

Seasonal algal blooms support sediment release of phosphorus via positive feedback in a eutrophic lake: Insights from a nutrient flux tracking modeling

Rui Zou^{a,e,f,1}, Zhen Wu^{a,g,1}, Lei Zhao^b, James J. Elser^c, Yanhong Yu^d, Yihui Chen^d, Yong Liu^{a,*}

^a College of Environmental Science and Engineering, State Environmental Protection Key Laboratory of All Materials Flux in Rivers, Peking University, Beijing, 100871, China

^b Yunnan Normal University, Kunming, 650500, China

^c Flathead Lake Biological Station, University of Montana, Polson, Montana, 59860, USA

^d Yunnan Key Laboratory of Pollution Process and Management of Plateau Lake-Watershed, Kunming, 650034, China

^e Rays Computational Intelligence Lab (RCIL), Beijing Intelway Environmental Science & Technology, Ltd., Beijing, 100191, China

^f Nanjing Innowater Environmental Science & Technology, Ltd., Nanjing, 210012, China

^g Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, MA, 02139, USA

ARTICLE INFO

Keywords:

Internal nutrient cycling
Phosphorus release
Water quality model
Scenario analysis
Algae feedback
Lake Dianchi

ABSTRACT

Despite the great effort of nutrient loading reduction, lake rehabilitation often suffers from the impacts of internal nutrient cycling. However, the mechanisms of internal nutrient cycling, specifically the feedback of algal blooms on nutrients cycling is still an open question. Management of Lake Dianchi, the most eutrophic lake in China, has involved a series of costly measures but without significant algal bloom decreasing. In view of the difficulty to evaluate the importance of internal cycling only by monitoring data, a three-dimensional model-based flux tracking approach was performed to identify the contributions of internal cycling. The results highlighted the role of nitrogen (N) and phosphorus (P) benthic fluxes with high seasonal fluctuations, contributing ~29 % (N) and ~18 % (P) of total input. The scenario analysis indicated that N loading reduction was more efficient for lake restoration. Furthermore, A positive feedback was detected between algae biomass and benthic P flux. Benthic P flux varied from adsorption to release when algae biomass increased. This phenomenon implied that a close link existed between N and P cycles with algae acting as a strong integrator. Due to the positive feedback loop between benthic P flux and algal blooms as well as the high efficiency of N loading reduction, controlling both N and P loadings will benefit lake restoration, especially eutrophic lakes with heavy sediment nutrient loadings.

1. Introduction

External loading reduction of nitrogen (N) and phosphorus (P) has been conducted globally for lake eutrophication control (Conley et al., 2009; Davidson and Howarth, 2007; Seitzinger, 2008). However, there is an increasingly puzzle that it is not necessarily effective for all lakes (Ding et al., 2018; Liu et al., 2013; Yang et al., 2013), possibly due to impacts of unobserved internal nutrient cycling. Previous studies have found that, in eutrophic lakes, internal nutrient cycling like benthic fluxes of N and P, can be a significant part of nutrient input preventing or delaying lake recovery after external loading reduction, especially significantly enhancing algal growth as nutrients sources (Bergstrom and Jansson, 2006; Carpenter et al., 1999; Nowlin et al. 2005, Roy et al., 2012; Sondergaard et al., 2013; Wu et al., 2017; Zhou et al.,

2016). However, the driving factors of internal nutrient cycling processes are complex and often harder to control than those affecting external loadings. More importantly, Cottingham et al. (2015) raised a new finding that cyanobacterial blooms could in turn affect P cycling; a recent lab study also found a positive feedback loop where benthic P flux fuels algal blooms, which in turn enhance the release of P (Chen et al., 2018). Algae was considered as a “biological pump” in this positive feedback loop, while there is great need for more quantitative or empirical evidences. Therefore, for effective management of lake eutrophication, it is essential to consider the roles of internal nutrient cycling and to explore (a) how internal nutrient cycling processes respond to various nutrient management strategies; and (b) how algae will change the nutrient cycling dynamics.

The effectiveness of loading reduction has been well studied.

* Corresponding author.

E-mail address: yongliu@pku.edu.cn (Y. Liu).

¹ Rui Zou and Zhen Wu contribute equally to this study.

However, diverse patterns of internal cycling processes under different loading reduction scenarios have seldom been explored. Furthermore, isolated considerations of N or P cycling changes in response to changes in external N or P loading may be misleading if we ignore the potentially tight links of lake N and P cycles due to the highly constrained link of N and P in living biomass (Bernhardt, 2013). For example, Finlay et al. (2013) showed that reducing P loading alone may result in exceptionally high N storage in lakes, in which algae act as a primary link between N and P cycling (McCarthy et al., 2016; Suding et al., 2004). As primary producer, the biomass of algae can be extremely large compared with macrophytes and consumers in eutrophic lakes, meaning that nutrient uptake and release by algae might dominate the overall fluxes of N and P (Anderson et al., 2002; Friedrich et al., 2003; Qin, 2009; Ramin et al., 2012). Moreover, algal blooms can also cause a drastic change of chemical conditions at sediment-water interface favoring the release of Fe-bound P (Chen et al., 2018). Algae therefore have the potential to influence internal nutrient cycling.

Three specific questions arose during the attempts to understand the internal nutrient cycling in lakes: (a) Are there any changes in the contribution of internal cycling during load reduction? (b) If yes, will there be different patterns for N-, P-, or N and P loading reduction? and (c) Is there a feedback loop between algae and nutrient cycling? If so, what is the mechanisms of the feedback? Although some internal processes can be evaluated in lab or by in-situ experiments (Nowlin et al., 2005; Risgaard-Petersen et al., 2003), it is still difficult to establish the patterns of internal nutrient cycling fluxes for a whole lake in different seasons, considering spatial and temporal differences. Numerical modeling is a valuable and feasible tool to explore the dynamics of nutrient cycling, integrating existing knowledge of relevant biogeochemical processes (Boyd, 2012; Hu et al., 2006; Wang et al., 2003a, b). Here a three dimensional (3D) model derived from our previously developed, calibrated and validated model of Lake Dianchi was used to simulate temporal changes of nutrient budgets under nutrient loading scenarios to explore the mechanisms of nutrient cycling (Liu et al., 2014; Wang et al., 2014; Yi et al., 2016).

2. Methods

2.1. Study area and data sources

Lake Dianchi is the 6th largest lake in China and the largest plateau one in Yunnan Province, southwestern China (Fig. 1), with a surface area of 309 km², a volume of 1.56 × 10⁹ m³, a mean depth of 4.4 m and a watershed area of 2920 km². Historical monitoring has shown that lake water quality has deteriorated rapidly since late 1970s and especially since the 1990s. However, after over 20 years of restoration efforts, the water column N and P concentrations decreased but there is no sign of significant improvement as expected for algae biomass (Figure S1 in Supporting Materials). Lake Dianchi is a typical semi-enclosed lake with high inflow, low outflow, long residence time, and high evaporation, which highlights the potential importance of internal nutrient cycling (Gao et al., 2014; Wu et al., 2017). To facilitate more effective decision-making for eutrophication control and ecological restoration in Lake Dianchi, it is crucial to explore the dynamic processes of nutrient cycling and the responses of algae biomass in the lake. Monthly water quality data was collected from the routine monitoring program conducted by Kunming Environmental Monitoring Center. It provides the basis for calibrating and validating the model developed in this study. Atmospheric and meteorological data are from the National Meteorological Information Center. River flow and velocity data are from the Kunming Bureau of Hydrology and Water Resources (Please refer to Supporting Materials for the detailed configuration of boundary and initial conditions).

2.2. Model-based numerical tracking of nutrient fluxes and pools

Changes in nutrient pools and fluxes are important to evaluate the ecological status of lakes. While nutrient pools and fluxes can be estimated via direct measurements and experiments, these often cannot illustrate the picture of the whole lake due to limitations on sampling sites, impacts of vertical stratification, and limited spatial coverage. In contrast, the 3D model is useful to calculate nutrient pools and fluxes. The model for Lake Dianchi was derived from our previously developed, calibrated and validated 3D model which was used in various studies, like global sensitivity analysis and water diversion scenarios (Liu et al., 2014; Yi et al., 2016). The model was based on EFDC (Environmental Fluids Dynamics Code), an integrated 3D model to simulate hydrodynamics, temperature, and the cycles of carbon, nitrogen, phosphorus, and silicon in living, inorganic, and organic forms (refer to Content S1 and Figure S2 in Supporting Materials for modeling details). In the model of Lake Dianchi, nutrient pools and fluxes were calculated based on the mechanistic equations and spatial configuration. Fluxes and pools were calculated in each grid of the model. The integral for fluxes and pools of all the grids were obtained according to the computational grid of Lake Dianchi based on the same discrete distribution. The main equations for nutrient pools and fluxes are as below.

$$\text{Nutrientpool: } M(i, t) = \iiint c(i) dx dy dz \quad (1)$$

$$\text{Nutrientloading: } F_{WS}(i, t) = \sum_{k=1}^N Q(t, k) * C(t, k, i) \quad (2)$$

$$\text{Atmosphericdeposition: } F_{AIR}(i, t) = \iint (Dd(i, t) + Dw(i, t)) dx dy \quad (3)$$

$$\text{Output: } F_O(i, t) = \sum_{k=1}^M q(k, t) c(k, t, i) \quad (4)$$

$$\text{Benthicflux: } F_{Ben}(i, t) = \iint Ben(i, t) dx dy \quad (5)$$

$$\text{Sedimentation: } F_{Set}(i, t) = \iint Fs(i, t) dx dy \quad (6)$$

$$\text{Denitrification: } F_{Den}(t) = \iiint F_{dn}(t) dx dy dz \quad (7)$$

$$\text{Nitrogenfixation: } F_{Nfix}(t) = \iiint F_{NF}(t) dx dy dz \quad (8)$$

where, i represent different forms of nutrient; $c(i)$ is the concentration of i in water body; $Q(t, k)$ is the quantity of flow in inflowing river k on time t ; $C(t, k, i)$ is the concentration of i in inflowing river k on time t ; $Dw(i, t)$ is wet deposition of i ; $Dd(i, t)$ is dry deposition of i ; $q(k, t)$ is the quantity of flow in outflowing river k on time t ; $c(k, t, i)$ is the concentration of i in outflowing river k on time t ; $Ben(i, t)$ is the benthic flux rate of i ; $Fs(i, t)$ is sedimentation rate of i ; $F_{dn}(t)$ is the denitrification rate; $F_{NF}(t)$ is the N fixation rate (refer to S1.1 in Supporting Materials for detailed flux expressions).

2.3. Scenario definition

In order to explore the efficiency of nutrient loading reductions and the impact of loading reduction on internal cycling processes, three types of scenarios were evaluated: (a) reducing N loading only; (b) reducing P loading only; and (c) reducing both N and P loading (Table S2). In each type of scenarios, the reduction ratios are 10 %, 30 %, 50 %, 70 %, 80 % and 90 %. There are 19 scenarios in all including baseline scenario. The baseline scenario was defined as no reduction. The results of all the scenarios were the fifth year of each model run in order to get a steady state. The limiting nutrient of algae growth can be detected by the comparison of N-only scenarios and P-only scenarios. The relationship between internal cycling of P (or N) to algae biomass change could be effectively studied in scenarios of N (or P) loading reduction based on the water quality modeling and calculation of nutrient cycling fluxes.

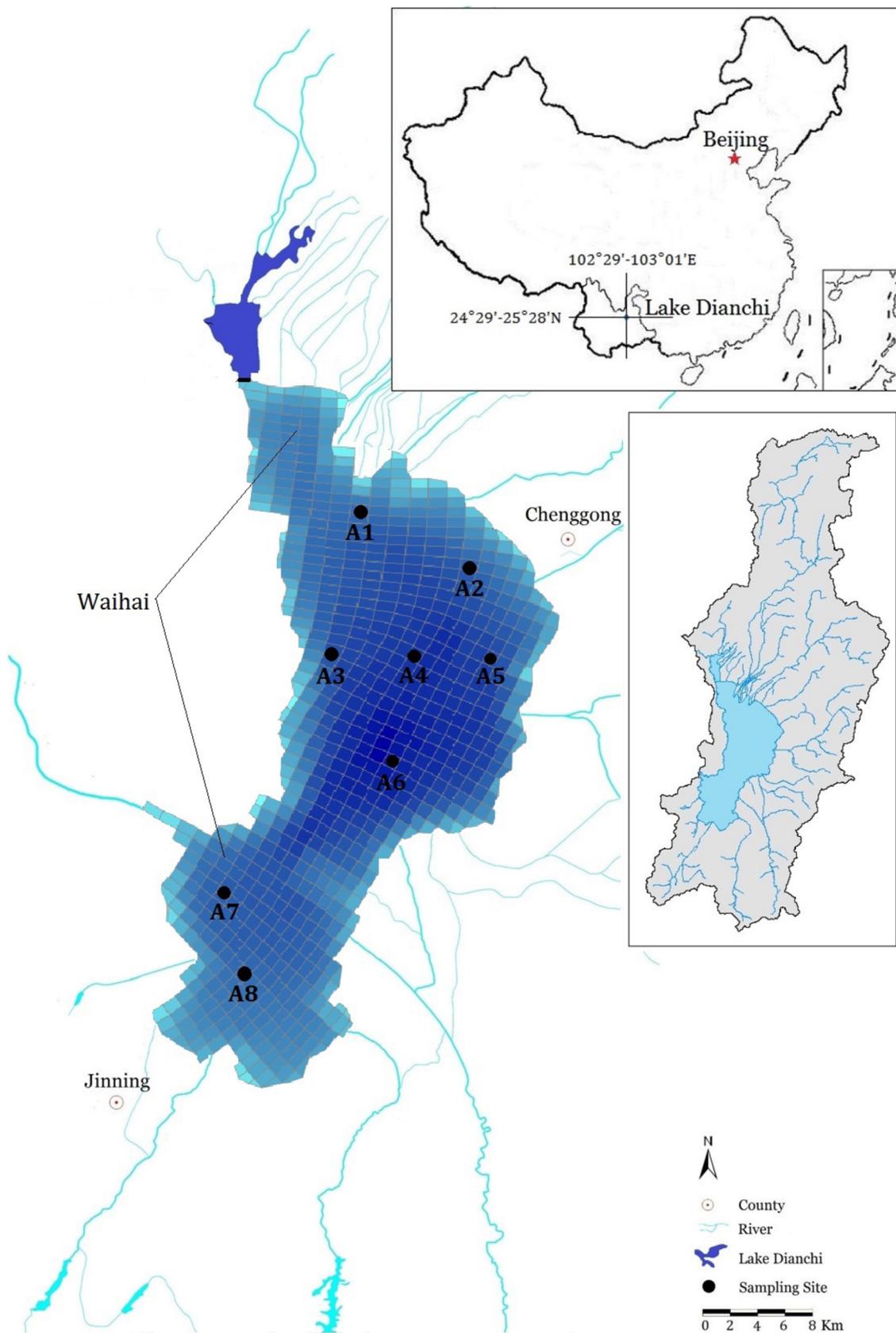


Fig. 1. Lake Dianchi including sampling sites and model grid. The grid consisted of 664 curvilinear cells per layer with six layers. A1 to A8 are the 8 routine monitoring stations in the lake.

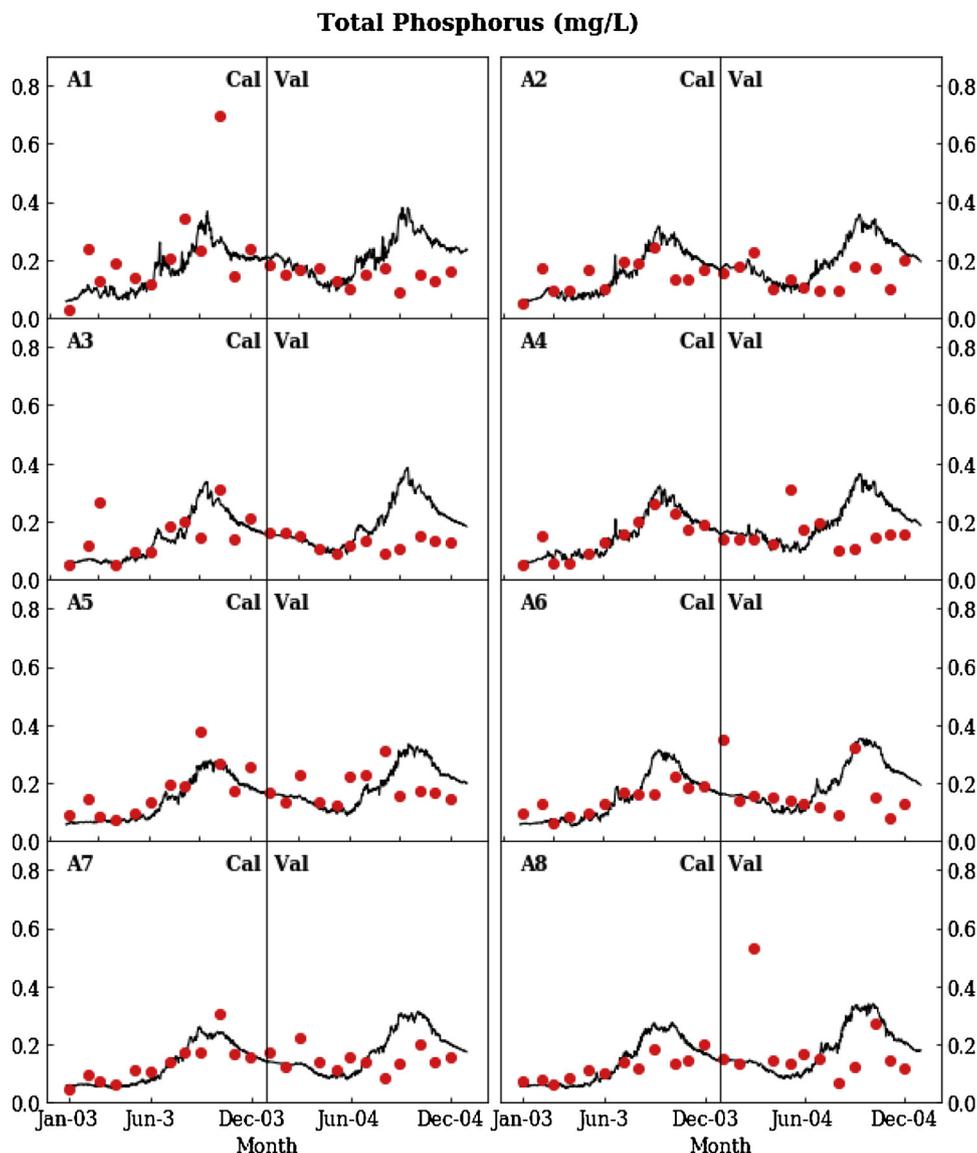


Fig. 2. Calibration and validation of TP of eight sampling sites. The red dots are observed data and the black line are model results.

3. Results and discussion

3.1. Model results

Before the model of Lake Dianchi could be used for the calculation of nutrient cycling fluxes as well as scenario analysis, its ability to represent in-lake water quality and processes of nutrient cycling were established through a model calibration and validation process. In this study, a data set consisting of two years of observations was used for calibration and validation. The hydrodynamic module was first calibrated with the temperature data. The water quality module was then calibrated with the observed data of chlorophyll-a (Chla), NH_4^+ , total phosphorus (TP), and DO. The simulated concentrations of Chla, NH_4^+ , TP, and DO in the surface layer are compared with observed data at eight routine monitoring stations in Lake Dianchi in Fig. 2 & S4. However, due to the lack of subsurface water column and surface sediment data, the model was calibrated only with surface water quality data. The calibrated values of for the key water quality parameters are listed in Table S3. Uncertainty analysis was conducted based on the LHS (Latin Hypercube Sampling) method to see the uncertainty of Chla, DO, TN, and TP and the sensitivity analysis was also conducted to see the response of Chla, DO, TN, and TP to 38 parameters based on Morris

method (Figure S5 and Table S5, Supporting Materials). Overall, the validation results showed that the model results fit well with observed water quality variations in Lake Dianchi and the model can serve as a computational platform for further analysis.

Some distinct seasonal patterns were found in the results of nutrient pools (Fig. 3). NH_4^+ and NO_3^- pools increased in November and December, but started to decrease in January and February, indicating that a huge sink of NH_4^+ and NO_3^- existed during warmer seasons when algae started to grow. This huge sink may result from the uptake of algae growth. Furthermore, a delay was detected between NH_4^+ and NO_3^- , indicating that nitrification took place in January and February leading to a rapid decrease of NH_4^+ and an increase of NO_3^- . Then, NO_3^- decreased rapidly and remained relatively low from April to October in contrast to NH_4^+ and total phosphate (TPO_4), likely because of the relatively high denitrification flux during algal bloom (from May to October). Different from NO_3^- , an increase of NH_4^+ and TPO_4 occurred from July to October, likely due to the sediment release of NH_4^+ and TPO_4 during algal bloom. In contrast to dissolved nutrients, algae biomass increased from March and decreased in November. Logically, algae uptake is likely the primary reason for the decrease of dissolved nutrients during algal bloom.

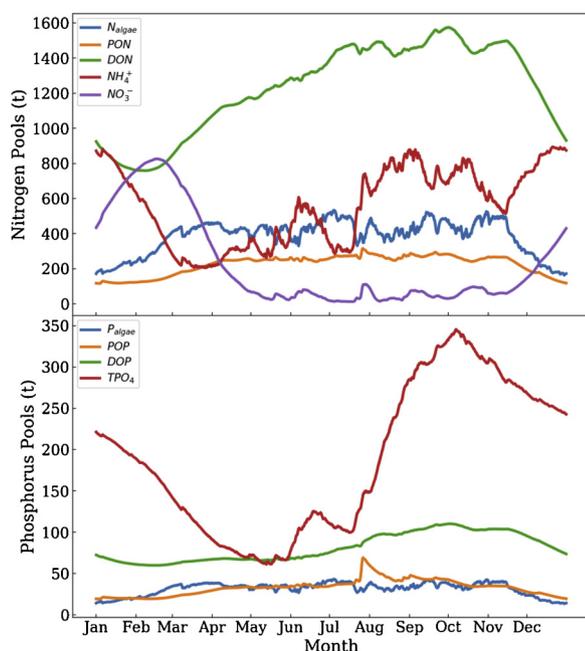


Fig. 3. The variations of nutrient pools (t). The figure shows the pools of different forms of N and P are calculated by the integral of all the model grids.

3.2. Contributions of nutrient internal cycling

Increasing evidence has shown that internal cycling of nutrients in shallow lakes may be one of the main factors maintaining eutrophication and preventing improvements in water quality (Jeppesen et al., 2005). Reductions of external nutrient loading have been implemented for decades in Lake Dianchi. However, there are still serious algal blooms with the summer maximum chlorophyll-a (Chla) reaching 209 $\mu\text{g/L}$ in recent years. Thus, exploring the dynamics of internal cycling of nutrients may offer useful insights for lake rehabilitation. The model results showed that, in Lake Dianchi, benthic fluxes of N and P accounted for $\sim 29\%$ of total N input and $\sim 18\%$ of total P input; these fluxes were second to external loadings, which contributed $\sim 68\%$ for N and $\sim 80\%$ for P (Fig. 4). Similar results have been shown in other studies. For example, in Lake Pontchartrain, benthic P flux contributed 30–44 % of annual P loading (Roy et al., 2012). In Lake Taihu, benthic fluxes of NH_4^+ contributed 20 %–25 % of total N loading while benthic P fluxes accounted for almost 50 % of total P loading (Qin and Zhu, 2006; Qin et al., 2006). Moreover, a great fluctuation was detected in benthic fluxes of nutrients throughout the year in the model (Fig. 4). Seasonal fluctuations of benthic nutrients fluxes in the Lake Dianchi are supported by previous studies, which showed that the benthic fluxes of nutrients vary monthly or seasonally (Sondergaard et al., 1992; Spears et al., 2012; Yang et al., 2013). The benthic P flux in Lake Dianchi acted as a source (sediment release) of P to the water column from May to October but acted as a sink (adsorption) in other months. Unlike TPO_4 , the benthic N flux was close to zero from January to March, which means an equilibrium existed between sediment release and adsorption of DIN (dissolved inorganic nitrogen). However, this equilibrium was broken in early March because of the uptake by algae. Low DO near the sediment as well as strong concentration gradients are likely the main driving factors enhancing benthic fluxes in systems like Lake Dianchi (Amirbahman et al., 2003; Li et al., 2016; Nowlin et al., 2005; Wu et al., 2014). In Lake Dianchi, benthic fluxes of N and P are synchronous with algae on account of the enhanced driving factors caused by biological uptake of algae as well as bottom hypoxia ($\text{DO} < 2 \text{ mg/L}$) resulting from algal bloom (Figure S5) (Paerl et al., 2011). Similar results were found in Lake Uzarzewskie, a hyper-eutrophic lake in Poland (Kowalczywska-Madura et al., 2015), where the highest P release rate

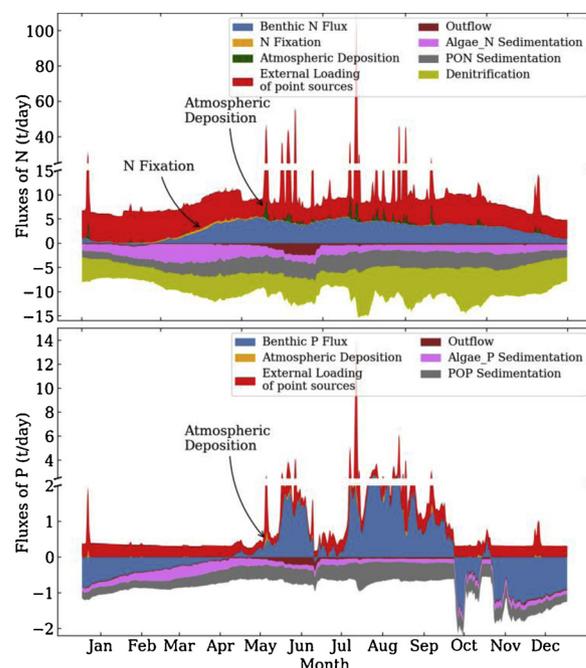


Fig. 4. The variations of nutrient fluxes (t/year). The figure shows the cumulative area plots are used to show the relative contributions of each cycling process of N and P. The fluxes of N are shown in the upper panel and the fluxes of P are shown in the lower panel with input processes above zero and output processes below zero.

was observed in autumn ($44.7 \text{ mg P/m}^2/\text{day}$) but P accumulation in sediments dominated over release in winter ($0.33\text{--}0.62 \text{ mg P/m}^2/\text{day}$).

Removal processes of nutrients are essential for Lake Dianchi because of its semi-closed morphology. In the absence of significant hydrologic outflow, sedimentation of particulate organic matter and denitrification were the main pathways of nutrient removal in Lake Dianchi. The outflow only accounted for 4.5 % of total N loss and 9.4 % of total P loss. Sedimentation was a major removal pathway for both N and P and accounted for 90.6 % of total P loss and 46.5 % of total N loss. Denitrification was a unique and important removal pathway of N internal cycling and accounted for $\sim 49\%$ of the total N loss, which is larger than sedimentation. This large contribution of denitrification may be explained by algal blooms and the resulting low benthic DO concentrations (Figure S6). It had been thought that hypoxia could not occur in Lake Dianchi because of its shallow depth. However, our previous model results showed that, 6.82 % of Lake Dianchi's volume was hypoxic annually which cannot be obtained from well-mixed or 2D models (Liu et al., 2014). Overall, our modeling effort highlights that benthic fluxes of N and P as well as denitrification are of great importance in eutrophic shallow lakes, especially semi-enclosed lakes.

3.3. Scenario analysis: efficiency of P vs N loading reduction

Eighteen scenarios (Table S2) were set based on the validated model configuration to explore the efficiency of loading reduction on algae regulation as well as N and P internal cycling. Overall, the scenario results showed that, as expected, algae biomass decreased when external loading was reduced. However, the efficiencies of N and P loading reduction were not the same. N loading reduction and dual-nutrient loading reduction had almost equal and higher performance for algae biomass than P loading reduction (Fig. 5a). The reason why the efficiencies of these two measures were similar is that nutrient limitation was decided by taking the minimal value of N and P limitation factors in the algae growth equation of the model (Hamrick, 1992). The lower efficiency of P loading reduction implied that bioavailable P was much more difficult to remove to the limiting level given

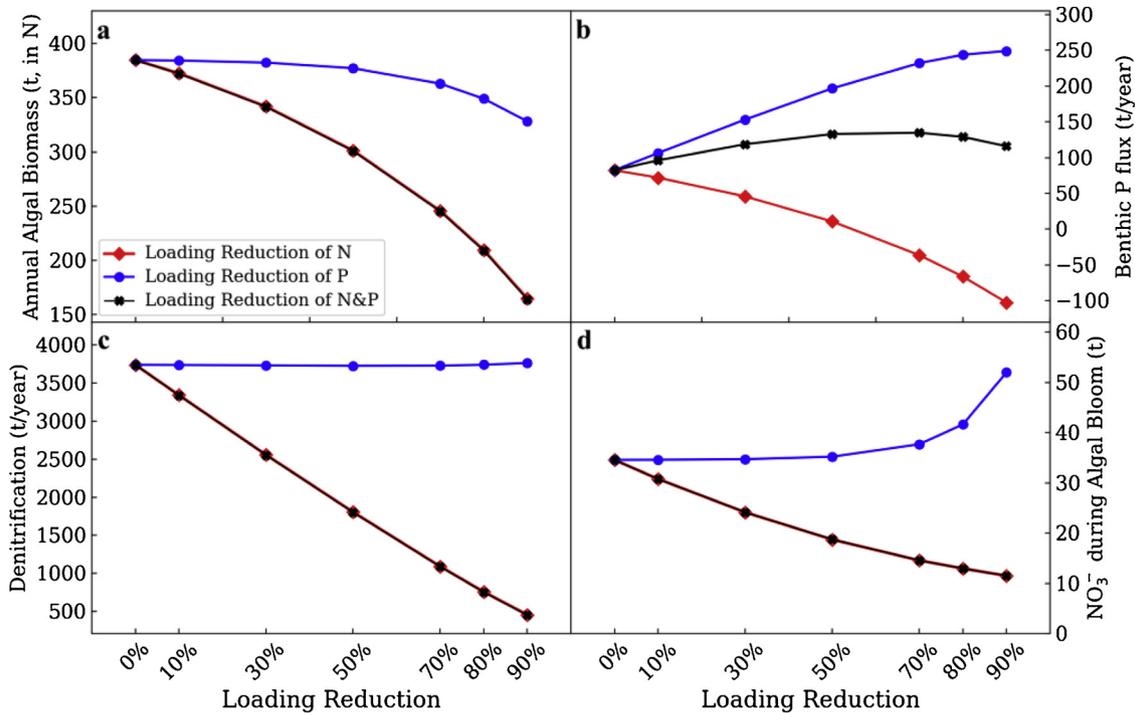


Fig. 5. Scenarios of external nutrient loading reduction on (a) annual algae biomass (in nitrogen), (b) annual benthic P flux, (c) annual denitrification, and (d) NO_3^- during algal bloom. Three types of scenarios are shown the four panels, including reduction of P alone (blue), reduction of N alone (red), and reduction of N and P simultaneously (black).

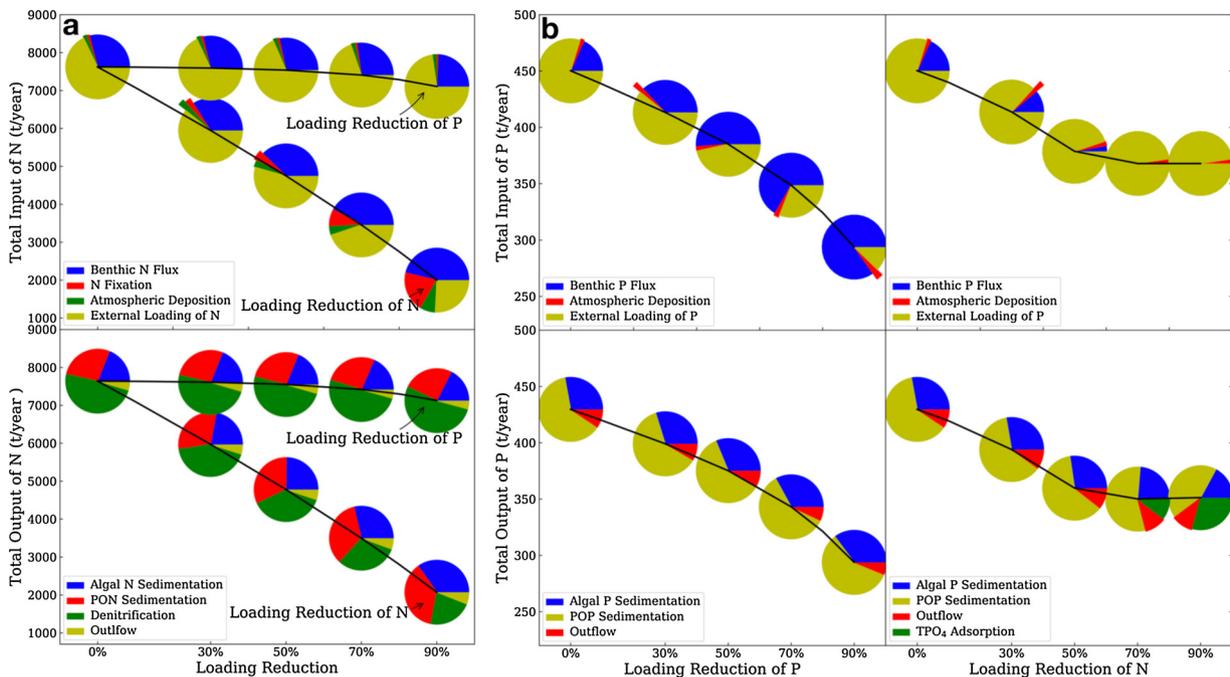


Fig. 6. The contributions of different nutrient cycling processes of N and P of all the scenarios: (a) shows the contributions of N cycling fluxes; (b) shows the contributions of P cycling fluxes. The position of each pie chart in each panel indicates the total input or output of N or P (y axis) in one scenario (x axis) and the sectors of different colors in each pie chart represent different input or output processes of N or P in this scenario.

the same nutrient loading reduction measures. Although N loading reduction was more efficient, a non-linear relationship between algae biomass and N loading reduction was still detected, the same as P loading reduction. In order to explore the non-linear relationships between algae biomass and nutrient loading reduction, N and P in different forms and fluxes of nutrient cycling processes were calculated in all scenarios (Fig. 6 & S7, Table S6 & S7).

The reason why N loading reduction was more efficient lay in the insufficiency of DIN, which implied that the internal source of DIN cannot support the uptake of algae. N loading reduction had a large impact on N cycling processes. Although the contribution of benthic N flux increased from 29.0%–46.3 % of total N input in N-loading reduction scenarios, the actual flux decreased. Compared with benthic P flux, the contribution of which increased from 18.3%–84.8 % of total P

input (actual flux increased from 82.4 t/year to 249.1 t/year, Figs. 5b & 6b) when P loading was reduced, internal N supply seemed to be the more insufficient one. Moreover, although N fixation fluxes increased from 91.4 t/year to 406 t/year and the relative contribution of N fixation increased from 1.2%–20.3% when N loading was reduced to 10% of baseline, the increase of N fixation still could not cover the total reduction of external N loading, in contrast to the scenarios proposed by Schindler et al. (2008). The reason for this difference could be differences in species composition and in time scales of studies. The theoretical basis for Schindler's view that N is not a limiting factor is that N fixation can eventually offset an N deficit. Indeed, this is true from a long time-scale. However, our model focused on yearly time scales. Since N fixation is also controlled by a number of physicochemical factors, it does not necessarily fully make up the N deficit in any given year, especially in the presence of intense denitrification, thus giving rise to N limitation in Lake Dianchi. The cyanobacteria species composition is another potential reason for N limitation in Lake Dianchi. Not all species of cyanobacteria are capable of fixing N. In Lake Dianchi, the N fixer *Aphanizomenon* only persists from March to May while non-fixing *Microcystis* dominates the lake throughout the year (Liu et al., 2006).

Non-linear relationships were detected in both N and P loading reduction scenarios. This kind of phenomenon was well studied as internal nutrient loading (Essington and Carpenter, 2000; Nowlin et al., 2005; Sondergaard et al., 2013). In this model, although N is the more insufficient nutrient, internal N sources including benthic N flux and N fixation still had a positive influence on the hysteresis in N remediation in Lake Dianchi. Moreover, the flux and contribution of denitrification decreased while N loading reduction increased. N supply and anaerobic conditions are the two primary factors for denitrification (Nizzoli et al., 2010). These were both removed by N loading reduction and resulting algae biomass reduction. Hence, decreased removal by denitrification in response to reduction of N loading could be another reason for the hysteresis in N remediation in Lake Dianchi. The strength of non-linear relationship could also reflect the relative abundance of nutrients. As bioavailable P, TPO_4 was more sufficient than DIN when P (or N) loading was reduced. Although the amount and fraction of TPO_4 decreased under P loading reduction, benthic P flux increased from 82.4 t/year to 249.1 t/year, the contribution of it increased from 18.3%–84.8%, which contributed more than benthic N flux to the maintenance of eutrophication. The increasing contribution of benthic fluxes of N and P with increasing load reduction support the hypothesis that internal loading has inhibited the remediation of eutrophication in Lake Dianchi and may be a similar role elsewhere. Together with the observed difference in the effects of N vs P loading reduction on algae biomass, this differential impact of N vs P reduction on N and P cycling implies that N is the main limiting nutrient in Lake Dianchi.

3.4. Algae feedback enhancing nutrient cycling

As Cottingham et al. (2015) pointed, algae could affect nutrient cycling as a positive feedback. However, there is little quantitative evaluation of the changes of nutrient cycling due to algal blooms. Since the limiting nutrient in Lake Dianchi appears to be N, the model of Lake Dianchi provides a perfect platform to explore the feedback of algae on P cycling, especially benthic P flux, in N loading reduction scenarios. Algae biomass can be controlled by the reduction of N loading which has no direct effect on P cycling. An interesting pattern was found in P cycling in a series of N loading reduction scenarios. The model simulations showed a negative non-linear correlation between TPO_4 and algae biomass (annual average values were used in this analysis, same below), which indicated that TPO_4 was consumed by algae when algae biomass increased (Fig. 7a). This was associated with the increasing demand of TPO_4 by algae that resulted from N loading increase. Besides, TPO_4 remained at a relatively low level when algae biomass reached 300 t N (algae biomass is counted in N) implying a significant

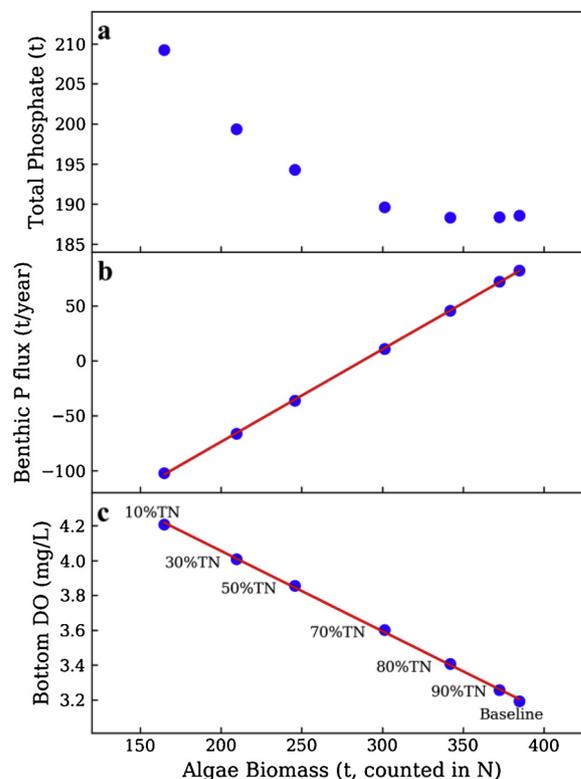


Fig. 7. Correlations of algae biomass to P cycling (a, b) and DO(c): (a) shows the non-linear relationship between algae biomass and TPO_4 . (b) shows the linear correlation of algae biomass and benthic P flux. (c) shows the linear correlation of algae biomass and bottom layer DO concentration at station A1. Labels in panel (c) represent the percentages of baseline N loading used in each scenario.

contribution of benthic P flux to P pool. Nevertheless, a strong positive linear correlation was found between benthic P flux and algae biomass: as algae biomass increased, the annual benthic P flux turned from negative to positive, from acting as a sink of P cycling and resulting in up to 29% of the total P loss to acting as a main source of P cycling and accounting for 18% of total P input (Fig. 7b). In this series of scenarios, external forcings of P remained the same as baseline scenario, implying that all the changes of P cycling were driven by the change of algae biomass. TPO_4 uptake by algae increased as the algae biomass increased in different scenarios causing a steep TPO_4 concentration gradient toward sediment, which was a benefit of P release. Besides, DO was also consumed by algal blooms increasing the occurrence of hypoxic condition, which was the driving factor of benthic P flux (Fig. 7c). As a result, benthic P flux switched from adsorbing P into sediment to releasing P into water column. Thus, the strong feedback of algae on benthic P flux in Lake Dianchi emphasized that algae played an important role as the primary linkage between N and P cycles.

Different lakes may have different types of algae feedback. Nutrient limitation of algae plays an important role in algae feedback by influencing the metabolism of algae and subsequently the cycling of nutrients. Even in Lake Dianchi, different algae feedback were observed. Of all the removal processes, sedimentation is a key nutrient cycling process in lake system. To some extent, sedimentation limits the availability of nutrients for regeneration and release (Poister and Armstrong, 2003). Moreover, sedimentation of organic materials drives hypolimnetic oxygen depletion, which further affects several biogeochemical processes, including sediment TPO_4 release and denitrification. In the model of Lake Dianchi, P sedimentation was the main removal pathway of total P loss. However, in the scenario analyses, sedimentation fluxes of refractory particulate organic phosphorus (RPOP), labile particulate organic phosphorus (LPOP), and algae

decreased more strongly with reduction of external N loading rather than with reduction of P when loading reduction is higher than 50 %, indicating a close link between N and P by algae (Figure S8). This phenomenon implies that considerable amounts of particulate organic phosphorus (POP) were from the metabolism of algae and zooplankton excretion instead of external loading, which could be affected by N loading reduction in an N-limited lake like Lake Dianchi (Genkai-Kato and Carpenter, 2005; Guildford and Taylor, 2011; Hantke et al., 1996; Qin and Zhu, 2006; Wetzel, 2001). In eutrophic lakes, the recycling ratio would be much higher than in oligotrophic or mesotrophic lakes, which means that the internal cycling of nutrients weighs much more than external loading in eutrophic lakes (Baines and Pace, 1994; Essington and Carpenter, 2000), consistent with our previous study (Wu et al., 2017).

Another kind of algae feedback was found in Finlay et al. (2013). N removal processes, especially denitrification, were closely related to algal blooms. Since P is viewed as the limiting nutrient in most lakes for algae growth, reducing external P loading can reduce algal blooms and the influence of hypoxia weakening the algae feedback on denitrification. Denitrification was thereby impaired because of the aerobic water column and surficial sediments (Chen et al., 2012; Knuth and Kelly, 2011). However, in the current study of Lake Dianchi, in spite of the increase of NO_3^- pool from 34.6 ton to 52.0 ton during algal bloom, the denitrification flux remained nearly the same when external P loading was reduced on different levels (Figure 5c&5d). Since N was the limiting nutrient according to Michaelis-Menten kinetics in the Lake Dianchi model, the lake remained eutrophic and hypoxic due to algal blooms even when external P loading was reduced. Furthermore, in this condition, rates of denitrification remained the same as in the baseline scenario. Accordingly, the main factor that likely leads to the difference between Finlay et al. (2013) and Lake Dianchi is the difference in the limiting nutrient for algae. The limiting nutrient in different lakes varies greatly; therefore, the effects of nutrient loading reduction differ among lakes (Abell et al., 2010; Jeppesen et al., 2007; Moon and Carrick, 2007). Thus, changes in nutrient limitation status may alter the mechanisms of the feedback loop of algae and nutrient cycles which should be taken in to consideration for lake restoration efforts.

4. Conclusion

A 3D model-based nutrient flux tracking approach was developed to identify the fate and transport of nutrients, along with algae growth in Lake Dianchi, China. The contributions of internal nutrient cycling and the response of nutrient cycling to external loading were explored. The model results and scenario analysis highlighted a positive feedback loop between algal bloom and sediment release of P as well as the importance of internal nutrient cycling in Lake Dianchi.

- The annual fluxes of external loadings were 5164 t for N and 359 t for P, accounting for 67.8 % for N and 79.8 % for P. Second to external loading were the benthic fluxes: 2213 t for N and 82.4 t for P, accounting for 28.04 % for N and 18.30 % for P. Denitrification was the biggest N removal processes at 3741 t per year, contributing 49 % of total N loss. Sedimentation of POP accounted for 62.8 % of total P loss, the largest component of P losses.
- Benthic fluxes of N and P fluctuated considerably during the year with peaks in July. Benthic P flux in Lake Dianchi acted as a source of P to the water column from May to October but as a sink in other months. In contrast to P, benthic N fluxes were close to zero from January to March and increased rapidly from March to April. The rapid increase of benthic fluxes of both N and P reflected the onset of hypoxia and establishment of concentration gradients.
- The results of scenario analyses showed that N was the primary and seasonal limiting nutrient for algae growth in Lake Dianchi. In addition, a positive feedback was detected between algal bloom and sediment release of P with different N loading reduction scenarios.

Algae could support the sediment release of P by forming a steep TPO_4 concentration gradient toward sediment as well as DO consumption.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

This paper was supported by the National Science Foundation of China (51779002), National Basic Research Program of China (2015CB458900), and Yunnan Key Laboratory of Pollution Process and Management of Plateau Lake-Watershed.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ecolmodel.2019.108881>.

References

- Abell, J.M., Oezkundakci, D., Hamilton, D.P., 2010. Nitrogen and phosphorus limitation of phytoplankton growth in New Zealand lakes: implications for eutrophication control. *Ecosystems* 13 (7), 966–977.
- Amirbahman, A., Pearce, A.R., Bouchard, R.J., Norton, S.A., Kahl, J.S., 2003. Relationship between hypolimnetic phosphorus and iron release from eleven lakes in Maine, USA. *Biogeochemistry* 65 (3), 369–385.
- Anderson, D.M., Glibert, P.M., Burkholder, J.M., 2002. Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. *Estuaries* 25 (4), 704–726.
- Baines, S.B., Pace, M.L., 1994. Relationships between suspended particulate matter and sinking flux along a trophic gradient and implications for the fate of planktonic primary production. *Can. J. Fish. Aquat. Sci.* 51 (1), 25–36.
- Bergstrom, A.K., Jansson, M., 2006. Atmospheric nitrogen deposition has caused nitrogen enrichment and eutrophication of lakes in the northern hemisphere. *Glob. Chang. Biol.* 12 (4), 635–643.
- Bernhardt, E.S., 2013. Cleaner lakes are dirtier lakes. *Science* 342 (6155), 205–206.
- Boyd, I.L., 2012. The art of ecological modeling. *Science* 337 (6092), 306–307.
- Carpenter, S.R., Ludwig, D., Brock, W.A., 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecol. Appl.* 9 (3), 751–771.
- Chen, M., Ding, S., Chen, X., Sun, Q., Fan, X., Lin, J., Ren, M., Yang, L., Zhang, C., 2018. Mechanisms driving phosphorus release during algal blooms based on hourly changes in iron and phosphorus concentrations in sediments. *Water Res.* 133, 153–164.
- Chen, X., Yang, L., Xiao, L., Miao, A., Xi, B., 2012. Nitrogen removal by denitrification during cyanobacterial bloom in Lake Taihu. *J. Freshw. Ecol.* 27 (2), 243–258.
- Conley, D.J., Paerl, H.W., Howarth, R.W., Boesch, D.F., Seitzinger, S.P., Havens, K.E., Lancelot, C., Likens, G.E., 2009. Controlling eutrophication: nitrogen and phosphorus. *Science* 323 (5917), 1014–1015.
- Cottingham, K.L., Ewing, H.A., Greer, M.L., Carey, C.C., Weathers, K.C., 2015. Cyanobacteria as biological drivers of lake nitrogen and phosphorus cycling. *Ecosphere* 6 (1), art1.
- Davidson, E.A., Howarth, R.W., 2007. Environmental science - nutrients in synergy. *Nature* 449 (7165), 1000–1001.
- Ding, S., Chen, M., Gong, M., Fan, X., Qin, B., Xu, H., Gao, S., Jin, Z., Tsang, D.C.W., Zhang, C., 2018. Internal phosphorus loading from sediments causes seasonal nitrogen limitation for harmful algal blooms. *Sci. Total Environ.* 625, 872–884.
- Essington, T.E., Carpenter, S.R., 2000. Nutrient cycling in lakes and streams: insights from a comparative analysis. *Ecosystems* 3 (2), 131–143.
- Finlay, J.C., Small, G.E., Sterner, R.W., 2013. Human influences on nitrogen removal in lakes. *Science* 342 (6155), 247–250.
- Friedrich, J., Dinkel, C., Grieder, E., Radan, S., Secrieru, D., Steingruber, S., Wehrli, B., 2003. Nutrient uptake and benthic regeneration in Danube Delta lakes. *Biogeochemistry* 64 (3), 373–398.
- Gao, W., Howarth, R.W., Hong, B., Swaney, D.P., Guo, H.C., 2014. Estimating net anthropogenic nitrogen inputs (NANI) in the Lake Dianchi basin of China. *Biogeosciences* 11 (16), 4577–4586.
- Genkai-Kato, M., Carpenter, S.R., 2005. Eutrophication due to phosphorus recycling in relation to lake morphometry, temperature, and macrophytes. *Ecology* 86 (1), 210–219.
- Guildford, S.J., Taylor, W.D., 2011. Evidence supporting the importance of nutrient regeneration by nano- and micrograzers for phytoplankton photosynthesis in Lake Malawi/Nyasa. *J. Great Lakes Res.* 37, 54–60.
- Hamrick, J.M., 1992. A Three-dimensional Environmental Fluid Dynamics Computer Code: Theoretical and Computational Aspects, Virginia Institute of Marine Science.

- College of William and Mary.
- Hantke, B., Fleischer, P., Domany, I., Koch, M., Pless, P., Wiendl, M., Melzer, A., 1996. P-release from DOP by phosphatase activity in comparison to P excretion by zooplankton. Studies in hardwater lakes of different trophic level. *Hydrobiologia* 317 (2), 151–162.
- Hu, W., Jørgensen, S.E., Zhang, F., 2006. A vertical-compressed three-dimensional ecological model in Lake Taihu, China. *Ecol. Modell.* 190 (3–4), 367–398.
- Jeppesen, E., Meerhoff, M., Jacobsen, B.A., Hansen, R.S., Sondergaard, M., Jensen, J.P., Lauridsen, T.L., Mazzeo, N., Branco, C.W.C., 2007. Restoration of shallow lakes by nutrient control and biomanipulation—the successful strategy varies with lake size and climate. *Hydrobiologia* 581, 269–285.
- Jeppesen, E., Sondergaard, M., Jensen, J.P., Havens, K.E., Anneville, O., Carvalho, L., Coveney, M.F., Deneke, R., Dokulil, M.T., Foy, B.O.B., Gerdeau, D., Hampton, S.E., Hilt, S., Kangur, K., Kohler, J.A.N., Lammens, E.H.H.R., Lauridsen, T.L., Manca, M., Miracle, M.R., Moss, B., Noges, P., Persson, G., Portielje, R.O.B., Romo, S., Schelske, C.L., Straile, D., Tatrai, I., Willen, E.V.A., Winder, M., 2005. Lake responses to reduced nutrient loading - an analysis of contemporary long-term data from 35 case studies. *Freshw. Biol.* 50 (10), 1747–1771.
- Knuth, M.L., Kelly, J.R., 2011. Denitrification rates in a Lake Superior coastal wetland. *Aquat. Ecosyst. Health Manag.* 14 (4), 414–421.
- Kowalczywska-Madura, K., Goldyn, R., Dera, M., 2015. Spatial and seasonal changes of phosphorus internal loading in two lakes with different trophy. *Ecol. Eng.* 74, 187–195.
- Li, H., Song, C.L., Cao, X.Y., Zhou, Y.Y., 2016. The phosphorus release pathways and their mechanisms driven by organic carbon and nitrogen in sediments of eutrophic shallow lakes. *Sci. Total Environ.* 572, 280–288.
- Liu, E.F., Shen, J., Yuan, H.Z., Zhang, E.L., Du, C.C., 2013. The spatio-temporal variations of sedimentary phosphorus in Taihu Lake and the implications for internal loading change and recent eutrophication. *Hydrobiologia* 711 (1), 87–98.
- Liu, Y., Chen, W., Li, D., Shen, Y., Liu, Y., Song, L., 2006. Analysis of paralytic shellfish toxins in Aphanizomenon DC-1 from Lake Dianchi, China. *Environ. Toxicol.* 21 (3), 289–295.
- Liu, Y., Wang, Y., Sheng, H., Dong, F., Zou, R., Zhao, L., Guo, H., Zhu, X., He, B., 2014. Quantitative evaluation of lake eutrophication responses under alternative water diversion scenarios: a water quality modeling based statistical analysis approach. *Sci. Total Environ.* 468–469, 219–227.
- McCarthy, M.J., Gardner, W.S., Lehmann, M.F., Guindon, A., Bird, D.F., 2016. Benthic nitrogen regeneration, fixation, and denitrification in a temperate, eutrophic lake: effects on the nitrogen budget and cyanobacteria blooms. *Limnol. Oceanogr.* 61 (4), 1406–1423.
- Moon, J.B., Carrick, H.J., 2007. Seasonal variation of phytoplankton nutrient limitation in Lake Erie. *Aquat. Microb. Ecol.* 48 (1), 61–71.
- Nizzoli, D., Carraro, E., Nigro, V., Viaroli, P., 2010. Effect of organic enrichment and thermal regime on denitrification and dissimilatory nitrate reduction to ammonium (DNRA) in hypolimnetic sediments of two lowland lakes. *Water Res.* 44 (9), 2715–2724.
- Nowlin, W.H., Everts, J.L., Vanni, M.J., 2005. Release rates and potential fates of nitrogen and phosphorus from sediments in a eutrophic reservoir. *Freshw. Biol.* 50 (2), 301–322.
- Paerl, H.W., Xu, H., McCarthy, M.J., Zhu, G., Qin, B., Li, Y., Gardner, W.S., 2011. Controlling harmful cyanobacterial blooms in a hyper-eutrophic lake (Lake Taihu, China): the need for a dual nutrient (N & P) management strategy. *Water Res.* 45 (5), 1973–1983.
- Poister, D., Armstrong, D.E., 2003. Seasonal sedimentation trends in a mesotrophic lake: influence of diatoms and implications for phosphorus dynamics. *Biogeochemistry* 65 (1), 1–13.
- Qin, B., 2009. Lake eutrophication: control countermeasures and recycling exploitation. *Ecol. Eng.* 35 (11), 1569–1573.
- Qin, B., Zhu, G., 2006. The nutrient forms, cycling and exchange flux in the sediment and overlying water system in lakes from the middle and lower reaches of Yangtze River. *Earth Sci.* 49, 1–13.
- Qin, B.Q., Zhu, G.W., Luo, L.C., Gao, G., Gu, B.H., 2006. Estimation of internal nutrient release in large shallow Lake Taihu, China. *Earth Sci.* 49, 38–50.
- Ramin, M., Perhar, G., Shimoda, Y., Arhonditsis, G.B., 2012. Examination of the effects of nutrient regeneration mechanisms on plankton dynamics using aquatic biogeochemical modeling. *Ecol. Modell.* 240, 139–155.
- Risgaard-Petersen, N., Nielsen, L.P., Rysgaard, S., Dalsgaard, T., Meyer, R.L., 2003. Application of the isotope pairing technique in sediments where anammox and denitrification coexist. *Limnol. Oceanogr. Methods* 1, 63–73.
- Roy, E.D., Nguyen, N.T., Bargu, S., White, J.R., 2012. Internal loading of phosphorus from sediments of Lake Pontchartrain (Louisiana, USA) with implications for eutrophication. *Hydrobiologia* 684 (1), 69–82.
- Schindler, D.W., Hecky, R., Findlay, D., Stainton, M., Parker, B., Paterson, M., Beaty, K., Lyng, M., Kasian, S., 2008. Eutrophication of lakes cannot be controlled by reducing nitrogen input: results of a 37-year whole-ecosystem experiment. *Proc. Natl. Acad. Sci. U. S. A.* 105 (32), 11254–11258.
- Seitzinger, S., 2008. Out of reach. *Nature* 452, 162–163.
- Sondergaard, M., Bjerring, R., Jeppesen, E., 2013. Persistent internal phosphorus loading during summer in shallow eutrophic lakes. *Hydrobiologia* 710 (1), 95–107.
- Sondergaard, M., Kristensen, P., Jeppesen, E., 1992. Phosphorus release from re-suspended sediment in the shallow and WIND-EXPOSED Lake Arreso, Denmark. *Hydrobiologia* 228 (1), 91–99.
- Spears, B.M., Carvalho, L., Perkins, R., Kirika, A., Paterson, D.M., 2012. Long-term variation and regulation of internal phosphorus loading in Loch Leven. *Hydrobiologia* 681 (1), 23–33.
- Suding, K.N., Gross, K.L., Houseman, G.R., 2004. Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.* 19 (1), 46–53.
- Wang, H., Appan, A., Gulliver, J.S., 2003a. Modeling of phosphorus dynamics in aquatic sediments: I—model development. *Water Res.* 37 (16), 3928–3938.
- Wang, H., Appan, A., Gulliver, J.S., 2003b. Modeling of phosphorus dynamics in aquatic sediments: II—examination of model performance. *Water Res.* 37 (16), 3939–3953.
- Wang, Z., Zou, R., Zhu, X., He, B., Yuan, G., Zhao, L., Liu, Y., 2014. Predicting lake water quality responses to load reduction: a three-dimensional modeling approach for total maximum daily load. *Int. J. Environ. Sci. Technol.* 11 (2), 423–436.
- Wetzel, R.G., 2001. *Limnology: Lake and River Ecosystems*. Academic Press, San Diego.
- Wu, Y.H., Wen, Y.J., Zhou, J.X., Wu, Y.Y., 2014. Phosphorus release from lake sediments: effects of pH, temperature and dissolved oxygen. *KSCE J. Civ. Eng.* 18 (1), 323–329.
- Wu, Z., Liu, Y., Liang, Z., Wu, S., Guo, H., 2017. Internal cycling, not external loading, decides the nutrient limitation in eutrophic lake: a dynamic model with temporal Bayesian hierarchical inference. *Water Res.* 116, 231–240.
- Yang, L., Lei, K., Yan, W., Li, Y., 2013. Internal loads of nutrients in Lake Chaohu of China: implications for lake eutrophication. *Int. J. Environ. Res.* 7 (4), 1021–1028.
- Yi, X., Zou, R., Guo, H.C., 2016. Global sensitivity analysis of a three-dimensional nutrients-algae dynamic model for a large shallow lake. *Ecol. Modell.* 327, 74–84.
- Zhou, Y., Zhang, Y., Jeppesen, E., Murphy, K.R., Shi, K., Liu, M., Liu, X., Zhu, G., 2016. Inflow rate-driven changes in the composition and dynamics of chromophoric dissolved organic matter in a large drinking water lake. *Water Res.* 100, 211–221.