Coloso et al., 2011b). Spatial heterogeneity of the aquatic metabolism in lakes can be related to lake morphometry and hydrodynamic processes within the system (van de Bogert et al., 2007, 2012; Staehr et al., 2010, 2012; Coloso et al., 2011; Brighenti et al., 2015). Long-term variability is often related to phosphorus availability and the concentrations of chlorophyll-*a* and dissolved carbon in the water (Sand-Jensen and Staehr, 2007, 2009). Short-term variability of the aquatic metabolism is suggested to respond to primary production, water temperature, and exchanges among the different compartments due to hydrodynamics (Hanson et al., 2006; Staehr and Sand-Jensen, 2007).

Estimates of lake metabolism are often based on a single dissolved-oxygen sensor in the pelagic zone (e.g., Cole et al., 2000; Hanson et al., 2003, 2006; Tsai et al., 2008; Staehr et al., 2010; Brighenti et al., 2015). However, dissolved-oxygen concentration is spatially variable, and metabolism estimates performed at single points, usually in the pelagic zone, fail to capture the existing spatial-temporal ecosystem heterogeneity (van de Bogert et al., 2012). Estimation of the metabolism based on a single dissolved-oxygen sensor has been suggested to be very different from the metabolism of the entire system, for many reasons: (a) lake zones (i.e. littoral, pelagic, photic, aphotic, and benthic) can contribute in different ways (Lauster et al., 2006; Sadro et al., 2011; Giordano et al., 2012; van de Bogert et al., 2012); (b) a point assessment can mask the influence of hydrodynamics (van de Bogert et al., 2007, 2012); (c) a dissolved-oxygen sensor is unable to track oxygen variations due to the sediments, where benthic organisms can cause significant variations (Sadro et al., 2011); and (d) the variability of dissolved oxygen is not related exclusively to metabolism-related activities and air-water fluxes, but also to groundwater input, physical and chemical interactions, photo-respiration of dissolved organic carbon, and external forces such as wind and precipitation (Hanson et al., 2003, 2006). Therefore, a complete representation of the lake metabolism using process-based models that include

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physical, chemical, and biological processes might be an useful alternative to better represent the aquatic metabolism (Coloso et al., 2011; Staehr et al., 2012).

Process-based models are commonly used to assess water quality in aquatic environments (e.g., Straskraba, 1979; Hamilton and Schladow, 1997; Brookes et al., 2004; Fragoso et al., 2011; Trolle et al., 2014). These models can be useful for understanding the spatial heterogeneity in systems such as large shallow lakes (Fragoso et al., 2011), because of the potential differences between the littoral and pelagic zones (Zanden and Vadeboncoeur, 2002; Vadeboncoeur et al., 2008). In lakes where hydrodynamic processes are intense, the aquatic metabolism may be spatially and temporally heterogeneous (Antenucci et al., 2013; van de Bogert et al., 2007; Coloso et al., 2011; Hanson et al., 2008), and may be associated with the spatial patchiness of phytoplankton and nutrients (Cardoso et al., 2012; Cardoso and Motta-Marques, 2003, 2004, 2009; Fragoso et al., 2008). The use of empirical/mathematical models to estimate lake metabolism is recent (e.g., Holtgrieve et al., 2010; Holtgrieve and Schindler, 2011; McNair et al., 2013). The process-based approach allows us to estimate, amongst other things, hydrodynamic effects on the ecosystem (Fragoso et al., 2011; Trolle et al., 2014) and metabolism (Antenucci et al., 2013; McNair et al., 2013). This approach also allows continuous diel estimates of ecosystem respiration, which is an advantage over the classic free-water approach (McNair et al., 2013).

Recent studies using an empirical single-point approach have suggested that the hydrodynamics may influence the estimates of lake metabolism in tropical and temperate lakes (van de Bogert et al., 2007; Coloso et al., 2011; Staehr et al., 2012; Brighenti et al., 2015). Nonetheless, the authors were unable to quantify the degree to which physical processes affect dissolved-oxygen dynamics. In large shallow lakes, the influence of hydrodynamics on limnological variables (such as nutrient concentration and phytoplankton biomass) can be strong, especially for wind-driven hydrodynamics (Cardoso and Motta-Marques, 2009; Fragoso et al., 2011), which may increase the effect of hydrodynamic processes on dissolved oxygen concentration. Recent publications regarding process-based modeling of lake metabolism use hydrodynamic models linked to metabolism estimates in order to understand these dynamics (Antenucci et al., 2013; McNair et al., 2013). However, these studies indirectly represent the individual processes that compose gross primary production and ecosystem respiration estimates (Cremona et al., 2014).

Metabolism in aquatic ecosystems is spatially and temporally dynamic, and many individual processes make significant and different contributions. In this study, we used a complex and spatially distributed ecosystem model, in order to evaluate individual processes (physical, chemical, and trophic web) on the metabolism of a shallow subtropical lake, based on the dissolved-oxygen budget, and considering spatial and temporal heterogeneity.

2. Methodology

2.1. Study area

Lake Mangueira (Fig. 1) is a large shallow lake in southern Brazil, located between 32°20′S and 33°00′S, and 052°20′W and 052°45′W. The lake surface area is approximately 820 km^2, with a mean depth of 2.6 m and maximum depth of 6.5 m, elongated, with a maximum length of 90 km and width of 10 km. The trophic state varies from oligotrophic to mesotrophic, with a mean annual PO_4 concentration of 35 mg m^{-3}, ranging from 5 to 51 mg m^{-3}. The lake is surrounded by dunes and two wetlands. This heterogeneous landscape harbors an exceptional biological diversity, which motivated the Brazilian federal authorities to protect part of the entire hydrological system as the TAIM Ecological Station, in 1991 (Motta-Marques et al., 2002). The watershed (ca. 415 km^2) is used primarily for rice production.

2.2. Model description

The IPH-TRIM3D-PCLake model (Fragoso et al., 2009), also known as IPH-ECO (freely available in: https://sites.google.com/site/iphecomodel), describes the main physical (water temperature and density, velocity fields, and free-water elevation), chemical and biological (e.g., nutrients and trophic structure) processes existing in the aquatic ecosystem. The model can be used in an individual assessment, allowing the user to evaluate physical and water-quality processes separately, or it can be used to evaluate physical processes, water-quality processes, and biological structures simultaneously in one, two, or three dimensions.

The IPH-ECO hydrodynamic module solves the Reynolds-Averaged Navier–Stokes Equation using a semi-implicit discretization on structured staggered grids (see Casulli and Cheng, 1992; Cheng et al., 1993, for more details). The non-linear convective terms existing in the TRIM solution (Cheng et al., 1993) are solved using an explicit Eulerian-Lagrangian finite-difference scheme. To increase the stability and accuracy, the θ-method was also implemented (Casulli and Cattani, 1994). The parameter of horizontal eddy viscosity can be calibrated manually, and vertical eddy viscosity is modeled as an empirical relationship (Pacanowski and Philander, 1981). To perform the coupling between physical and biological processes, IPH-ECO uses an explicit finite-difference scheme to solve an advection-diffusion-reaction type equation of the form:

$$\frac{\partial C}{\partial t} + \nabla(\mathbf{v}C) = \nabla(\Gamma\nabla(C)) + S_C \tag{1}$$

where C is the scalar concentration being transported, which can be regarded as different ecosystem variables (e.g., nutrients, biomass, chlorophyll-*a*, or water temperature); $\mathbf{v}$ is the velocity field, which is given by the hydrodynamic model; Γ is the diffusivity tensor, regarded in the model as turbulent eddy diffusivity; and S_C is a source/sink term that takes into account a wide variety of processes that can cause changes in the scalar concentration (e.g., settling, resuspension, and biological processes).

The water quality-module of IPH-ECO, i.e., the chemical and biological dynamics in the water column and sediment bed, is based largely on PCLake (Janse, 2005). Each water-quality variable has its own source/sink term, allowing IPH-ECO to describe nutrients (phosphorus, nitrogen, and silica) and dissolved-oxygen dynamics based on different processes. The model is also able to describe biological biomasses, splitting the phytoplankton and fish biomasses into three functional groups, the aquatic macrophytes into four functional groups, and the zooplankton as one functional group, and the zooplankton as one functional group; and describes in a simplified manner the benthic fluxes and sediment diagenesis. Some improvements have been added to the model since its first release, such as a resuspension flux that is a function of wind fetch (Fragoso et al., 2011), and the day length as a function of latitude. In order to evaluate the metabolism dynamically, we implemented a process-based algorithm to evaluate the aquatic metabolism based on individual processes composing O_2 dynamics, which is described next.

2.3. Process-based algorithm for aquatic metabolism

Our process-based algorithm for aquatic metabolism was based on the assumption that processes involved in the dissolved-oxygen (O_2) budget are related to NEP (Odum, 1956). The mathematical formulation proposed here and implemented in IPH-ECO describes O_2 dynamics in a more detailed form, taking into account more