



What maintains seasonal nitrogen limitation in hyper-eutrophic Lake Dianchi? Insights from stoichiometric three-dimensional numerical modeling

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Abstract

One debate about lake restoration is whether there is overemphasis of a “Phosphorus (P)-only” paradigm, while overlooking the limiting effect of nitrogen (N). In particular, the roles of internal nutrient cycling which could act as drivers of algal blooms are not yet well assessed. However, it is hardly possible to identify the complex mechanisms of nutrient limitation patterns in lakes only by in-situ experiments or monitored data. Numerical modeling can serve as a complementary approach by providing quantitative internal variations with high spatial and temporal resolutions. A three-dimensional model-based N:P stoichiometric approach was developed to explore the storage pools and fluxes that affect the limiting nutrient in hyper-eutrophic Lake Dianchi, the most eutrophic large lake in China with seasonal N limitation. The results highlighted the role of benthic P fluxes, which fluctuated considerably within a year and could supply enough P for algae, contributing over 50% of P input and leading to relative N deficiency during algal bloom. Further insights into N cycling indicated that N deficiency could be attributed to low N fixation and extremely high N losses from denitrification (~50% of total loss). Considering the continuous sediment P release and N losses that promote N deficiency, controlling both N and P loadings will benefit lake restoration.

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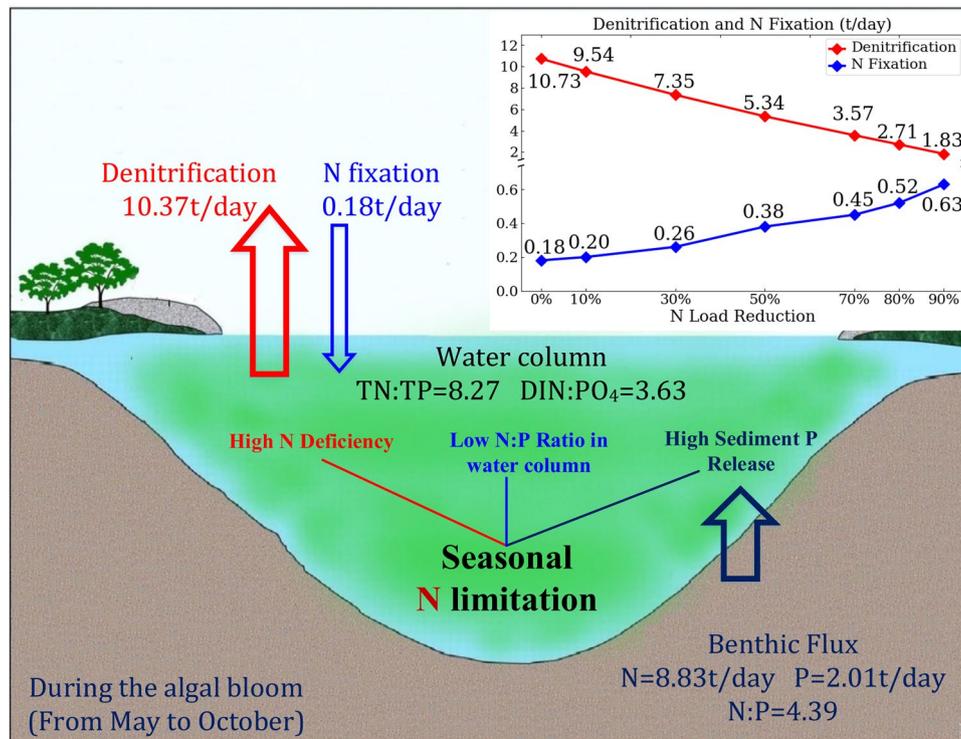
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Graphic abstract



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Introduction

Eutrophication is a long-standing global threat to natural lakes (Conley et al. 2009; Davidson and Howarth 2007; Seitzinger 2008), which is caused by excessive anthropogenic nutrient inputs and can also be amplified by internal nutrient cycling (also known as internal nutrient loading) (Kim et al. 2013; Malecki et al. 2004; Sondergaard et al. 2013). For decades, the problem of eutrophication was addressed by reducing external phosphorus (P) loading because of the presumption that P is universally the primary limitation on algae growth in lakes (Carpenter 2008; Schindler 1974; Schindler and Hecky 2009; Smith and Schindler 2009). The P reduction has indeed been successful in many lakes (Schindler et al. 2016). However, there are still some lakes do not recover after P loading reduction, like Lake Taihu, Lake Rotorua, and Lake Erie because of high benthic P flux or seasonal N deficiency due to the lack of N fixation (Ding et al. 2018; Paerl et al. 2016; Smith et al. 2016).

Attempts to explore the nutrient limitation mechanisms often focus on lake N:P stoichiometry (Bergstrom 2010; Cha et al. 2016; Grantz et al. 2014). Redfield (1958) first found that the mass ratio of N:P in oceanic phytoplankton was 7.2:1. More recently, studies of N:P ratios of different

nutrient pools and retention rates are becoming valuable tools in understanding nutrient effects on phytoplankton (Grantz et al. 2014; Vanni et al. 2011; Verburg et al. 2013). For example, stoichiometric imbalance was detected in N and P retention and recycling rates leading to an inference of N deficiency in eutrophic reservoirs due to enhanced denitrification and inefficient N fixation (Grantz et al. 2014). The input and removal processes of N and P dominate the N:P stoichiometry in the water column and thus can alter patterns of nutrient limitation of primary producers in lakes. A current debate is focusing on the effects of N fixation and denitrification on changes of nutrient limitation status (Schindler 2012; Schindler et al. 2008; Schindler and Hecky 2009). Some have argued that N fixed by cyanobacteria in lakes can readily ameliorate N deficiency when N loading is reduced, maintaining P limitation in lakes (Schindler et al. 2008). However, analyses by Scott and McCarthy (2010) have indicated that N fixation by cyanobacteria is not sufficient to cover the N loading decrease. Furthermore, removal processes can also influence N:P stoichiometry in the water column, such as disproportionate removal of N by denitrification, which can cause up to ~30% of total N loss in some lakes (Bruesewitz et al. 2012; Nishri and Hamilton 2010; Yao et al. 2016). Overall, it seems that the factors which

impact N:P stoichiometry are still under discussion and therefore, more work on nutrient dynamics and its impact on lake N:P stoichiometry should be done to help resolve the debate on nutrient limitation for remediation of lake eutrophication.

Lake Dianchi, one of the three most eutrophic large lakes in China cannot recover only from P loading reduction. The algal blooms in Lake Dianchi can be observed through the whole year, with the summer maximum chlorophyll-a (Chla) reaching 209 $\mu\text{g/L}$ (annual average of $78.8 \pm 30.9 \mu\text{g/L}$) and cyanobacteria density reaching $2.3 \times 10^9 \text{ cell/L}$ in recent years. Despite decades of restoration efforts, there is still no significant decrease in algal blooms in Lake Dianchi (Chen et al. 2018). It seems that in some shallow hyper-eutrophic lakes, nutrients would not always be the primary limiting factor due to the excessive storage of N and P (Iachetti and Eugenia Llamas 2015; Kolzau et al. 2014; Scheffer 1998). However, severe N deficiency was still detected in Lake Dianchi during the summer seasons according to observed N:P ratios as well as our previous model results (Fig.S1). We found a positive feedback between algae biomass and benthic P flux leading to a higher efficiency of N loading reduction in Lake Dianchi (Zou et al. 2020). However, it is still not clear why Lake Dianchi tends to be N limited from a nutrient stoichiometric perspective. Due to the lack of PO_4 (phosphate) data, which phytoplankton take up directly, DIN:TP ratio (DIN, dissolved inorganic nitrogen; TP, total phosphorus) instead of DIN: PO_4 ratio was calculated according to observations from 2002 to 2015 namely 3.07 ± 0.60 which still indicated that bioavailable N (mainly DIN) was insufficient, not P. While observations could only provide evidence for seasonal N limitation, more efforts are needed to explore nutrient limitation patterns. Therefore, it is a high priority to explore the mechanisms of nutrient limitation for more effective lake restoration.

It is hardly possible to identify the mechanisms that affect nutrient limitation patterns in Lake Dianchi only by in-situ experiments and observed water quality data because of the discrepancy of the spatial and temporal patterns of nutrient cycling processes in the whole lake (Dolman et al. 2016; Saunders and Kalff 2001; Sondergaard et al. 2017). One additional and feasible solution alongside in-situ experiments is numerical modeling, which can provide quantitative water quality and flux variations with high spatial and temporal resolutions (Boyd 2012; Wang et al. 2003a, b). Our previous study developed a well-mixed dynamic nutrient-driven model and found that algae in Lake Dianchi were strongly N limited due to impacts of internal nutrient cycling processes that make more P available (Wu et al. 2017). The advantage of the well-mixed model lies in its ability to explore the temporal variations across years (Wu et al. 2017), while it simplified some detailed internal processes. In this

study, a three-dimensional (3D) numerical model modified from Zou et al. (2020) was applied to Lake Dianchi to simulate the lake nutrient cycling in a more spatially and temporally efficient way. The N:P ratios of different forms of nutrients and stoichiometric imbalance of nutrient cycling processes were studied based on three types of nutrient loading reduction scenarios (P-only, N-only, and NP together) to assess the changing mechanisms of algae nutrient limitation. More specifically, this study addressed the following primary research questions: (a) Will internal nutrient cycling play an important role in the alteration of limiting nutrients? (b) If yes, which process or what processes jointly drive N:P stoichiometry in lakes and (c) Is Lake Dianchi unique for being N-limited or is there any common ground of nutrient cycling dynamics of N-limited eutrophic lakes?

Materials and methods

Study site

Lake Dianchi is the sixth largest lake in China and the largest plateau lake in Yunnan Province, southwestern China (Fig. 1). It has a surface area of 309 km^2 , a mean depth of 4.4 m, a volume of $1.56 \times 10^9 \text{ m}^3$, and a watershed area of 2920 km^2 . Lake Dianchi has been experiencing impacts from rapid urbanization of millions of people and increasing agricultural activities. Historical water quality data showed that nutrient concentrations have increased rapidly since late 1970s and peaked in the 2000s (Fig. S2). After over 10 years of restoration efforts, water quality deterioration has been stabilized, total nitrogen (TN) decreased from 3.01 mg/L (annual average of 2007) to 1.95 mg/L (annual average of 2017) and TP decreased from 0.33 mg/L (annual average of 1999) to 0.13 mg/L (annual average of 2017). However, no sign of significant reduction of Chla has been detected (Fig. S2). Lake Dianchi is a semi-enclosed lake with high inflow, low outflow, high evaporation and long residence time (~ 3.5 years), which highlights the potential importance of internal nutrient cycling in the water column and surface sediment (Gao et al. 2014; Wu et al. 2017; Zhang et al. 2016). Two years of monthly water quality data collected by Kunming Environmental Monitoring Center were used for model calibration and validation. Atmospheric and meteorological data from the National Meteorological Information Center and river flow and velocity data from the Kunming Bureau of Hydrology and Water Resources were collected for the boundary conditions of the model (Please refer to Supporting Materials for the detailed configuration of boundary and initial conditions).

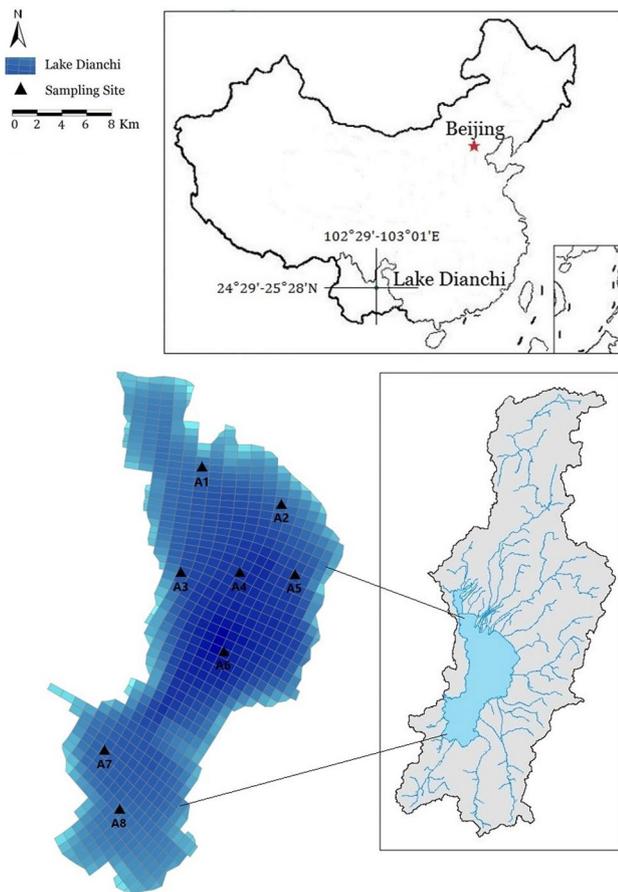


Fig. 1 Watershed of Lake Dianchi including sampling sites and model grid. The grid consisted of 664 curvilinear grid cells per layer. Each cell was represented using six layers, which resulted in 3984 computational cells

Modeling framework

The 3D numerical model for Lake Dianchi was derived from Wang et al. (2014) which was applied in nutrient flux tracking modelling (Zou et al. 2020), water diversion scenarios modeling (Liu et al. 2014), and global sensitivity analysis (Yi et al. 2016). The model was originally developed based on Environmental Fluids Dynamics Code (EFDC) (Hamrick 1992; Park et al. 1995; Zhang et al. 2016; Zou et al. 2006), an integrated 3D model that is capable of simulating hydrodynamics, salinity, temperature, and the cycling of carbon, nitrogen, and phosphorus through inorganic, living, and dissolved and particulate organic forms (refer to Content S1 in Supporting Materials for model details). In the model of Lake Dianchi, a boundary-fit curvilinear grid was used to truly represent the lake topography. The grid was composed

of 664 grid cells per layer and 6 vertical layers in all (Fig. 1). The algae simulated in the model were grouped based on the known responses of specific taxa to environmental conditions, such as water temperature, nutrients, and light. For Lake Dianchi, three algae groups representing functionally important taxa were simulated: green algae, diatoms, and cyanobacteria. However, in Lake Dianchi, only a small part of cyanobacteria can fix N, which is *Aphanizomenon*, but the dominant species, *Microcystis*, cannot fix N (Liu et al. 2006; Yu et al. 2015). In the model, nutrient limitation factor of algae growth was calculated by Michaelis–Menten equation. The limiting factor was decided by taking the minimum value of different nutrient limitation factors and the limiting nutrient was the nutrient with lowest nutrient limitation factor. Algae of all the three groups consume nutrients in the same constant stoichiometric ratio according to the limiting nutrient.

N:P stoichiometry of nutrient pools and fluxes

The fluxes and pools of N and P were calculated in each cell of the model grid, and then integrated according to the computational grid with the same discrete distribution based on the mechanic equations of biogeochemical processes and spatial division (Zou et al. 2020). The outputs of nutrient pools and fluxes were presented with a 12-h time step. The N:P ratios of nutrient storage pools were calculated in four different forms, namely particulate organic form, dissolved organic form, dissolved inorganic form, and the total amount of nutrient. The N:P ratios of fluxes were also calculated in various processes as below.

$$\text{External input : } IN_{N:P}(t) = \frac{F_{WS}(N, t) + F_{AIR}(N, t) + F_{Nfix}(t)}{F_{WS}(P, t) + F_{AIR}(P, t)} \quad (1)$$

$$\text{Benthic flux : } BEN_{N:P}(t) = \frac{F_{Ben}(N, t)}{F_{Ben}(P, t)} \quad (2)$$

$$\text{Outflow : } OUT_{N:P}(t) = \frac{F_O(N, t)}{F_O(P, t)} \quad (3)$$

$$\text{Retention : } RET_{N:P}(t) = \frac{F_{WS}(N, t) + F_{AIR}(N, t) + F_{Nfix}(t) - F_O(N, t)}{F_{WS}(P, t) + F_{AIR}(P, t) - F_O(P, t)} \quad (4)$$

$$\text{Net sedimentation: } NETSED_{N:P}(t) = \frac{F_{Set}(N, t) - F_{Ben}(N, t)}{F_{Set}(P, t) - F_{Ben}(P, t)} \quad (5)$$

$$\text{Potential recycle : } PR_{N:P}(t) = \frac{F_{WS}(N, t) + F_{AIR}(N, t) + F_{Nfix}(t) - F_O(N, t) - F_{Den}(t)}{F_{WS}(P, t) + F_{AIR}(P, t) - F_O(P, t)} \quad (6)$$

where, $F_{WS}(N,t)$ and $F_{WS}(P,t)$ represent the external loadings of N and P at time t ; $F_{Air}(N,t)$ and $F_{Air}(P,t)$ represent the atmospheric deposition of N and P at time t ; $F_{Nfix}(t)$ represents the N fixation by cyanobacteria at time t ; $F_{Ben}(N,t)$ and $F_{Ben}(P,t)$ represent the benthic fluxes of DIN and total phosphate (TPO₄) at time t ; $F_{O}(N,t)$ and $F_{O}(P,t)$ represent the outflow of N and P at time t ; $F_{Set}(N,t)$ and $F_{Set}(P,t)$ represent the sedimentation of particulate N and P at time t ; $F_{Den}(t)$ represents the denitrification in the lake at time t . The N:P stoichiometry was calculated in three different time scales, namely monthly, seasonal and annual scale. The twelve months in one year were divided into two seasons, wet season (May to September) and dry season (January to April and October to December). Over 70% of the annual precipitation in Lake Dianchi Watershed happened in wet season, and it was also the period when algal blooms occurred.

Scenarios definition

Anthropogenic nutrient input is one of the main sources of the nutrients in Lake Dianchi. By applying different nutrient input scenarios to the model which has detailed biogeochemistry, we can explore how nutrient loading reductions will influence nutrient limitation of algae as well as the responses of nutrient dynamics. Three types of scenarios were investigated: (a) reducing N loading only; (b) reducing P loading only; and (c) reducing both N and P loadings. The percentages of loading reduction applied in the scenarios were 10%, 30%, 50%, 70%, 80%, and 90% in each type of scenarios, resulting in 18 scenarios in total (Table S3). The results of all the scenarios were the fifth year of each model run in order to get a steady state. The limiting nutrient for algae

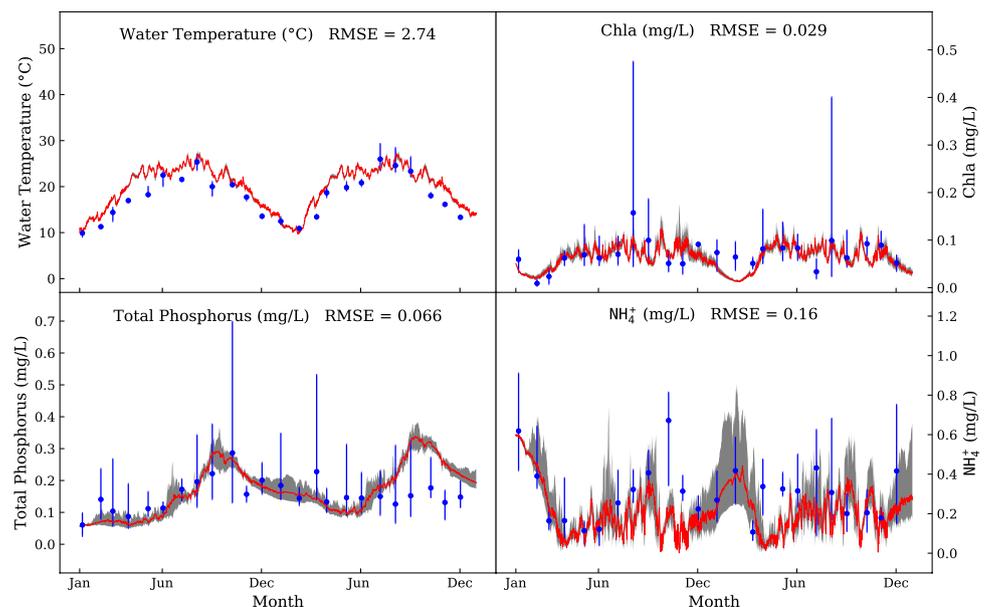
growth can be inferred by comparison of N-only scenarios and P-only scenarios. Furthermore, the responses of internal cycling to external loading reduction especially the response of P cycling to N loading reduction were studied based on the nutrient cycling fluxes and related N:P stoichiometry of various scenarios.

Results

Model calibration

To support the nutrient stoichiometric analysis of Lake Dianchi, the capability of the model to reproduce the in-lake water quality and the processes of nutrient cycling were confirmed through model calibration. In this study, two years of independent data were used to calibrate and validate the hydrodynamic and water quality components of the Lake Dianchi model according to our previous study (Zou et al. 2020). The hydrodynamic model was calibrated with surface water temperature data. The dynamic water quality model was then calibrated using the observed data for Chla, ammonium (NH₄⁺), and TP. The simulated concentrations of these state variables in the surface layer against the observed data at eight sampling sites in Lake Dianchi are shown in Fig. 2. The results showed that the model output fit well with the observed water quality data in Lake Dianchi and thus the model can serve as a computational platform for further analysis on nutrient limitation and effectiveness of nutrient loading reduction strategies. The calibrated values of EFDC parameters are listed in Table S3.

Fig. 2 Calibration and validation of water temperature, Chla, TP, and NH₄⁺. The first year is calibration and the second year is validation. The blue dots are observed data of 8 sampling sites with error bars. The red lines represent the surface spatial average of simulation results. The shadow represents the maximum and minimum of the simulation



Stoichiometric patterns of nutrient pools

N:P ratios of different nutrient pools were calculated based on the result of nutrient budgets. The TN:TP ratio (annual average) was 7.86 (by mass) which is quite close to Redfield ratio (7.2 by mass) implying a plausible co-limitation of algae growth by both N and P (Guildford and Hecky 2000). However, the N:P ratios of different forms varied greatly. At annual scale, the particulate organic N:P (PON:POP) ratio was 6.82, dissolved organic N:P (DON:DOP) ratio was 15.1 and dissolved inorganic N:P (DIN:DIP) ratio (which serves as the biologically available share of nutrients) was 4.20. This low DIN:DIP ratio indicates that N was the limiting nutrient in Lake Dianchi. Furthermore, a distinct seasonal pattern of DIN:DIP ratios was detected at the monthly scale (Fig. 3). DIN:DIP ratios kept decreasing from February to November acting differently with TN:TP ratios. On the contrary, the DON:DOP ratios followed the trend of TN:TP ratios increasing in dry season and decreasing in wet season. Despite of the difference of DIN:DIP, DON:DOP and TN:TP in dry season, the consistent decrease indicated that denitrification removed significant amount of N from lake when algal blooms occurred. Besides, the DIN:DIP ratios were most affected by loading reduction of N and P, decreasing from 4.20 to 0.58 (7.24 times) when N loading was reduced from 100 to 10% of original loading, but increased from 4.20 to 14.6 (3.48 times) when P loading was reduced from 100 to 10% of original loading.

Stoichiometric patterns of nutrient fluxes

The evidence of nutrient limitation patterns could also be found in N:P ratios of nutrient fluxes. The annual average of $IN_{N:P}$ and $OUT_{N:P}$ were 14.7 and 8.57. The $IN_{N:P}$ was

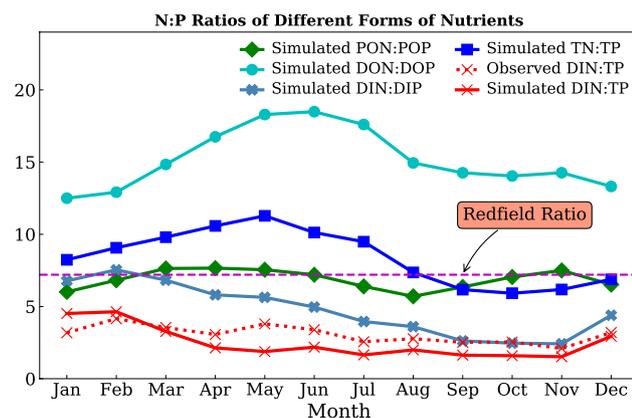


Fig. 3 Monthly N:P ratio patterns of nutrient storages. The purple dashed line represents the Redfield Ratio. The N:P ratios below this line imply relative N deficiency and above this line P deficiency. Observed DIN:TP was calculated by multiple-year average of DIN and TP of each month from 2002 to 2015

greater than $OUT_{N:P}$ in all the P loading reduction scenarios and N loading reduction scenarios lower than 50% reduction. The difference of these two ratios implied that N was retained at an even higher ratio than $IN_{N:P}$ to P in the lake. In addition, similar seasonal patterns were found in $IN_{N:P}$ and $RET_{N:P}$ as a result of extremely low outflow of Lake Dianchi (Fig. 4). The highly correlated $IN_{N:P}$ and $RET_{N:P}$ indicated that most N and P in Lake Dianchi were retained in the lake (or removed by denitrification, only for N). The annual $BEN_{N:P}$ was 26.9 which is indicative of P deficiency. However, this high annual $BEN_{N:P}$ is somewhat misleading when looking into monthly and seasonal scales. The monthly $BEN_{N:P}$ varied from -118.4 to 15.7 because of the strong fluctuations between release and adsorption of benthic TPO_4 (Fig. 5, the negative of $BEN_{N:P}$ means that benthic TPO_4 flux is negative, TPO_4 tends to be adsorbed by sediment). $PR_{N:P}$ was also calculated to represent the ratio of N and P stored within the lake and sediment which was the potential source for nutrient release. The annual average of $PR_{N:P}$ was 4.07, much lower than $RET_{N:P}$ indicating that denitrification accounted for a large part of N retention. The low $PR_{N:P}$ also showed that the source of N release was relatively lower than P which suggested a high possibility of N deficiency in Lake Dianchi. However, when P loading was reduced to 10% of original loading, $PR_{N:P}$ increased to 50.14, implying a deficiency of P.

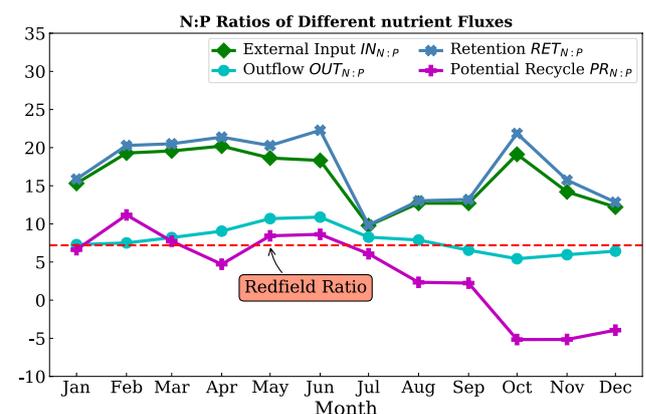


Fig. 4 Monthly N:P ratio patterns of nutrient fluxes. The red dashed line represents the Redfield Ratio. The N:P ratios below this line imply relative N deficiency and above this line P deficiency. The negative values of $PR_{N:P}$ are resulted from the huge denitrification leading to negative potential recycle of N

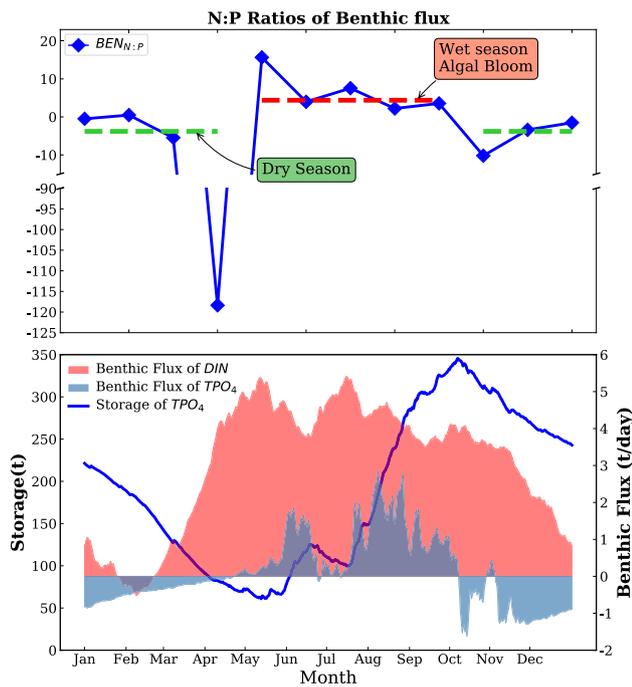


Fig. 5 Monthly $BEN_{N:P}$ patterns. The red dashed line represents the average $BEN_{N:P}$ in wet season (4.39). The green dashed line represents the average $BEN_{N:P}$ in dry season (-3.80). The negative values in $BEN_{N:P}$ result from the negative benthic P flux, which means that TPO_4 tends to be adsorbed by sediment. The benthic fluxes of DIN (red) and TPO_4 (blue) are shown below. Benthic TPO_4 flux is more accessible during algal blooms and it is a major source of TPO_4 (blue solid line) (color figure online)

Discussion

P is more accessible than N from benthic fluxes in wet season

As mentioned in 3.2, DIN:DIP ratios changed more rapidly in N loading reduction scenarios than in P loading reduction scenarios indicating that N loading reduction was more effective in reducing DIN. Further implication could be made that the benthic N flux is lower than benthic TPO_4 flux because benthic N flux cannot cover the amount of N reduced from external loading. However, the annual $BEN_{N:P}$ was 26.9 suggesting a much stronger benthic N flux than expected. This is because of the large fluctuation of benthic TPO_4 flux as mentioned in 3.3. The annual benthic TPO_4 flux could be extremely small and lead to a high $BEN_{N:P}$ due to its large fluctuations, which has also been found in other eutrophic lakes in previous studies (Kowalczyńska-Madura et al. 2015; Spears et al. 2012; Yang et al. 2013). In the previous long temporal study of Lake Dianchi, fluctuations of benthic TPO_4 fluxes were also detected and regarded as the controlling factor for nutrient limitation variation (Wu et al. 2017). Benthic TPO_4 flux acts distinctively from N because

their mechanisms are different. Benthic fluxes of both TPO_4 and NH_4^+ are mainly controlled by the oxygen concentration at the surface sediment; hypolimnetic hypoxia would significantly enhance TPO_4 release and impairs nitrification, which is a main consumption pathway for NH_4^+ (Chen et al. 2016, 2018; Liu et al. 2016; Malecki et al. 2004). However, hypolimnetic hypoxia would simultaneously enhance denitrification, which depletes NO_3^- and indirectly reduces benthic N flux (Nowlin et al. 2005). In N cycling dynamics, the intense denitrification in Lake Dianchi could be a major removal pathway of stored N in sediments, accounting for 49% of total N loss, which may cause N deficiency of benthic N flux (Hasegawa and Okino 2004; Holmroos et al. 2012; Yao et al. 2016). Hence, benthic N flux was mainly determined by the concentration gradient of NO_3^- between interstitial water and overlying water as well as hypolimnetic DO concentration (Small et al. 2014).

According to the patterns of the fluctuation, $BEN_{N:P}$ was calculated for two seasons: 4.39 in wet season and -3.80 in dry season. The low $BEN_{N:P}$ in wet season indicated that N was likely insufficient relative to P when algal blooms occurred implying that more P was released from the sediment. This is consistent with previous studies which indicated that TPO_4 was easier to release in a hypoxic condition than DIN (Li et al. 2016; Orihel et al. 2015). However, during the dry season when algal blooms ended, the excessive TPO_4 turned its benthic flux to adsorption, resulting in a negative $BEN_{N:P}$. A similar result was found in Lake Uzarzewskie, a hyper-eutrophic lake in Poland, where P accumulation in sediments dominated over release in winter (0.33–0.62 mg P/m²/day) and the highest P release rate was observed in autumn (44.7 mg P/m²/day) (Kowalczyńska-Madura et al. 2015). These huge direction-changing fluctuations indicated that TPO_4 could be released more easily than DIN from the sediment when TPO_4 was lacking in water column. Furthermore, $NETSED_{N:P}$ was also calculated to indicate the difference between sedimentation and benthic fluxes. Annual $NETSED_{N:P}$ was 4.38, implying a faster sediment accumulation for P than N which could ultimately be a potential pool for nutrient release. However, $NETSED_{N:P}$ turned negative (-1.57) in wet season because benthic TPO_4 flux was greater than P sedimentation. Benthic N fluxes decreased from 7.63 to 3.20 gN/m²/year when N loading was reduced from 100 to 10%, which was another reason for N deficiency besides the intense denitrification. This result is also consistent with DIN:DIP ratios as mentioned in 3.2 suggesting a low capacity for sediment N release. However, $BEN_{N:P}$ increased from 4.39 to 9.41 in wet season during the algal bloom when N loading was reduced from 100 to 10% due to a concurrently more rapid decrease of benthic TPO_4 flux (Fig.S4). The P cycling was strongly affected by N loading reduction via the decrease of algae biomass implying a closely coupled N and P cycling, which demonstrated in

Finlay et al. (2013). In contrast to N, without the influence of denitrification, the annual benthic P fluxes increased from 0.28 to 0.86 gP/m²/year when P loading was reduced from 100 to 10%, consistent with numerous previous studies on internal P loading (Carpenter 2008; Liu et al. 2016; Sondergaard et al. 2013). Thus, $BEN_{N:P}$ remained low in wet season (~4.5) and became positive in the dry season when P loading was reduced, indicating benthic TPO₄ flux turned from adsorption to release in the dry season and met the demand of TPO₄ by algae. Accordingly, P deficiency caused by algae uptake can easily be offset by benthic TPO₄ flux.

Permanent N removal by denitrification greatly exceeded N fixation

Denitrification is a permanent N removal pathway by transforming NO₃⁻ into N₂ escaping from the lake in a gas phase. In Lake Dianchi, a large amount of “retained” N was removed by denitrification. The annual average rate of denitrification in Lake Dianchi was 12.9 gN/m²/yr, accounting for ~50% of the total N loss, among the highest denitrification rates observed in lakes (Pina-Ochoa and Alvarez-Cobelas 2006; Saunders and Kalff 2001). Therefore, denitrification could be a significant driving force inducing stoichiometric imbalance of nutrients in lake water and resulting in sustained N limitation of algal growth. Similar results have been found in previous studies (Grantz et al. 2014; Holmroos et al. 2012). These findings implied that denitrification in P-enriched eutrophic lakes could be so intense to drive these lake ecosystems towards N deficiency (Finlay et al. 2013) due to enhanced denitrification. In contrast with N, all retained P appeared to be stored in sediments. The stored nutrients in sediments were assumed to be the major source of nutrient release. The $PR_{N:P}$ was 4.07 at annual scale, 5.13 in wet season, and 2.57 in dry season, indicative of strong N deficiency and conform to the patterns of $BEN_{N:P}$.

The internal N and P cycling tended to drive the lake towards N deficiency because of efficient denitrification and stoichiometric imbalance of benthic fluxes. However, some previous studies have found that N fixation by cyanobacteria can cover the deficiency of N caused by loading reduction and denitrification (Schindler et al. 2008; Schindler and Hecky 2009). Whereas for Lake Dianchi, the amount of N fixed by cyanobacteria only accounted for 1.2% of the total input of N, namely 0.32 gN/m²/year. Assuming all the other inputs and outputs remained constant, to cover the N removal by denitrification, average annual N fixation rate would have to be approximately 40 times greater than estimated. Even when external N loading was reduced to 10%, the rate of N fixation increased from 0.32 to 1.40 gN/m²/year, accounting for 20.3% of total N input, which could only replenish 6.8% of the reduced N loading. Moreover,

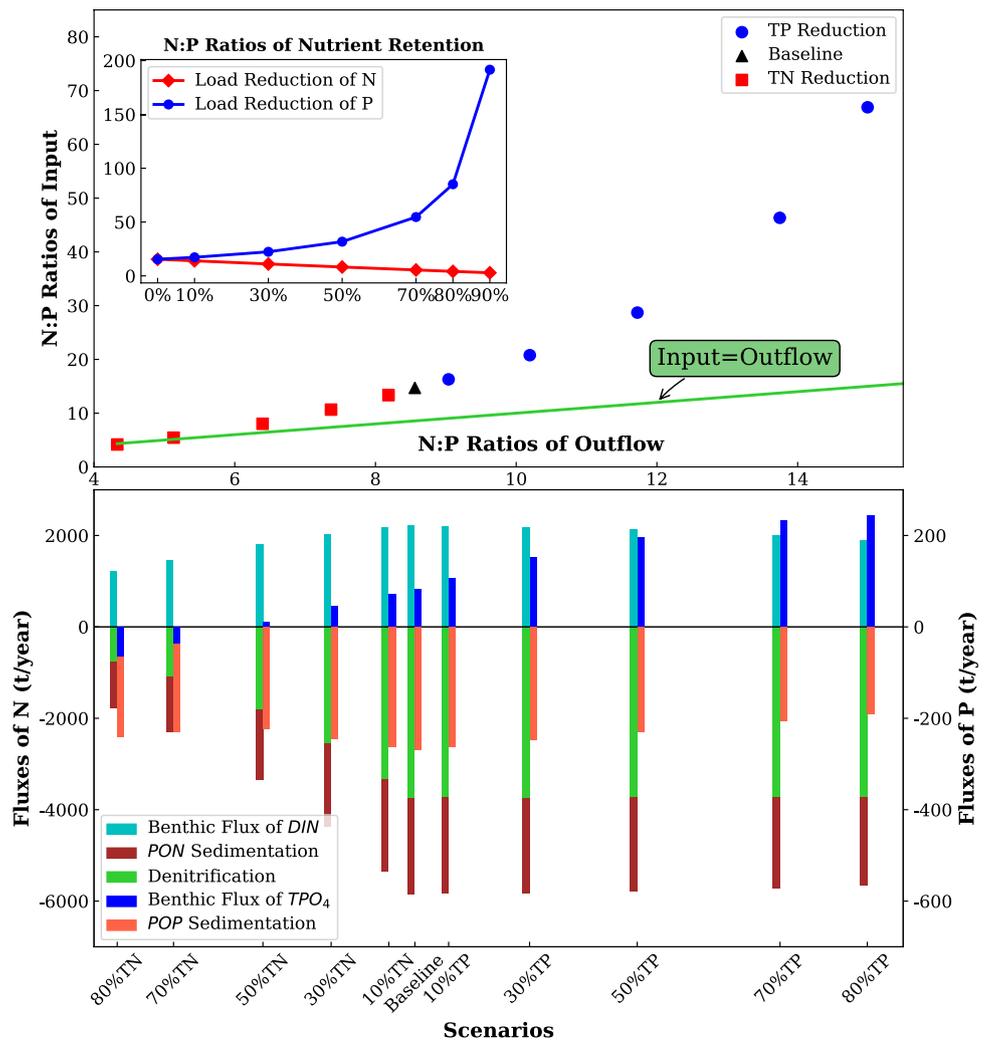
denitrification rate decreased from 12.9 to 1.57 gN/m²/year when external N loading reduced to 10%, it was still greater than N fixation, leading to the N deficit, as argued by Paerl et al. (2014) and Scott et al. (2010) (Fig.S5). The species composition of cyanobacteria may be a primary reason for sustained N deficiency in Lake Dianchi. Not all species of cyanobacteria are capable of fixing N. *Aphanizomenon*, the dominant N fixer in Lake Dianchi, only exists from March to May, while *Microcystis*, which cannot fix N, dominates the lake throughout the year (Havens et al. 2003; Liu et al. 2006). Hence, when algal blooms occur in summer, the dominant species is not *Aphanizomenon*. N fixation thereby cannot offset the severe N deficiency experienced in summer. Another potential reason why N fixation cannot balance the N pool is that our model focused on a relatively short time scale, namely only one year. The dominant species may not shift quickly enough to cover the N deficiency.

Nutrient retention can change nutrient limitation patterns

Nutrient retention is defined as a positive difference between external inputs and outputs (Dittrich et al. 2013; Sondergaard et al. 2001). Differences in the retention of N and P may reflect various mechanisms and alter nutrient limitation patterns of algal growth. High $RET_{N:P}$ was observed in Lake Dianchi with an annual average of 15.5, indicating that more N was retained than P. The monthly $RET_{N:P}$ ranged from 9.84 to 22.3, also reflecting a higher N retention than P. As discussed above, in Lake Dianchi, the joint effects of high benthic TPO₄ flux, high denitrification rate, and extremely low N fixation led to high N retention and low P retention, namely high $RET_{N:P}$ leading to N limitation. It was still true even when 50% of N loading was reduced (Fig. 6). The high N retention in these scenarios maintained relatively low N storage and resulted in N limitation with the assistance of high benthic TPO₄ flux to offer enough P for algal growth. Besides, the mismatch of low DIN:DIP and high DON:DOP also indicated that conversion of N from inorganic form to organic form by algae is much stronger than P. This phenomenon implied a high demand of N by algal growth and could be potential evidence for N limitation.

In order to identify the influence of retention on nutrient limitation of algal growth, the $IN_{N:P}$ and $OUT_{N:P}$ of over 20 lakes were collected from literatures (Fig.S6). There were several lakes with similar nutrient retention patterns of Lake Dianchi, such as Lakes Rotorua, Chaohu and Müggelsee (Kohler et al. 2005; Kong et al. 2015; Smith et al. 2016), reported as seasonal N-limited or high sediment release of P. In Lake Müggelsee, a seasonal shift between N-limitation and P-limitation was detected like Lake Dianchi. A very high P release from sediment and

Fig. 6 $IN_{N:P}$, $OUT_{N:P}$ and nutrient dynamics of different TN and TP loading reduction scenarios. $IN_{N:P}$ and $OUT_{N:P}$ of different scenarios were shown in the upper plot. The green line represents $IN_{N:P} = OUT_{N:P}$. The important fluxes of N and P internal dynamics were shown in the lower plot. $RET_{N:P}$ reduced when N loading was reduced but increased when P loading was reduced



a relatively high N retention led to N-limitation in summer in Lake Müggelsee. Moreover, in the hyper-eutrophic period of Lake Müggelsee, *Planktothrix agardhii*, which cannot fix N, dominated the algae in summer (Kohler et al. 2005). Different from the above lakes, high $OUT_{N:P}$ lakes usually had strong N-fixation fluxes and tended to be P-limited, such as Lakes Donghu, Elmdale and Fayetteville (Grantz et al. 2014; Havens et al. 2001). The N fixation rates measured with acetylene reduction method in Lakes Elmdale and Fayetteville were among the highest ever reported, namely 10 to 11 gN/m²/year, contributing ~30% of N input (Grantz et al. 2014). Overall, internal dynamics dominate the nutrient retention patterns in eutrophic lakes and different retention patterns may lead to various nutrient limitations of algae growth.

For Lake Dianchi, regulation of N loading should thereby be more effective in controlling algal blooms, in contrast to various previous studies of a number of lakes because of its low N fixation and high sediment P release rates (Schindler 2012; Schindler et al. 2016; Schindler and Hecky 2009;

Wang and Wang 2009). There are also a number of studies that emphasize the importance of reducing N loading, although N management is more difficult and costly (Abell et al. 2010; Moss et al. 2013; Müller and Mitrovic 2015; Paerl et al. 2011; Smith et al. 2016; Xu et al. 2010). Furthermore, the accumulated N will eventually lead to high external N inputs to downstream N-limited freshwater and coastal ecosystems (Bernhardt 2013; Finlay et al. 2013). Despite our emphasis on the importance of external N loading regulation in this study, we do not imply that decision-makers should relax the control of P. Both N and P loading regulations are necessary for reliable rehabilitation of lake ecosystems.

Conclusions

A 3D model-based N:P stoichiometric approach was developed to explore the mechanisms that affect the limiting nutrient in hyper-eutrophic Lake Dianchi. The N:P ratios of different nutrient pools and fluxes were calculated and

analyzed. The results and analysis highlighted the importance of internal nutrient cycling on the seasonal N limitation in Lake Dianchi.

- a. Benthic P fluxes fluctuated considerably within a year and could supply enough P for algae, contributing over 50% of P input and leading to relative N deficiency during algal bloom. However, during the other period of a year when the demand of P is small, benthic P fluxes became a considerable sink of P adsorbing TPO₄ from water column to the sediment.
- b. N fixation contributed only ~ 1% of total N input, it could not meet the N demand by algae. Even when 90% of N load was reduced, N fixation, accounting for 20.3% of total N input, could only replenish 6.8% of the reduced N loading.
- c. Denitrification was an extremely high N removal pathway, accounting for ~ 50% of total loss in this hyper-eutrophic lake. When 90% of N loading was reduced, denitrification rate decreased from 12.9 to 1.57 gN/m²/year. However, it was still greater than N fixation, leading to the N deficit.
- d. The joint effects of high benthic P flux, high denitrification, and extremely low N fixation led to a discrepancy between N and P retention resulting in seasonal N limitation in Lake Dianchi. It was still true even when 50% of N loading was reduced.

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