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Cross-lake comparisons of physical and biological settling of phosphorus: A phosphorus budget model with Bayesian hierarchical approach

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ABSTRACT

Phosphorus (P) is viewed as one limiting factor for phytoplankton growth in freshwater lakes. Simple budget models are very efficient for cross-lakes comparisons, while neglecting key distinction between algal P and other forms. Here, a phosphorus budget model was developed to balance between process resolution and cross-system applicability, in which lake total phosphorus (TP) was divided into algal-bound P and other fractions. The model was tested for six lakes on the Yunnan Plateau, China and the Markov Chain Monte Carlo (MCMC) algorithm of Bayesian hierarchical inference was employed for parameters estimation. The model results showed that (a) both algal species composition and P loading are key factors that influence the efficiency of converting phosphorus into algal P; (b) variability of the settling velocity of non-algal P and algal P decreases with increasing TP concentrations, representing a lower capacity for restoration; and (c) settling velocity declined exponentially with the increase of trophic state index, indicating a potential rapid rise of P removal rates during eutrophication restoration. Two conceptual models were then proposed to identify the prior countermeasures for eutrophication restoration in the lakes: (a) for Conceptual Model II, e.g. Lake Lugu, increasing the physical settling of phosphorus should be paid extra attention.

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1. Introduction

Phytoplankton is a critical component of the aquatic food web and is the important contributor to primary production (Wetzel, 1964; Snit'ko and Snit'ko, 2014). However, with increasing anthropogenic nutrient inputs, eutrophication, including the proliferation of harmful algal blooms, has been recognized worldwide (Conley et al., 2009; Heini et al., 2013). The increasingly common increase in Cyanophyta have special ecological characteristics of low light requirements, a wide temperature tolerance, special floating mechanism and strong abilities of absorbing nutrients, which result in its excessive growth and reproduction (Burford and Davis, 2011). Regime shifts from macrophyte to phytoplankton dominance has also been widely reported, such as Lake Christina, Lake Kariba and Lake Krankesjon (Theissen et al., 2012; Mahere et al., 2014; Randsalu-Wendrup et al., 2014), which can be driven by various

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http://dx.doi.org/10.1016/j.ecolmodel.2016.07.011 0304-3800/© 2016 Elsevier B.V. All rights reserved. factors, such as climate, nutrients, depth and lake size (Scheffer and van Nes, 2007). It is therefore essential to develop the appropriate nutrient management strategy to reduce eutrophication and phytoplankton growth.

Despite the debates on nitrogen (N) vs. phosphorus (P) as the primary limiting factors for lake eutrophication (Smith et al., 2006; Elser et al., 2007; Finlay et al., 2013; Davis et al., 2015), P availability is widely viewed as the most important determinant causing excessive phytoplankton growth (Schindler, 1977; Smith and Atkinson, 1984; Müller et al., 2014; Peacock and Kudela, 2014). In addition to P inputs and outflows, in-lake P concentration is strongly influenced by algal assimilation of soluble phosphorus and subsequent sedimentation of particulate phosphorus. Two general classes of models have been developed over the past decades for exploring the P changes in lakes: (a) simple and one-equation budget model, treating lakes as completely mixed reactors in steady state describing P settlement, inputs, and outputs (Vollenweider, 1969; Reckhow, 1979; Chapra, 1982); and (b) more detailed, often three-dimensional, mechanistic models describing detailed sedimentation and ecological processes (Cerco and Cole, 1993;







Astrakhantsev et al., 1996; Muhammetoğlu and Soyupak, 2000; León et al., 2005; Zhao et al., 2012). The benefits of simple budget models lie in their effectiveness for cross-lakes comparisons and along long temporal scales, while they neglect the important biological processes converting dissolve phosphate into algal biomass (Arhonditsis et al., 2006; Scavia and Liu, 2009). The more detailed mechanistic models connect phytoplankton biomass, usually represented using chlorophyll-a (Chla), with P; however, they are time consuming and require substantially more data for both input drivers and calibration, which limits its application in exploring cross-lake comparisons (Beck, 1981). Therefore, we propose a relatively simple model that provides a balance between process resolution and cross-system applicability. The simple model can be extremely useful for lakes with limited data, for example lack of data in different phosphorus forms, such as organic and inorganic P, or dissolved and particulate P, which limits the application of complex mechanistic model and hinders the further understanding of aquatic ecosystem. However, it is crucial to reveal the relationship of phytoplankton with P and provide deeper insight and information of eutrophication restoration mechanisms with limited observations.

Vollenweider (1969) proposed that phosphorus concentration in phytoplankton should be proportional to the water-column P concentration for P-limited lakes; therefore the effect of phytoplankton sedimentation on P could be represented as watercolumn P sedimentation. Based on this view, the ratio of P:C and C:Chla (C means carbon) could be introduced to distinguish algalbound P (particulate organic P) with non-algal P (dissolved and adsorbed inorganic P). Herein, the losses of P in the lakes could be divided into the sedimentation of non-algal P and algal-bound P. The settling velocity of non-algal P depends on suspended solids and algal-bound P has the same settling velocity as algae. Using the modified model, the following questions can be addressed: (a) How to distinguish algal-bound P and non-algal P in a simple budget model? (b) Is the ratio of algal-bound P and non-algal P same among lakes, and if not, what factors might cause the efficiency differences of converting phosphorus into algal P? (c) How can physical and biological factors influence the settling velocities of algal-bound P and non-algal P, such as water depth, TP concentration and trophic state? (d) What ecological information and management countermeasures can be revealed for lake eutrophication restoration by introducing new model parameters?

2. Materials and methods

2.1. Study area

Plateau lakes in China are a good class of lakes for this study because they are highly susceptible to eutrophication due to the low water exchange, strong light irradiation, and severe anthropogenic disturbances (Xie and Chen, 2001). The six plateau lakes in this study are Lake Lugu (LG), Lake Fuxian (FX), Lake Erhai (EH), Lake Chenghai (CH), Lake Yilong (YL) and Lake Dianchi (DC) (Fig. 1). Lake Fuxian and Lugu are both oligotrophic. Lake Erhai is the second largest lake of Yunnan Plateau with accelerated eutrophication. Lake Chenghai is a typical, enclosed lake where surface evaporation is about three times as much as precipitation. Lake Yilong has a relatively small surface area and has been proved to experience regime shift from a macrophytic lake to an algal one during 2008-2009 (Zhao et al., 2013). Lake Dianchi has been seriously polluted since the 1990s and is among the three most eutrophic lakes in China. Different aquatic environment results to different distributions of algae species: the dominant algae is diatom in Lake Lugu, Chlorophyta in lakes Fuxian and Erhai, and Cyanophyta in lakes Yilong and Dianchi (Table 1). The six lakes cover a wide range of depths (2.8-87 m), lake surface $(31.0-309.0 \text{ km}^2)$, watershed area $(240.4-2920.0 \text{ km}^2)$, and total phosphorus (TP) concentrations (0.005-0.185 mg/L) (Table 1). Both TP and Chla were observed once a month in the plateau lakes except that Lake Lugu was annually sampled because of the constant concentrations.

2.2. Model development

Chapra (1982) proposed a model that considers P loads, flushing, and physical settlement, with the latter integrating the net of particulate P settling, conversion of dissolved P to particulate P with subsequent settling, and release of P from the sediments (Eq. (1)):

$$V\frac{\Delta TP}{\Delta t} = L_{in} - S - L_{out} \tag{1}$$

where, *V* is the lake volume; *t* is time, i.e. month; *TP* is the total phosphorus concentration i.e. mg/L; L_{in} is the *TP* load, i.e. t/month; L_{out} is the *TP* export, i.e. t/month; *S* is the rate of mass loss, i.e. t/month.

Here, we expand that model modestly, by dividing *TP* into algal P (*TP*_B, g/m³) and non-algal P (*TP*_W = *TP*-*TP*_B, g/m³). *TP*_B is calculated from observed chlorophyll a (*Chla*) as *TP*_B = $\alpha \cdot APC \cdot Chla$, where *APC* is the P:C ratio (0.0244 mgP/mgC, Redfield ratio) (Schindler, 1971; Hecky et al., 1993) and α is the C:*Chla* ratio, which was set as 50 mgC/mgChla in all six lakes (Bowie et al., 1985; Ji, 2008), except the Lake Yilong after regime shift, which was estimated as a constant value by Bayesian inference. That was because C:*Chla* ratio changed when the conversion of macrophytes to algae dominance occurred in Lake Yilong (Zhao et al., 2012; Wei and Tang, 2014). Similarly, *S* was separated into *WW*, the mass loss of *TP*_W, i.e. t/month, and *WB*, the mass loss of *TP*_B, i.e. t/month:

$$V\frac{\Delta TP}{\Delta t} = L_{in} - WW - WB - L_{out}$$
(2)

WW and WB are calculated as:

$$WB = wb \cdot V \cdot TP_B/z = wb \cdot V \cdot \alpha \cdot APC \cdot Chla/z$$
(3)

$$WW = ww \cdot V \cdot TP_W/z = ww \cdot V \cdot (TP - TP_B)/z$$

$$= ww \cdot V \cdot (TP - \alpha \cdot APC \cdot Chla)/z \tag{4}$$

Where, *wb* is the algal settling velocity (m/d), *ww* is the settling velocity of non-algal P(m/d); *z* is mean depth. There are large differences of depths among the six lakes. Two concepts were proposed to eliminate the influence of lake depth, including (a) removal efficiency (RE), net remove rate divided by depth, that is (*ww* + *wb*)/*z*; and (b) removal amount unit volume (RAUV), i.e. (WW + WB)/V. Further, by replacing $L_A = L/A = (L_{in} - L_{out})/A$ (*A* is the surface area of lakes), the rate of net mass input of *TP* per unit area, i.e. t/(mon·m²), Eq. (1) can be reorganized as:

$$\frac{\Delta TP}{\Delta t} = \frac{L_A - ww \cdot TP - (wb - ww) \cdot \alpha \cdot APC \cdot Chla}{z}$$
(5)

where, $\triangle TP | \triangle t$ at time *n* can be calculated from observations as TP_{n+1} - TP_n .

The semi-dynamic model ($\Delta TP/\Delta t$ at time *n* as observed data) in Eq. (5) provides lake internal changes, while the steady one can provide more hints on some general eutrophication mechanisms. In order to put forward scientific suggestions for lake management, the model was further assumed to be steady with constant L_A and $\frac{\Delta TP}{\Delta t} = 0$, so Eq. (5) was converted as:

$$TP_W = \frac{wb}{wb - ww} \cdot TP + L_A \cdot \frac{1}{ww - wb}$$
(6)

$$TP_B = \frac{ww}{ww - wb} \cdot TP + L_A \cdot \frac{1}{wb - ww}$$
(7)

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