Modelling the plankton groups of the deep, peri-alpine Lake Bourget

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ABSTRACT

Predicting phytoplankton succession and variability in natural systems remains to be a grand challenge in aquatic ecosystems research. In this study, we identified six major plankton groups in Lake Bourget (France), based on cell size, taxonomic properties, food-web interactions and occurrence patterns: cyanobacterium *Planktothrix rubescens*, small and large phytoplankton, mixotrophs, herbivorous and carnivorous zooplankton. We then developed a deterministic dynamic model that describes the dynamics of these groups in terms of carbon and phosphorus fluxes, as well as of particulate organic phosphorus and dissolved inorganic phosphorus. The modular and generic model scheme, implemented as a set of modules under Framework for Aquatic Biogeochemical Models (FABM) enables run-time coupling of the plankton module an arbitrary number of times, each time with a prescribed position across the autotrophy/heterotrophy continuum. Parameters of the plankton groups were mainly determined conjointly by the taxonomic and allometric relationships, based on the species composition and average cellular volume of each group. The biogeochemical model was coupled to the one-dimensional General Ocean Turbulence Model (GOTM) and forced with local meteorological conditions. The coupled model system shows very high skill in predicting the spatiotemporal distributions of water temperature and dissolved inorganic phosphorus for five simulated years within the period 2004 to 2010, and intermediate skill in predicting the plankton succession. We performed a scenario analysis to gain insight into the factors driving the sudden disappearance of *P. rubescens* in 2010. Our results provide evidence for the hypothesis that the abundance of this species before the onset of stratification is critical for its success later in the growing season, pointing thereby to a priority effect.

1. Introduction

Mechanistic ecosystem models are not only ideal media for synthesizing data and theory and thereby improving our understanding of the functioning of ecosystems, but they are also useful tools for supporting decision-making processes. Implementation of ecosystem models in aquatic systems has been increasingly appearing in the form of coupled hydrodynamic-biogeochemical models, reflecting the increasing recognition that biogeochemistry is often strongly driven by hydrodynamics, as well as the advances in computing power (Robson, 2014).

While coupled hydrodynamic-biogeochemical models can often provide reliable estimates of physical parameters such as temperature and salinity, prediction of chemical and biological parameters,

and especially occurrence of certain plankton species or functional groups are more difficult to predict (Shimoda and Arhonditsis, 2016). Problems start there already at the very preliminary stage of conceptual model building: what constitutes a functional group? From a global perspective, Hood et al. (2006) defined a functional group as an entity that plays a particular role in a certain biogeochemical pathway, such as nitrogen fixation or silification. However, shifts in the community structure under focus might be driven by competition for the shared resources or trophic interactions, intensity of which may change across seasonal to interdecadal scales, e.g., with thermal stratification dynamics and changes in nutrient loading (Sommer et al., 2012; Kerimoglu et al., 2013). In such cases, traits relating to growth rate, grazer defense, resource utilization, temperature response and motility (Litchman et al., 2010) should (also) be considered for identifying the functional groups, for which, ample examples indeed exist (Jöhnk et al., 2008; Mieleitner and Reichert, 2008; Carraro et al., 2012).

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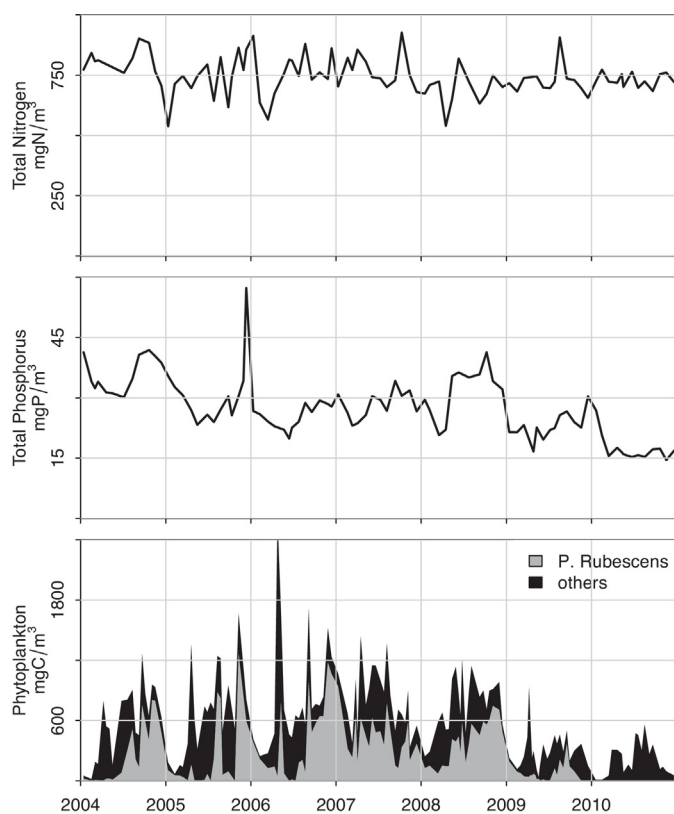E-mail address: kerimoglu.o@gmail.com (O. Kerimoglu).

Fig. 1. Observed concentrations of total phosphorus and total nitrogen (0–140 m average), and total phytoplankton and contribution by *P. rubescens* in Lake Bourget (0–20 m average) for the period 2004–2010.

The system under investigation here, Lake Bourget, France, has been recovering from eutrophication since the 1980s (Vinçon-Leite et al., 1995; Jacquet et al., 2014a). Starting from 1996, the toxic cyanobacterium, *Planktothrix rubescens* became a dominant species in the lake (Vinçon-Leite et al., 2002; Jacquet et al., 2005, see also Fig. 1). *P. rubescens* is a wide-spread cyanobacterial species especially prevalent in peri-alpine lakes (e.g., Ernst et al., 2009; Salmaso et al., 2012; Dokulil and Teubner, 2012; Posch et al., 2012), but also observed elsewhere (e.g., Konopka, 1982; Halstvedt et al., 2007; Naselli-Flores et al., 2007; Padisák et al., 2010). Being a potentially microcystin producing species (Briand et al., 2005), its occurrence in lakes and reservoirs has been of major concern for livestock and human health (Naselli-Flores et al., 2007; Ernst et al., 2009). In 2010, *P. rubescens* suddenly disappeared (Jacquet et al., 2014b) from Lake Bourget, whereas the mixotrophic and small phytoplankton species became relatively more abundant, latter being typical for oligotrophic systems (Anneville et al., 2004; Chen and Liu, 2010; Mitra et al., 2014). Accordingly, mixotrophy and traits associated with cell size should be taken into account for understanding the mechanisms driving the changes in phytoplankton community composition, and in particular, the disappearance of *P. rubescens* in Lake Bourget.

Since long, phytoplankton cell size has been recognized to be an important aspect in determining the ecophysiology of phytoplankton (e.g., Finkel et al., 2010; Litchman et al., 2010, and references therein), and cell size has been increasingly used as a 'master trait' (Litchman et al., 2010) in theoretical modelling studies (e.g., Grover, 1991; Armstrong, 1994; Litchman et al., 2009; Kerimoglu et al., 2012, submitted), although the integration of size concept in realistic ecosystem models attempting to reproduce mesocosm or field observations at relevant ecological time scales has been gaining momentum only recently (but see, e.g., Ward et al., 2012;

Wirtz, 2013; Terseleer et al., 2014). Following many decades of dichotomous classification of planktonic organisms as 'autotrophs' and 'heterotrophs' (Flynn et al., 2012), importance of mixotrophy in ecosystem functioning has been increasingly recognized (Mitra et al., 2014, and references therein). Mixotrophy has been addressed mainly by theoretical work so far (e.g., Thingstad et al., 1997; Flynn and Mitra, 2009; Crane and Grover, 2010; Berge et al., 2017). The recent work of Ward and Follows (2016) constitutes the first example where mixotrophy is resolved in a global ocean model.

Environmental control of the occurrence of *P. rubescens* blooms is still under debate. Analysis of the long-term changes in individual lakes and inter-comparison between lakes suggest that phosphorus (and nitrogen, see Posch et al., 2012) availability is the primary determinant (Dokulil and Teubner, 2012; Jacquet et al., 2014b; Anneville et al., 2015). *P. rubescens* is characterized by their slow growth rates (Bright and Walsby, 2000) and tolerance to low light conditions (Walsby and Schanz, 2002). As a result of the latter, it often develops thin and intense layers within the metalimnion during the growing season (e.g., Jacquet et al., 2014b), where they are the first to harvest the nutrients leaking from the nutrient-rich layers beneath the thermocline. On the other hand, occurrence of *P. rubescens* displays extreme interannual variability in deep lakes, which is suggested to be driven by meteorological conditions (Vinçon-Leite et al., 2002; Salmaso, 2010; Jacquet et al., 2014b; Anneville et al., 2015): after warm winters, *P. rubescens* have been observed to be at relatively high abundances, which is usually followed by their sustained dominance throughout the growing season (Salmaso, 2010; Posch et al., 2012).

In this study, we had the following objectives: (1) developing a plankton model that resolves mixotrophy and relies on allometric relationships for the parameterization of plankton groups; (2) implementing the plankton model in a 1-D coupled hydrodynamical-biogeochemical modeling framework for the simulation of the surface layer dynamics of Lake Bourget; (3) quantifying the performance of the model with respect to both the bulk characteristics of the system and plankton groups; (4) gaining insight into the reasons for the relative importance of low phosphorus concentrations and low starting inoculum at the beginning of the growth season for the disappearance of *P. rubescens* in Lake Bourget.

2. Study site and data

The study site is Lake Bourget, a peri-alpine (45°44′N, 5°52′E, 231 m altitude) lake with a maximum depth of 145 m and a surface area of approximately 45 km^2. It has a north-south aligned, elongated basin with a length of 18 km and a maximal width of 3 km at the surface. Within the study period (2004–2010), average total phosphorus and nitrogen concentration ranged between approximately 15–45 mg/m^3 and 550–800 mg/m^3, respectively (Fig. 1), classifying it as a mesotrophic system. Further details about the lake can be found in Vinçon-Leite et al. (1995) and Jacquet et al. (2014b).

Meteorological data required to force the hydrodynamical model (see Section 4.3) were taken from the Météo-France station at Vouglans, located at the southern tip of Lake Bourget. In-situ data used in this study were sampled at the deepest location of Lake Bourget. Sampling was performed usually biweekly during the growth season and monthly during winter. Water temperature was measured at high vertical resolution with a conductivity-temperature-depth probe, and interpolated on a regular grid of 1-m intervals. Nutrient data were collected at several irregular depths (2, 10, 15, 20, 30, 50, 80, 110, 130, 140 m), and interpolated also to a regular 1-m grid. For the phytoplankton species counts, an