



Internal cycling, not external loading, decides the nutrient limitation in eutrophic lake: A dynamic model with temporal Bayesian hierarchical inference



Zhen Wu^a, Yong Liu^{a,b,*}, Zhongyao Liang^a, Sifeng Wu^a, Huaicheng Guo^a

^a College of Environmental Science and Engineering, Key Laboratory of Water and Sediment Sciences (MOE), Peking University, Beijing 100871, China

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

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ABSTRACT

Lake eutrophication is associated with excessive anthropogenic nutrients (mainly nitrogen (N) and phosphorus (P)) and unobserved internal nutrient cycling. Despite the advances in understanding the role of external loadings, the contribution of internal nutrient cycling is still an open question. A dynamic mass-balance model was developed to simulate and measure the contributions of internal cycling and external loading. It was based on the temporal Bayesian Hierarchical Framework (BHM), where we explored the seasonal patterns in the dynamics of nutrient cycling processes and the limitation of N and P on phytoplankton growth in hyper-eutrophic Lake Dianchi, China. The dynamic patterns of the five state variables (Chl_a, TP, ammonia, nitrate and organic N) were simulated based on the model. Five parameters (algae growth rate, sediment exchange rate of N and P, nitrification rate and denitrification rate) were estimated based on BHM. The model provided a good fit to observations. Our model results highlighted the role of internal cycling of N and P in Lake Dianchi. The internal cycling processes contributed more than external loading to the N and P changes in the water column. Further insights into the nutrient limitation analysis indicated that the sediment exchange of P determined the P limitation. Allowing for the contribution of denitrification to N removal, N was the more limiting nutrient in most of the time, however, P was the more important nutrient for eutrophication management. For Lake Dianchi, it would not be possible to recover solely by reducing the external watershed nutrient load; the mechanisms of internal cycling should also be considered as an approach to inhibit the release of sediments and to enhance denitrification.

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1. Introduction

Lake eutrophication has been recognized widely as a global challenge (Conley et al., 2009; Edmondson, 1970; Xu et al., 2010), and it results in excessive phytoplankton growth, low dissolved oxygen, degeneration of submerged macrophytes, and increased frequency of algae blooms (Wetzel, 2001). The increasing anthropogenic discharge of nutrients has long been viewed as the primary cause of eutrophication. Previous studies have proven that the supply of nitrogen (N) or phosphorus (P) limits phytoplankton growth and thus, this supply of nutrients can be

regarded as the key factor of that changes in biomass in lakes (Seitzinger, 2008). For effective management of lake eutrophication, it is therefore essential to discover (a) which nutrient (N or P) should be priority for control; and (b) whether it will alter, and if yes, what will drive the temporal variations? Since the 1970s, the importance of P limitation has been emphasized in management of eutrophication (Carpenter, 2008a; Schindler, 1974; Schindler et al., 2008b). However, the assumed emphasis on P limitation has been challenged by some studies that show that N limitation or co-limitation frequently influences phytoplankton growth more than P limitation (Elser et al., 2009; Paerl et al., 2016; Scott and McCarthy, 2010; Wang and Wang, 2009). In addition, the role that N and P limitation plays in controlling eutrophication differs dynamically throughout the year and among years (Xu et al., 2015; Paerl et al., 2014).

Whether N or P limitation is dominant in the system is

* Corresponding author. College of Environmental Science and Engineering, Key Laboratory of Water and Sediment Sciences (MOE), Peking University, Beijing 100871, China.

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

dependent on modification of lake nutrient dynamics (i.e., N and P cycling) and hydrological conditions (McLauchlan et al., 2013; vanderMolen and Boers, 1996). Considering the effect of N and P limitation on phytoplankton growth, great effort has been made to reduce external N and P (especially P) sources. Some lakes responded rapidly to such reductions, but a delay often occurred in other lakes (Carpenter, 2005; Jeppesen et al., 2005). Clearer lakes were more vulnerable to changes in external sources, such as atmospheric deposition and anthropogenic input (Fuentes et al., 2013; Zhou et al., 2016). For example, atmospheric nitrogen deposition can alter the effect of nutrient limitation in unproductive lakes, but it has little effect on eutrophic lakes (Bergstrom et al., 2005). Similar results were found in remote watersheds in the northern hemisphere (Bergstrom and Jansson, 2006; Holtgrieve et al., 2011). For example, in Lake Constance, which is a large nonhumic oligotrophic lake, allochthonous matter dominated the sedimentary flux of organic matter (Fuentes et al., 2013). Compared to clearer lakes, internal loading (i.e. sediment release) has proven to be so persistent that the improvement of water quality was prevented for as long as decades in eutrophic lakes (Sondergaard et al., 2003; Jeppesen et al., 2005). The anoxic condition of the shallow bottom water and the high sediment surface per volume of water accelerated the release of nutrients from sediments (Malecki et al., 2004; Nowlin et al., 2005); therefore, sediment release can equal or exceed external loading, which can be a significant part of the total loading (Sondergaard et al., 2013).

In spite of the important role of internal loading, few measures can be taken to reduce internal loading because the sediment sink and release process is complex. Internal loading affects, and it will also be affected by other internal nutrients cycling process, especially removal processes, such as denitrification. Therefore, internal loading changes greatly throughout the year. For example, in some lakes, the removal by denitrification contributed approximately 30% of the total loss of N in a lake (Bruesewitz et al., 2012; Zhao et al., 2015). The N/P ratio of lake water can be affected by denitrification, and to some extent this can affect the factors that limit phytoplankton growth (Holmroos et al., 2012). The rate of denitrification varies among lakes in different trophic states, but it tends to be higher in eutrophic lakes (Saunders and Kalf, 2001). In view of the difficulty of reducing internal loading and the contribution of the removal by denitrification, some questions must be presented before taking restoration measures: a) What is the role of internal cycling (i.e., sediment release, nitrification and denitrification) in the temporal changes of nutrients in the lake water column and in growth limitation of phytoplankton? b) How should we measure the dynamics quantitatively?

The dynamics of nutrient cycling can be explored both by experiments and models. The real status of the lake can be revealed by observation experiments. The inner processes can be imitated in the laboratory; however, the internal processes are usually monitored poorly and it is impossible to hindcast the coupling effects of N and P dynamic cycling when considering temporal changes across years (Wang et al., 2003). Numerical modeling is developed based on the existing knowledge of biogeochemical processes, and it is tested against observations. The well-calibrated model can capture the temporal variations in the lake and therefore be a valuable tool to explore the dynamics of nutrient cycling, especially the temporal changes across years (Boyd, 2012; Cho et al., 2016; Menshutkin et al., 2014; Shen et al., 2015). Parameter estimation and uncertainty analysis can be challenging for modeling, but it can be accomplished by framing the implicit assumptions into equations and using a Bayesian inference (Arhonditsis et al., 2008; Clark, 2005; Qian et al., 2010; Wike, 2003). For example, Arhonditsis et al. (2008) outlined how they attained realistic predictive links between management actions

and ecosystem response through a probabilistic framework using Markov chain Monte Carlo (MCMC) simulations. Li et al. (2015) used a simple dynamic nutrient-driven model to simulate the internal loadings with Bayesian estimated parameters in Lake Yilong. These previous studies proved that Bayesian approach could solve this problem to some degree by providing an effective method that incorporates existing information with current observations to obtain future ecosystem responses (Fiechter et al., 2013; Liu and Scavia, 2010; Liu et al., 2011; Scavia and Liu, 2009; Zhang and Arhonditsis, 2009). However, many intertwined spatiotemporal environmental processes are included in a relatively long time series. For example, seasonal variations of temperature, precipitation, solar irradiation and other external disturbances will lead to changes in nutrient supply, phytoplankton growth, and internal cycling processes (Arhonditsis et al., 2008; Clark, 2005; Wike, 2003). It is usually difficult to simulate lake biogeochemical processes with spatial and temporal heterogeneity based on a simple model because of the absence of hydrodynamic equations and complex seasonal patterns (Clark, 2005; Qian et al., 2010; Qian and Shen, 2007). Bayesian Hierarchical Model (BHM) has been used widely in process-based models, like aquatic biogeochemical models, to distinguish and identify the spatial complexity (Zhang and Arhonditsis, 2009). It can decompose complex problems into manageable levels, thereby offering a maneuverable means for resolving the complexity of lake ecosystems (Qian et al., 2009; Wike, 2003). The model can thereby be decomposed into relatively independent sub-models on the basis of different hydrodynamic conditions or seasonal patterns; while more can be conducted for the usage of Bayesian hierarchical framework in the temporal way. Since internal cycling processes cannot be observed easily or measured in eutrophic lakes with spatial and temporal heterogeneity (Wang et al., 2003); it is necessary to simulate the internal cycling processes in a dynamic way using Bayesian hierarchical framework.

Lake Dianchi is one of the three most eutrophic lakes in China. It is characterized by extremely high concentrations of N and P in the water column and annual algae blooms. Previous studies have shown that, after decades of intensive restoration efforts, lake water quality has improved, but not so manifest as expected (Gao et al., 2014; Wang et al., 2014). Three issues arose during the attempts at lake restoration: (a) Besides external loading of the watershed, how much do the internal cycling processes contribute to eutrophication? (b) Which element, N or P, should be prioritized for control? (c) Will internal cycling in the lake result in an alternation between which nutrients are limiting? To answer the above questions, a mass-balance model was developed to simulate monthly changes across years. The Bayesian hierarchical framework was introduced to explore the seasonal patterns in the release of N and P in sediments, the dynamics of nutrient cycling processes, and the limitation of N and P on phytoplankton growth.

2. Materials and methodology

2.1. Study area and data sources

Lake Dianchi is the largest plateau lake in Yunnan Province, southwestern China (Fig. S1 in Supporting Materials). It is in the south of Kunming City with a surface area of 309 km², a volume of 1.56 billion cubic meters, a mean depth of 4.4 m, and a maximum depth of 10.2 m. The lake does not freeze and it is mixed completely because of the subtropical monsoon climate and wind perturbation. Lake Dianchi is the only water body to receive the pollutants of the entire watershed of millions of people. Rapid urbanization has impacted the health of the lake. Historical monitoring has shown

that the water quality of the lake has deteriorated more and more rapidly since late 1970s and became worse in the 1990s. Even though the nutrients have been under control since 2010s, eutrophication is still the main problem (Fig. S2 in Supporting Materials). Lake Dianchi is a typical semi-enclosure lake with high inflow, low outflow, and long residence time, which highlights the importance of internal cycling for changes in the water column nutrients (Gao et al., 2014). To facilitate effective decision-making on eutrophication control and ecological restoration in Lake Dianchi, it is crucial to explore the dynamic processes of nutrient cycling and phytoplankton biomass variations within the lake. Monthly data on water quality of surface layer (total phosphorus (TP), ammonia ($\text{NH}_4^+ \text{-N}$), nitrate ($\text{NO}_3 \text{-N}$), organic nitrogen (ON-N) and chlorophyll *a* (Chla)) were collected from the routine monitoring program conducted by Kunming Environmental Monitoring Center from 1999 to 2015; monthly data on external nutrient loading were from previous studies during 2002–2009 (92 data sets in all) (Sheng and Guo, 2015).

2.2. Model development

A nutrient-driven lake eutrophication model was developed in this study to explore the temporal relationship among phytoplankton biomass and N/P internal cycling. The model relates monthly average phytoplankton biomass to TP, $\text{NH}_4^+ \text{-N}$, $\text{NO}_3 \text{-N}$ and ON-N monthly loading and lake hydrodynamic characteristics. The model describes a completely mixed water body because of the wind perturbation and shallowness of the lake. The model structure was simplified, nevertheless we still considered the basic ecological processes based on phytoplankton and N/P cycling dynamics in the lake. The governing equation of phytoplankton considers phytoplankton production and outflow losses, sinking loss, mortality and loss due to grazing by zooplankton (Arhonditsis et al., 2007; Liu and Scavia, 2010). Nutrient limitation on phytoplankton growth follows the Michaelis-Menten kinetics. According to Liebig's law of the Minimum, previous studies have used the minimum of N limitation factor and P limitation factor on phytoplankton growth (Li et al., 2015). In this study, the multiplication of N and P limitation factor was applied because both N and P will contribute to (in spite of the relatively importance one) and also be affected by the algal growth (Finlay et al., 2013) and there will be synergy of these two main nutrients (Davidson and Howarth, 2007). Considering the simplification of the processes in the model, the multiplication model was much better for the connection between algae and both N and P. Sinking loss and mortality loss were modeled as first-order processes, but loss of phytoplankton due to zooplankton grazing was modeled as a quadratic process similar to the approach used to model zooplankton mortality ($L \cdot B^2$ in Equation. (1)) (Arhonditsis et al., 2008; Scavia and Liu, 2009).

The cycling of N and P were considered in the model. Due to the lack of TDP (total dissolved phosphorus) data, P cycling was simplified as external loading that entered the lake, outflow loss, phytoplankton uptake, and net sink of TP, which incorporated TP release from the sediment and TP sink of the water body. N cycling was relatively complicated, considering three state variables of nitrate, ammonia, and organic nitrogen including. Included in the model were external loading, outflow loss, phytoplankton uptake of nitrate and ammonia, net sink of organic nitrogen, nitrification and denitrification (Fig. 1). Atmosphere deposition and N fixation were not included in the model. In hyper-eutrophic Lake Dianchi, the previous studies showed that atmosphere deposition and N fixation contribute quite little (less than 10%) to the total nutrients loading (Patoine et al., 2006; Wang et al., 2014). The equations are shown below:

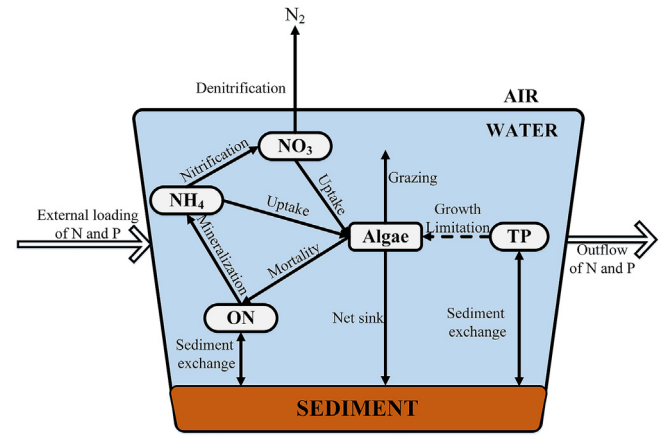


Fig. 1. Schematic description of modeling processes for eutrophication in Lake Dianchi, China.

$$\frac{dB}{dt} = \left(M \cdot f_N \cdot f_P - mo - \frac{vs}{h} \right) \cdot B - L \cdot B^2 - \frac{Q}{V} \cdot B \quad (1)$$

$$B = Chla \cdot ca \quad (2)$$

$$f_N = \frac{NH_4 + NO_3}{NH_4 + NO_3 + K_N} \quad (3)$$

$$f_P = \frac{TP}{TP + K_P} \quad (4)$$

$$\frac{dTP}{dt} = \frac{L_P}{V} + S_P \cdot TP - \frac{Q}{V} \cdot TP \quad (5)$$

$$\frac{dNH_4}{dt} = \frac{L_{NH}}{V} + a \cdot ON - ni \cdot NH_4 - \frac{NH_4}{NH_4 + NO_3} \cdot M \cdot f_N \cdot f_P \cdot r_1 \cdot B - \frac{Q}{V} \cdot NH_4 \quad (6)$$

$$\frac{dNO_3}{dt} = \frac{L_{NO}}{V} + ni \cdot NH_4 - de \cdot NO_3 - \frac{NO_3}{NH_4 + NO_3} \cdot M \cdot f_N \cdot f_P \cdot r_2 \cdot B - \frac{Q}{V} \cdot NO_3 \quad (7)$$

$$\frac{dON}{dt} = \frac{L_{ON}}{V} + p \cdot mo \cdot B + S_N \cdot ON - a \cdot ON - \frac{Q}{V} \cdot ON \quad (8)$$

where, B is the biomass of phytoplankton (gC/m^3); M is the maximum growth rate of phytoplankton (day^{-1}); mo is the mortality of phytoplankton ($0.3, \text{day}^{-1}$) (Hu et al., 2006); vs is the sinking velocity of phytoplankton ($0.3 \text{ m}/\text{day}$) (Zhang et al., 2003); h is the lake mean depth (4.4 m); V is the lake volume ($1.546 \times 10^9 \text{ m}^3$); L is the rate of grazing loss ($0.42, \text{m}^3\text{gC}^{-1} \text{ day}^{-1}$) (Zhang and Arhonditsis, 2009); Q is the out flow of the lake (m^3/day); ca is the C:Chla ratio in algae (3.72) (Riemann et al., 1989); S_P is the sediment exchange rate of total phosphorus (positive means release and negative means sink, day^{-1}); S_N is the sediment exchange rate of organic N (positive means release and negative means sink, day^{-1}); r_1 is the nitrogen to carbon ratio of ammonia in algae (0.053) (Hu et al., 2006); r_2 is the nitrogen to carbon ratio of nitrate in algae (0.127) (Hu et al.,

2006); p is the nitrogen to carbon ratio of organic nitrogen in dead algae (0.114) (Hu et al., 2006); a is the mineralization rate of organic nitrogen ($0.018, \text{day}^{-1}$) (Arhonditsis et al., 2008); de is the denitrification rate (day^{-1}); ni is the nitrification rate (day^{-1}); L_P , L_{NH} , L_{NO} , and L_{ON} represent the external loading entering the lake of total phosphorus, ammonia, nitrate and organic nitrogen respectively (g/day); K_N is the Michealis-Menten constant for N ($\text{g}\cdot\text{m}^{-3}$); K_P is the Michealis-Menten constant for P ($\text{g}\cdot\text{m}^{-3}$). In the study, K_N and K_P were estimated with the following priors: $K_N \sim N(0.2, 0.01)$, $K_P \sim N(0.04, 0.01)$. The numbers in the brackets represent the mean and standard deviation.

2.3. Bayesian hierarchical structure for parameter estimation

Based on the seasonal pattern of heterogeneity in the study area, such as light and water temperature, one year is divided into four parts (Gao et al., 2014; Wang et al., 2014): (a) February, March, and April; (b) May, June, and July; (c) August, September, and October; and (d) November, December, and January (next year). Each quarter of a certain year is regarded as a sub-model. Because we simulated eight years, the BHM had 32 sub-models. Parameters of each sub-model representing the same process shared the same prior distributions. The 32 parameters representing the same process in 32 sub-models consist a time series that can show the seasonal patterns. Five processes were chosen to build the hierarchical framework, algae growth (M), sediment exchange of P (S_P), sediment exchange of N (S_N), denitrification (de), and nitrification (ni).

$$M_i \sim N(m_M, \sigma_M) \quad i = 1, 2, 3, 4, 5, 6, 7, \dots, 31, 32 \quad (9)$$

$$de_i \sim N(m_{de}, \sigma_{de}) \quad i = 1, 2, 3, 4, 5, 6, 7, \dots, 31, 32 \quad (10)$$

$$ni_i \sim N(m_{ni}, \sigma_{ni}) \quad i = 1, 2, 3, 4, 5, 6, 7, \dots, 31, 32 \quad (11)$$

$$S_{P_i} \sim N(m_{SP}, \sigma_{SP}) \quad i = 1, 2, 3, 4, 5, 6, 7, \dots, 31, 32 \quad (12)$$

$$S_{N_i} \sim N(m_{SN}, \sigma_{SN}) \quad i = 1, 2, 3, 4, 5, 6, 7, \dots, 31, 32 \quad (13)$$

In this structure, m_M , m_{de} , m_{ni} , m_{SP} and m_{SN} were global parameters for M , de , ni , S_P and S_N respectively, and M_i , de_i , ni_i , S_{P_i} , and S_{N_i} were the equivalent parameters for each sub-model. M_i followed a normal distribution with m_M as the average and σ_M as the standard deviation (SD), de_i followed a normal distribution with m_{de} as the average and σ_{de} as the SD, ni_i followed a normal distribution with m_{ni} as the average and σ_{ni} as the SD, S_{P_i} followed a normal distribution with m_{SP} as the average and σ_{SP} as the SD, and S_{N_i} followed a normal distribution with m_{SN} as the average and σ_{SN} as the SD. The five global parameters in the hierarchical structure M , de , ni , S_N , and S_P were estimated with priors as following: $m_M \sim N(1, 0.5)$ (Zhang and Arhonditsis, 2009), $m_{de} \sim N(0.1, 0.1)$ (Pardo et al., 2012), $m_{ni} \sim N(0.1, 0.1)$ (Spiteri et al., 2008), $m_{SN} \sim N(0, 0.01)$, and $m_{SP} \sim N(0, 0.01)$, and their hierarchical parameters followed the structure with the SD as follows: $\sigma_M \sim N(1, 1)$, $\sigma_{de} \sim N(0.1, 0.1)$, $\sigma_{ni} \sim N(0.1, 0.1)$, $\sigma_{SP} \sim N(0.1, 0.1)$, and $\sigma_{SN} \sim N(0.1, 0.1)$.

In this study, the Markov chain Monte Carlo (MCMC) estimates of the mean and SD parameter values were used to update the model in WinBUGS (version 1.4.3). It was conducted using the WinBUGS differential Interface (WBDiff), an interface that allows for the numerical solution of systems of ordinary differential equations within the WinBUGS software. The MCMC sampling was carried out using three chains, each with 2000 iterations (first 1000 discarded after model convergence).

3. Results and discussions

3.1. Modeling results

The Bayesian inference was used for state variables and parameter estimation. The MCMC sequence of the model converged rapidly (≈ 1000 iterations) and the statistics reported in this study were based on the last 1000 draws by keeping every 2nd iteration (thin = 2). The results of estimates of constant parameters and the hierarchical parameters, which changed often with the time series, suggested that the seasonal patterns had a strong impact on the ecological processes of Lake Dianchi (Table 1 and Table S1 (Supporting Materials)). The model produced an acceptable fit to the observed Chl a , TP, NH_4^+ -N, NO_3^- -N, and ON-N (Fig. 2). The observed values were within the 95% confidence intervals. The assessment of the model simulation of the observations was conducted by examining the root means squared error (RMSE). The RMSE values were 0.0239 g/m^3 for Chl a , 0.0389 g/m^3 for TP, 0.1398 g/m^3 for NH_4^+ -N, 0.0810 g/m^3 for NO_3^- -N and 0.3091 g/m^3 for ON-N. The results are acceptable even though some extremely high and low values of Chl a , TP, NH_4^+ -N, NO_3^- -N, and ON-N did not fit well. Despite the hydrological changes and simplicity of N and P cycling, the model should work well for practical management of lake ecosystem.

The rates of phytoplankton and nutrient cycling processes were calculated based on the model equations by the Runge-Kutta method with a time step of one day (Fig. 3). The actual growth rate of phytoplankton ($M \cdot f_N \cdot f_P$) was $0.111 \text{ g C/m}^3/\text{day}$ with a range of $0.0350\text{--}0.220 \text{ g C/m}^3/\text{day}$. The sediment exchange of P and N ($S_P \cdot \text{TP}$ and $S_N \cdot \text{ON}$) performed oppositely on annual average. The sediment exchange of P acted as a net sink, $-0.00152 \text{ g P/m}^3/\text{day}$ on average with a range of -0.0222 to $0.0171 \text{ g P/m}^3/\text{day}$, and the sediment exchange of N acted as a net release, $0.0175 \text{ gN/m}^3/\text{day}$ on average with a range of -0.274 to $0.282 \text{ gN/m}^3/\text{day}$. Considering the complexity of N cycling in Lake Dianchi, N circulates by microorganism metabolism without phytoplankton (Gao et al., 2014; Wang et al., 2014), and N can be removed from the lake in the form of N_2 . Unlike the process of N uptake, denitrification changes NO_3^- to N_2 , which means that N is removed completely. Denitrification is an indispensable pathway for N removal. The denitrification rate in Lake Dianchi was $98.2 \text{ mg N/m}^2/\text{day}$ with a range of $66.9\text{--}189 \text{ mg N/m}^2/\text{day}$ (Denitrification was supposed to occur mainly in the water column above sediment within 1 m (Nowlin et al., 2005)). The process of denitrification comprised 27% of the total loss of N in Lake Dianchi, which was second to sedimentation on an annual basis. Compared with $14\text{--}104 \text{ mg N/m}^2/\text{day}$ in the Lake Superior Estuary and $92 \text{ mg N/m}^2/\text{day}$ in river networks of Lake Taihu, which accounted for 43% of the total loading, denitrification in Lake Dianchi appeared to be higher than in these two systems because of the benthic hypoxia and hyper-eutrophication (Bellinger et al., 2014; Zhao et al., 2015).

3.2. Temporal dynamics of N and P limitation

Some interesting patterns in the dynamics of nutrient (N/P) limitation and N:P ratio were detected in the model results. The nutrient limitation patterns were monitored by f_N (N limitation) and f_P (P limitation), based on the Michaelis-Menten kinetics and the monthly growth of phytoplankton (Fig. 4). The TN (total nitrogen):TP ratios in the lake were usually much higher than Redfield ratios (7:1 by weight) (Schindler et al., 2008a). The TN:TP ratio in Lake Dianchi was 15.7, with a range of 8.37–37.8. However, the DIN (NH_4^+ and NO_3^-):TP ratio in Lake Dianchi varied from 1.75 to 6.08, indicating that the bioavailable N accounted for less than 20% of TN. It seems that N was the more limiting nutrient (Guildford and

Table 1
Calibrated parameter values.

Parameter	Mean	SD	MC error	2.5%	Median	97.5%	References
K_N	0.194	0.0115	0.000632	0.173	0.194	0.219	0.2 (Hu et al., 2006)
K_P	0.0525	0.00639	0.000448	0.0414	0.0519	0.0672	Calibration

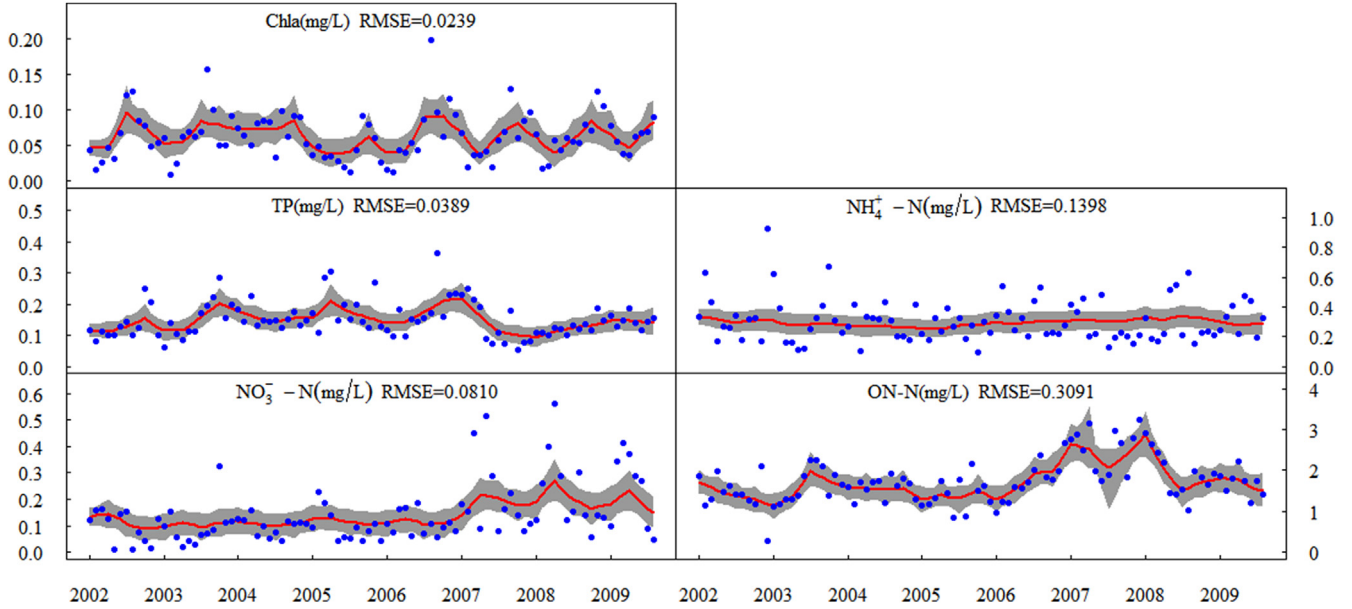


Fig. 2. Modeling fitting results. The five state variables (Chla, TP, $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, and ON-N) are shown in the figure (Jan 2002–Aug 2009). The blue dots represent the observed values, the red lines represent the simulated means, and the shadow represents the 95% confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

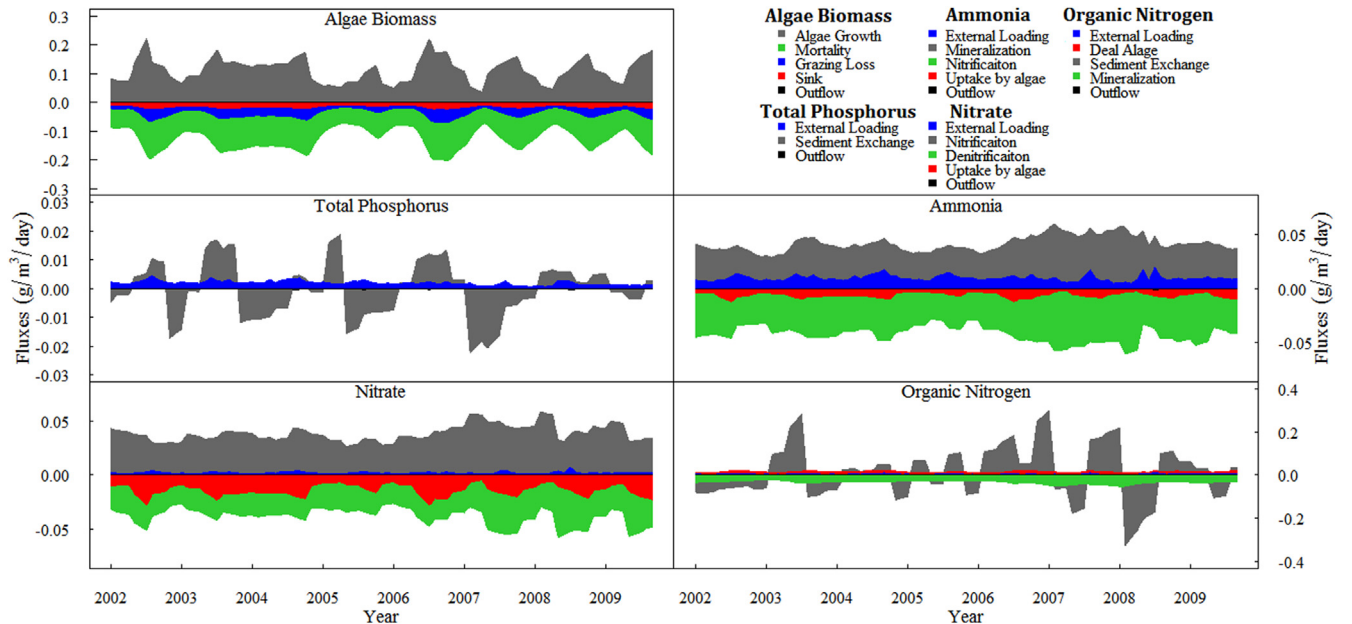


Fig. 3. Rates of phytoplankton and nutrient cycling processes ($\text{g}/\text{m}^3/\text{day}$). Cumulative area plots are used to show the relative contributions of each cycling process of phytoplankton and nutrients. Internal cycling processes, for example, sediment exchange, nitrification, denitrification, and mineralization, contribute much more than external loading.

Hecky, 2000; Verburg et al., 2013). But it was still in suspense for the missing data of TDP. The f_N values were a bit lower on average than that of f_P which means that N was the stronger limiting nutrient on phytoplankton growth. The DIN in Lake Dianchi

remained stable throughout the simulation period, but TP fluctuated seasonally. The f_N and f_P followed the same trend as DIN and TP. A negative correlation was detected between f_P and DIN:TP (Fig. S3, Supporting Materials), which indicated that TP was a more

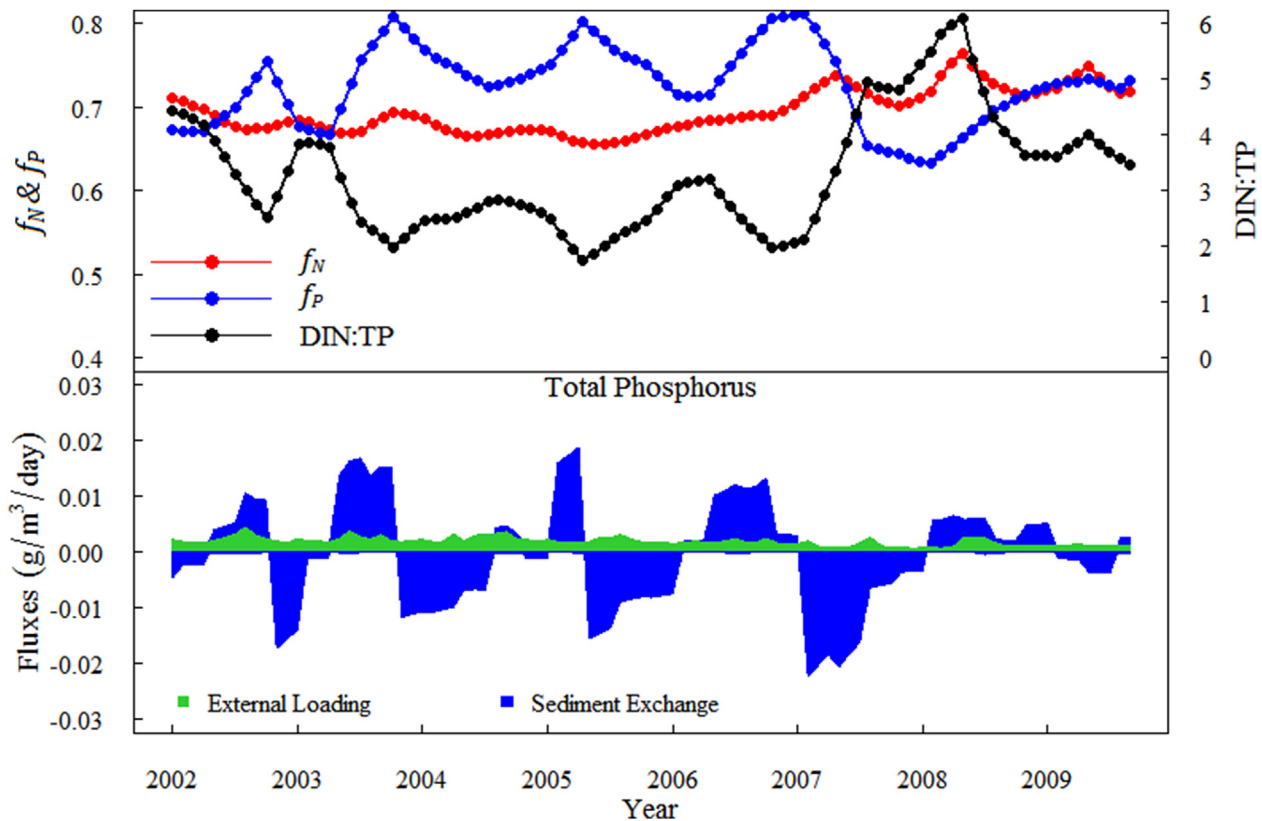


Fig. 4. The variation of nutrient limitation patterns. The nutrient limitation patterns (f_N and f_P) follow the axis on the left, and the ratios of DIN to TP follow the axis on the right. f_N and f_P were calculated based on Michaelis-Menten kinetics. The fluxes of TP are shown below. The sediment exchange of P made a great contribution to the peaks in TP concentration. And the sediment exchange of P dominated the trend of f_P .

important factor in the management of eutrophication. However, doubts still exist because of the lack of TDP data, which phytoplankton take up directly (Bergstrom, 2010; Carpenter, 2008b; Schindler et al., 2008a).

The co-limitation of N and P, which has been documented by previous studies, was also detected during Aug 2008–Aug 2009 (Crowley et al., 2012; Davidson and Howarth, 2007). During periods of P limitation (Oct 2007–Jul 2008), an increase of P accelerated phytoplankton growth and N uptake, which took N and organic matter to lake sediments when phytoplankton sank and died. This process decreased N in the lake and caused the relative insufficient of N compared to N demand of the lake. Thus, the lake transfers into the co-limitation of N and P.

3.3. Contributions of internal cycling to nutrient dynamics

Increasing evidence shows that the internal loading of N and P in shallow lakes is probably one of the main forces that maintains the eutrophication of lakes and prevents improvements in water quality (Jeppesen et al., 2005). Reductions in nutrient loadings were conducted for decades in Lake Dianchi. However, the average annual biomass of phytoplankton and the concentration of N and P did not change greatly during the study period. To explore the dynamic changes in internal loading may provide practical suggestions for ecological restoration of Lake Dianchi. In this study, the fluxes of sediment exchange were calculated separately as sediment release (internal loading, when $S_{N(P)}$ was positive) and sedimentation (when $S_{N(P)}$ was negative). The contributions of internal loading ($S_P \cdot TP$ and $S_N \cdot ON$) were 77% (TP) and 72% (TN), which dominated the total loading throughout the study period

(Figs. 3 and 5). The sharp fluctuations in sediment exchanges that we documented are counterintuitive, because the transition and migration of N and P in sediments are usually slow and constant, according to classical theory. But recent studies have shown that the rate of sediment release could vary monthly or seasonally (Spears et al., 2012; Yang et al., 2013). The dynamic sediment exchange patterns in Lake Dianchi are similar to other studies. Sondergaard et al. (2013) used 21 years of monthly water quality data from six shallow lakes to conclude that internal loading could be equal or higher to the external loading in summer, and that internal loading could delay lake recovery for approximately a decade in the lake with a reduction in external loading. Furthermore, benthic P flux contributed 30–44% of the annual P loading in Lake Pontchartrain, but in Lake Chaohu, benthic N flux contributed only 10% of the annual N loading (Roy et al., 2012; Yang et al., 2013).

Although sediment exchange of P acted as a net sink on annual basis in Lake Dianchi, the sediment release of P should not be ignored because its amplitude was large. The sediment release of P made a great contribution to the peaks in TP concentration. The sediment exchange of P dominated the trend of f_P . The limiting nutrient changed from P to N when P was released from the sediment, but when P settled to the sediment, the limiting nutrient changed to P (Fig. 4). In contrast to the process of P, the sediment exchange of N acted as a net release during the simulation period, which indicated that N was significantly insufficient in the water column. Mineralization was the second removal process of ON-N, which was also the most important source of NH_4^+-N , and this process accounted for 77% of the total input of NH_4^+-N . The fluxes of nitrification and denitrification also exceeded the inflow and

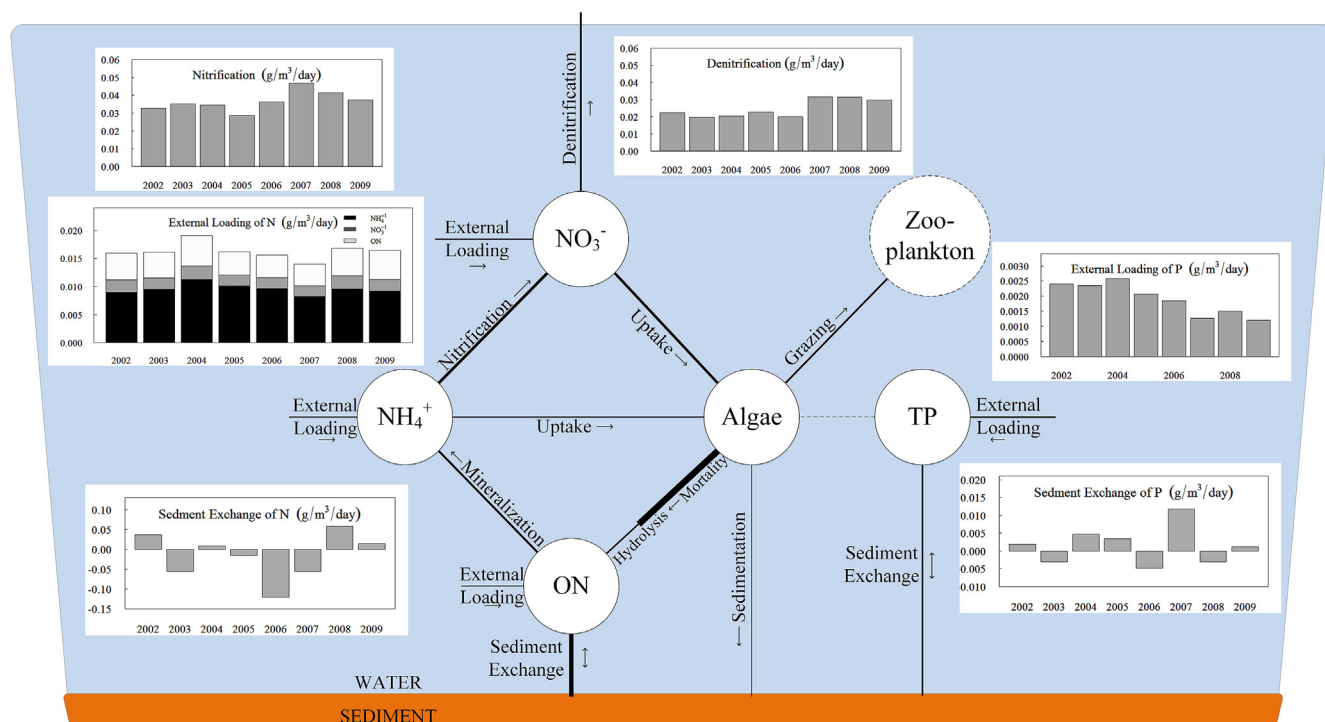


Fig. 5. Annual internal nitrogen and phosphorus cycling processes. External loading and internal cycling processes are shown in the figure on an annual basis. The width of each black line between state variables represent the amount of average annual fluxes of each process. The black block represents the external loading of ammonia, the grey block represents the external loading of nitrate, the white block represents the external loading of organic nitrogen.

outflow of NO_3^- -N, contributing 95% of the total input and 63% of the total output of NO_3^- -N. NH_4^+ -N acted as an intermediate component in N cycling and a large amount of N was finally removed from the lake by denitrification. A strong seasonal pattern of NO_3^- -N was detected from 2007 to 2009, with peaks in spring and valleys in winter. The deciding processes in this seasonal pattern were nitrification and denitrification. The fluxes of nitrification and denitrification showed an opposite trend during 2007–2009, where denitrification reached peaks in summer and nitrification reached peaks in winter. This seasonal pattern could be explained by algae blooms and benthic hypoxia ($\text{DO} \leq 2 \text{ mg/L}$). Lake Dianchi is a shallow lake with a mean depth of 4.4 m, where it is thought that hypoxia could not occur because of its shallowness. However, our previous study showed that 6.82% of Lake Dianchi volume was hypoxic (Liu et al., 2014). Hypoxia, which often starts in summer, can facilitate the process of denitrification and inhibit the process of nitrification (Bellinger et al., 2014; Small et al., 2013, 2014).

3.4. Analysis of scenarios for nutrient load reduction

Analysis of scenarios was conducted in a different way. A long time series was used as the input of the model including Q , L_P , L_{NH_4} , L_{NO_3} and L_{ON} . The input of the baseline was the observed data and parameters from Sep 2007–Aug 2009 (24 months in all). The time series consisted of 144 data sets of 12 years by month in which the 1st and 2nd years were the baseline, the 3rd and 4th years were a 20% reduction in N and P external loading based on the baseline, the 5th and 6th years were a 50% reduction in N and P external loading, and the 7th to 12th years were a 70% reduction in N and P external loading. The TP reduction scenario and the TN reduction scenario were also carried out to analyze efficiency of reducing P or N loading. A 12-year baseline scenario was conducted to show the model result under baseline.

The results showed that reducing the N and P loadings simultaneously can achieve better results than reducing N or P loading separately (Fig. 6). Reducing N loading was more efficient than reducing P loading. The result of the baseline indicated that TP accumulated due to the internal loading of P during the two years (Sep 2007–Aug 2009), but N was being removed due to the high denitrification rate and low internal loading. Because of the low internal loading of N and the high denitrification rate, phytoplankton biomass was reduced significantly even under the baseline scenario (Fig. 6).

In addition, when P loading was reduced alone, the concentration of NO_3^- increased rather than decrease (Fig. 6), which was the same result shown by Finlay et al. (2013). Reductions of P loading may cause negative impacts to N cycling in the lake (Bernhardt, 2013). The rising NO_3^- concentration could also lead to far-reaching impacts of climate change because nitrate is a main source of greenhouse-warming and nitrous oxide in the lake is a gas that destroys ozone (Beaulieu et al., 2014). Although we must point out that the scenario analysis was based on the existing conditions of internal cycling processes, more can be done to refine the scenario for future predictions.

4. Conclusions

A dynamic mass-balance model based on the Bayesian hierarchical framework was proposed in this study. It was used to simulate the temporal changes of Chl_a, TP, NH_4^+ -N, NO_3^- -N, and ON-N profiles in eutrophic Lake Dianchi. The dynamic patterns of the five state variables and internal cycling processes were explored. The model results and analysis highlighted the role of internal cycling of N and P in Lake Dianchi.

(a) The actual growth rate of phytoplankton was $0.111 \pm 0.041 \text{ g C/m}^3/\text{day}$. The sediment exchange of P and N

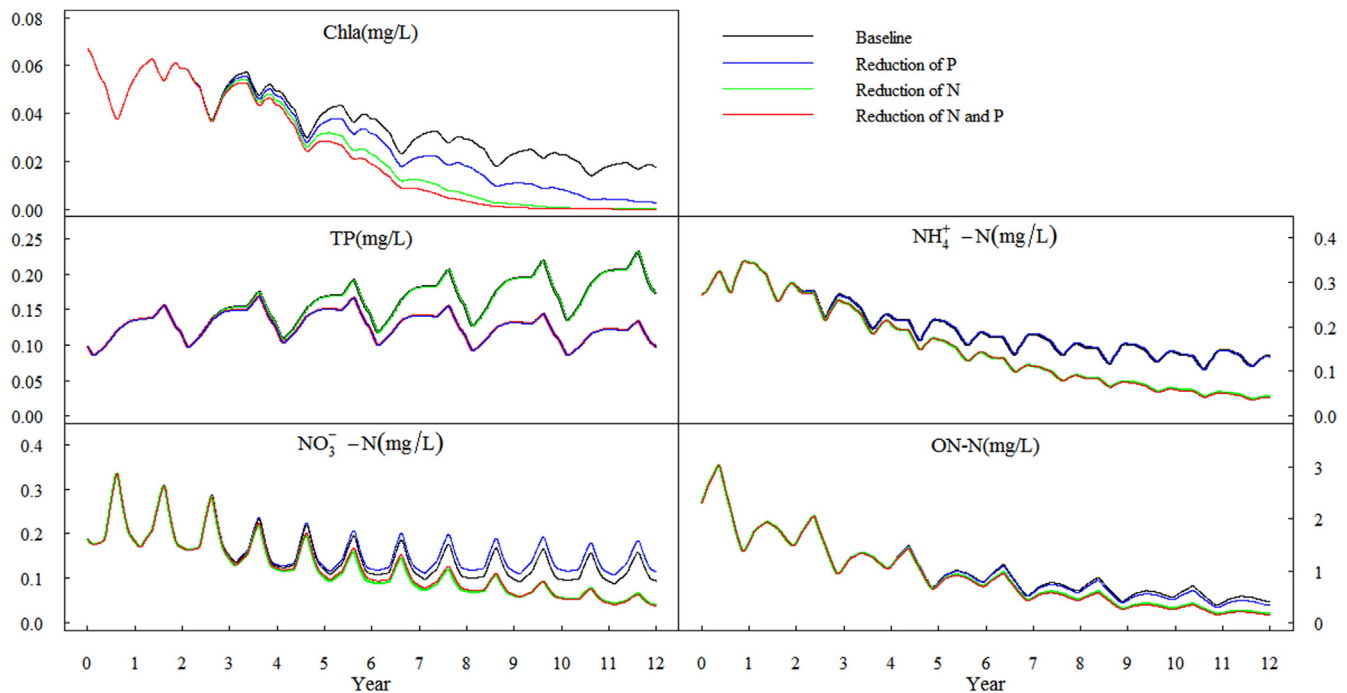


Fig. 6. Results of nutrient load reduction scenarios. Four scenarios are shown in the figure, that are baseline scenario (black), reduction of P alone (blue), reduction of N alone (green), and reduction of N and P simultaneously (red). The time series consisted of 144 data sets of 12 years by month in which the 1st and 2nd years were the baseline, the 3rd and 4th years were a 20% reduction in external loading based on the baseline, the 5th and 6th years were a 50% reduction in external loading, and the 7th to 12th years were a 70% reduction in external loading. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

performed oppositely on average. The sediment exchange of P acted as a net sink, -0.00152 ± 0.00851 g P/m³/day, but the sediment exchange of N acted as a net release, 0.0175 ± 0.102 gN/m³/day. The denitrification rate in Lake Dianchi was 98.2 ± 25.4 mg N/m²/day.

- (b) The contribution of internal loadings were 77% (TP) and 72% (TN), which dominated the total loading throughout the year. Nitrification and denitrification also exceeded the inflow and outflow of NO₃⁻-N, and they contributed 95% of the total input and 63% of the total output respectively.
- (c) The TN:TP ratio in Lake Dianchi was 15.7 ± 6.1 . However, the DIN:TP ratio in Lake Dianchi varied from 1.75 to 6.08, which indicated that bioavailable N accounted for less than 20% of TN. Further insights into the nutrient limitation analysis indicated that N was the more limiting nutrient most of the time, however, P was the more active nutrient for eutrophication management.
- (d) The result of scenario analysis found that when P loading was reduced alone, the concentration of NO₃⁻ increased rather than decreased providing evidence of N and P coupling effect that was reported in Finlay et al. (2013).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.watres.2017.03.039>.

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