

Impoundment-induced stoichiometric imbalance exacerbated phosphorus limitation in a deep subtropical reservoir: Implications for eutrophication management

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ABSTRACT

Impoundments play a vital role as nutrient sinks, capable of retaining and exporting nitrogen (N) and phosphorus (P) at different rates. The imbalance in N and P stoichiometry relative to phytoplankton demand often determines the limiting nutrient of phytoplankton biomass in these systems. This critical factor has a substantial impact on the management of eutrophication, encompassing the formulation of nutrient control strategies and the setting of regulatory thresholds. Nonetheless, research remains relatively limited on phytoplankton limiting factors and nutrient stoichiometry interactions in subtropical impoundment reservoirs. This study fills a critical gap in the current research by providing a comprehensive assessment of the influences of N and P on phytoplankton biomass in Lake Qiandaohu, China. Through field monitoring, nutrient addition experiments, and novel constraint line regression model, we provide new insights into the nutrient-phytoplankton dynamics within the lake. Both bioassay experiments and statistics indicated primarily P-limitation in Lake Qiandaohu owing to its dam-induced deep-water conditions, characterized by a nearly 1:1 linear relationship between chlorophyll *a* (Chl_a) and total P (TP) concentrations. This underscores the pivotal role of P management plays in controlling algal blooms. Utilizing the constraint line equation that relates TP to Chl_a, we have proposed TP thresholds designed to keep Chl_a within the specified target ranges, specifically below 10, 12, 20, 24, 40, and 60 µg/L. Furthermore, leveraging Vollenweider's models with these TP concentration thresholds, we established TP loading targets that accommodate a range of hydrological conditions, from normal to wet and dry years. Furthermore, both nutrient addition experiments and constraint line regression model indicates potential N and P co-limitation in specific regions, particularly the riverine zone, where the unsettled particulate matter results in relatively lower N:P ratios. To address this, we introduces TN thresholds and suggests localized control measures, including the use of floating macrophytes beds, as effective alternatives. Considering the uniform nutrient management policy currently applied across Chinese lakes and reservoirs, which may lead to under- or over-protection for individual water bodies, our research provides a flexible cost-effective eutrophication management framework tailored for the China's subtropical region.

1. Introduction

The excessive proliferation of phytoplankton, commonly known as blooms, poses a significant global environmental threat to freshwater ecosystems (Paerl 1988; Ho et al., 2019; Hou et al. 2022). These blooms

can produce algal toxins, taste and odor compounds, and hypoxia, which negatively impact drinking water supplies, food webs, ecosystem resiliency and local economic sustainability (Huisman et al. 2018; Codd et al. 2005; Ansari et al. 2010). Over-enrichment by nutrients, including phosphorus (P) and nitrogen (N), is considered the main driver of

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excessive phytoplankton growth (Conley et al., 2009). However, there is ongoing debate regarding whether freshwater lakes are limited solely by P or co-limited by both N and P, or even N-limited and consequently, whether strategies for sole P reduction or dual N&P control should be implemented (Schindler, 1974; Conley et al. 2009; Xu et al. 2010; Paerl et al. 2016; Shatwell and Köhler, 2019; Chorus and Spijkerman, 2021). Particularly, the imbalance in P and N stoichiometry relative to phytoplankton demand often determines the limiting nutrient for lakes at continental scales (Sterner and Elser, 2017). Guildford and Hecky (2000) found that N-deficient growth was apparent at the mass ratios of nitrogen and phosphorus (N:P) less than 9, while P-deficient growth was apparent at ratios greater than about 23. When P is strongly limiting, the yield of phytoplankton biomass per unit of N will be less than expected based on the supply of N, and vice versa when N is strongly limiting (Carlson and Havens, 2005). Thus, the nutrient stoichiometric imbalance can significantly influence the relationship between nutrients and phytoplankton biomass (Wurtsbaugh et al. 2019).

Recent studies have indicated that nutrient stoichiometry is associated with water depth, suggesting that deep and shallow lakes tend to be potentially P-limited and N&P-co-limited, respectively (Maberly et al. 2020; Qin et al. 2020). This implies that deep lakes should focus on P reduction, while shallow lakes should concentrate on N and N&P dual control. Fertile plains, with their robust agricultures, often export materials having relatively lower N:P ratios into nearby lakes. In contrast, lakes in mountainous regions receive materials with higher N:P ratios due to less human disturbance and more intact ecosystems (Downing, 1992). The topography typically results in plains hosting shallow lakes, while mountains more often harbor deeper ones, creating a geographical pattern where deep lakes tend to have higher N:P ratios and shallow lakes have lower ones. Moreover, deep lakes act as strong P sinks, but N loss through sedimentation is less efficient than for P because N is predominantly in dissolved bioavailable forms. Additionally, denitrification in shallow lakes can significantly counter N inputs (Scheffer, 1998). In recent decades, China has experienced a significant increase in dam construction, leading to the formation of large, deep reservoirs (Song et al. 2022). Based on the review of the influence of lake depth on phytoplankton limiting factors, phytoplankton biomass in these deep reservoirs is likely to be P-limited (Qin et al. 2020), indicating a need for P control strategies. However, this assumption requires further validation through field and experimental data. Moreover, the assumption might be too simplistic, considering the large size and significant variability in internal hydromorphic conditions of these reservoirs, which can greatly influence the dynamics of nutrient stoichiometry and phytoplankton limiting factors.

Determining the quantitative level of control needed is crucial, such as identifying nutrient concentration and inflow thresholds that can prevent excessive phytoplankton growth. With this knowledge, effective management strategies, such as targeted nutrient reduction measures, can be established to mitigate phytoplankton proliferation. However, empirical models linking nutrient concentration to phytoplankton biomass have primarily been developed for temperate lakes in developed countries (Vollenweider 1968; Jones and Lee 1982; Brown et al. 2000; Phillips et al. 2008; Filstrup et al. 2014), with relatively few studies in subtropical developing countries like China (Huo et al. 2014; Zou et al. 2020; Yu et al. 2022). Additionally, a scatter plot of phytoplankton biomass and nutrients often takes on a wedge shape in lake ecosystems, indicating that the causal relationship between nutrients and phytoplankton biomass is complicated by other factors. In such cases, it is usually necessary to use constrained line regression to explore the relationship between the biomass and nutrients, a method that has been widely applied in many developed countries (Carvalho et al. 2013; Phillips et al. 2019; Kelly et al. 2022; Phillips et al. 2024). However, in contrast, some developing countries in subtropical regions, such as China, have relatively rarely applied unconstrained line regression methods in lake ecological management, and this is mainly focused on shallow lakes (Zou et al. 2020; Liang et al., 2021), with little attention paid to the

constrained effects of nutrients on algal biomass in deep reservoirs. In recent years, the number of reservoirs in China has increased dramatically (Song et al. 2022), and they have trended towards deeper systems. The material cycling of N and P in reservoirs is vastly different from that in shallow lakes, so theoretically, constrained line regression may reveal different patterns in the relationship between phytoplankton and nutrients. Notably is that the current nutrient management in China adopts a "one-size-fits-all" policy (China State Environmental Protection Administration, 2002), which does not conform to the principle of economic cost-effectiveness and is seriously out of step with internationally advanced aquatic ecological management systems, such as the renowned Water Framework Directive. If China is to formulate a category-based lake ecological governance framework suitable for local conditions in the future, it may be necessary to carry out research and data analysis based on datasets native to China.

Here, we focused on Lake Qiandaohu, a typical large, deep reservoir in the Eastern China, as a case study. Through extensive monitoring and controlled experiments, we aim to quantitatively determine the effects of N and P enrichment on phytoplankton biomass and the associated mechanisms in this subtropical deep reservoir. The objectives of this study were to: 1) document the limnological conditions of Lake Qiandaohu, 2) quantify the impacts of N and P on phytoplankton biomass and explore the underlying mechanisms, and 3) propose management policies, such as nutrient control strategies and thresholds, for controlling algal blooms in subtropical deep lakes. Given the general nutrient management policy applied across Chinese lakes and reservoirs (China State Environmental Protection Administration, 2002), which may result in over- or under-protection for individual lakes, our research helps develop a cost-effective eutrophication management framework specifically tailored to the subtropical Eastern China.

2. Material and methods

2.1. Study area

Lake Qiandaohu, also known as Xin'anjiang Reservoir, is located at the boundary of western Zhejiang and southern Anhui provinces (Fig. 1). Situated in a subtropical monsoon climate zone, the lake experiences a warm, humid climate with abundant rainfall, distinct seasons, an average annual temperature of approximately 17 °C, and an average annual precipitation of 1636.5 mm. The lake's name, 'Qiandao,' meaning 'a thousand islands,' reflects the numerous islands that dot its surface. With a length of up to 150 km and a width of 50 km, the reservoir's elongated shape, with many bays, covers a surface area of 580 km² at its design water level of 108 m. Lake Qiandaohu has an average depth of 31 m, with the deepest points exceeding 100 m, and it has water volume of 178.6×10^8 m³ within a drainage basin of 10,480 km² (Zhang et al. 2015).

Monthly monitoring data from May 2020 to April 2021 shows that about 70% of the inflow to Lake Qiandaohu originates from the Xin'an River. Dongyuan River and Wuqiang River are the next significant contributors, with their combined inflow making up roughly 10% of the total inflow. The remaining 23 rivers account for 20% of the total inflow. The water exits the lake through a dam at its southeasternmost point (Fig. 1). Strategically, Lake Qiandaohu is a vital drinking water source for over ten millions of inhabitants in major cities of Hangzhou and Jiaying. However, the lake faces dual pressures from climate change and human activities, indicated by rising nutrient levels, reduced Secchi disk depth, and occasional algal blooms, which threaten the long-term safety and security of the drinking water supply (Li et al. 2020; Shi et al. 2023).

2.2. Sampling and measurement variables

Between May 2020 and April 2021, we conducted monthly surveys at 100 sites across Lake Qiandaohu (Fig. 1). At each site, we recorded

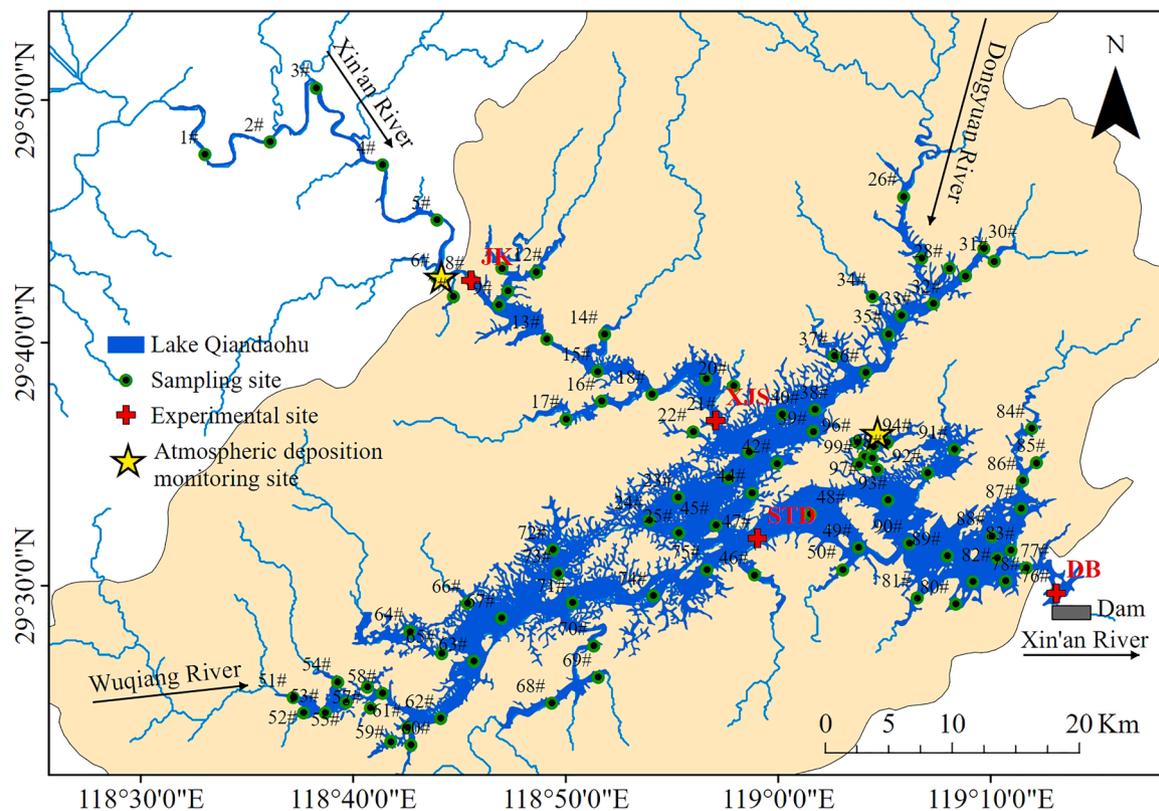


Fig. 1. A map illustrating the spatial distribution of various research activities in Lake Qiandaohu, including water sampling sites, locations for controlled nutrient addition experiments, atmospheric deposition monitoring, and the main rivers that flow into and out of the lake. The sites for the nutrient addition experiments are designated by the following abbreviations: Jiekou (JK), Xiaojinshan (XJS), Santandao (STD), and Daba (DB). The northwest region, where JK is situated, is recognized for its riverine features.

water depth (WD) and Secchi disk depth (SD) using a Speedtech SM-5 Portable Depth Sounder and a Secchi disc, respectively. The water temperature (WT) within the top 50 cm was measured in situ with an EXO2 multi-sensor sonde. For laboratory analysis, we collected surface water samples and determined concentrations of total N (TN), total P (TP), total dissolved N (TDN), and total dissolved P (TDP) spectrophotometrically after alkaline potassium persulfate digestion. TN and TP were measured on unfiltered samples, whereas TDN and TDP were measured on samples filtered through 0.7 μm GF/F glass fiber filters. Chlorophyll *a* (Chl_a) was extracted with hot 90% ethanol and measured spectrophotometrically at wavelengths of 665 and 750 nm (Jin and Tu, 1990). Total suspended solids (TSS) were quantified by collecting samples on pre-weighed 0.7 μm GF/F filters, followed by combustion in a muffle furnace at 550 $^{\circ}\text{C}$ for 4 h to obtain ash-free weight. Inorganic suspended solids (ISS) were calculated by the difference in weight before and after filtration. Organic suspended solids (OSS) were then derived as the difference between TSS and ISS.

2.3. Nutrient addition bioassay experiments

Phytoplankton nutrient limitation in Lake Qiandaohu was assessed using standard nutrient addition bioassay experiments conducted at four sites (JK, XJS, STD, and DB, in Fig. 1). Water samples from each site were transferred into 1 L 80% PAR transparent polyethylene cubitainers, which were then assigned to one of four treatment groups: a control with no added nutrients, a N only group, a P only group, and a group with both nutrients added. Each treatment had three replicates, resulting in a total of 48 cubitainers. We added 2 mg of N and 20 μg of P into the 1 L transparent plastic cubitainers, using potassium nitrate (KNO_3) and potassium dihydrogen phosphate (KH_2PO_4) as the nutrient sources. The experiment lasted for 2 days, and Chl_a concentrations were measured at

the start and end of this period in each bag.

2.4. Constraint line regression model

Constraint line regression is a statistical technique that examines the influence of a single predictor on the higher or lower quantiles of a response variable. This approach offers a nuanced perspective on the impact of N or P on algal biomass, revealing cause-effect relationships in ecological variables without the confounding effects of significant extraneous factors (Kaiser et al. 1994). In our study, we applied the 95% quantile model from the *quantreg* package in R to quantify the relationship between maximal lnChl_a and nutrients, specifically lnTP, when a discernible linear trend was present in our bivariate plots.

However, when nonlinear trends were observed in the scatter plots of lnChl_a versus lnTN, we turned to alternative methods to quantify the relationship. Initially, we used interval maxima regression, consistent with the statistical principles of the 95% quantile model, to ascertain the upper limits of lnChl_a. This process involved dividing lnTN into specific intervals and identifying the maximum lnChl_a values corresponding to each lnTN interval (Graham et al. 2004). Subsequently, we employed segmented regression, a versatile method that fits multiple models across different ranges, to measure the influence of lnTN on lnChl_a maxima. This analysis was performed using the *segmented* package in R.

2.5. Nutrient budget calculation

To determine the nutrient mass balances for Lake Qiandaohu, we quantified the inputs and outputs of N and P. Our assessment included total inputs from riverine sources and atmospheric deposition onto the lake's surface. Outputs were calculated from riverine outflows and resource extraction, including fisheries and drinking water supplies.

Lake Qiandaohu experiences few cyanobacterial blooms, and its nutrient concentrations are relatively low. Diatoms are the dominant phytoplankton throughout the year, and the N:P ratio typically exceeds the threshold of 22.6. This suggests that the lake is not likely to be N-limited and that N₂-fixing cyanobacteria are generally not a significant component of N input (Guildford and Hecky 2000). In addition, experimental results from three locations (JK, XJS and STD, Fig. 1) indicate undetectable denitrification potential in the water column and low potential in the sediment (about 5 μmol/kg/h), significantly lower than that observed in shallow lakes (Scheffer 1998; Xu et al. 2021). The annual N and P mass balances for Lake Qiandaohu were calculated using the equation:

$$R = M_{in} + M_{atmos} - M_{out} - M_{intake} - M_{fish} \quad (1)$$

Where R represents the nutrient retention, M_{in} is the riverine input, M_{atmos} is atmospheric deposition, M_{out} is the riverine output, M_{intake} is the drinking water intake, and M_{fish} is the fish catch output. To obtain these parameters, we employed the Soil and Water Assessment Tool (SWAT) model to simulate inflow into Lake Qiandaohu, calibrated and validated using observed streamflow data from 2001 to 2010 and validated for 2011 to 2014, showing a strong correlation with a coefficient of determination between 0.85 and 0.90 (Li et al. 2022). We then used this model to simulate water inflow from 25 rivers into the lake from May 2020 to April 2021 and estimated the total nutrient load from monthly N and P concentration measurements. Outflow through the dam site was quantified using monthly discharge data correlated with N and P measurements at the same location (i.e., DB in Fig.1). Atmospheric deposition of TN and TP was measured following established methods (Zhu et al. 2022). Drinking water consumption was estimated by multiplying the water consumption volume by the nutrient concentrations. M_{fish} was calculated as the fish catch multiplied by the average nutrient content of fish (0.31% for P and 4.65% N) (Xu et al. 2021).

2.6. Statistical analyses

We used the Paired t-Test to identify significant differences among WT, WD, TN, TDN, TP, TDP, N:P, SD, SS, ISS, OSS, and Chla between summer months and the entire year when the data met the assumptions of normality, independence, and homogeneity of variances. When these assumptions were not met, we applied the Wilcoxon Signed-Rank Test to assess differences. For analyzing Chla among various treatments in controlled experiments, we conducted a one-way ANOVA. Post hoc multiple comparisons of treatment means were carried out using Tukey's Honestly Significant Difference test. In all cases, the untransformed data fulfilled the assumptions of normality and homoscedasticity.

2.7. Chlorophyll a control target

In this study, we established a series of Chla control targets under different ecological risk levels or reference-based targets, and accordingly determine the thresholds for nutrient concentrations or loads. Firstly, by international standards, the WHO Guidelines for recreational use dictate that Chla levels should be greater than 12 μg/l for Alert Level 1 and 24 μg/L for Alert Level 2. These levels are considered thresholds for potential health risks. At Alert Level 1, further assessment is necessary to determine potential risks to swimmers or animals, and inquiries are made regarding toxin producers. Alert Level 2 involves monitoring for algal scums and advising users to avoid activities that could lead to the inhalation of toxins, particularly for children (WHO, 2021). In the context of reference-based targets, for instance, Poikane et al. (2014) defined the 'good-moderate' status boundaries for Chla in moderately deep European lakes as 10 μg/L. Lastly, for lakes and reservoirs in China, mild algal blooms typically occur when Chla levels range from 20 to 40 μg/L, causing a slight impact on water supply safety. As Chla levels rise to between 40 and 60 μg/L, the algal blooms become more severe,

posing a significant threat to water supply safety. If Chla exceeds 60 μg/L, the algal bloom becomes extremely severe, potentially leading to the interruption of water supply (Ministry of Ecology and Environment of the People's Republic of China, 2021). Therefore, this study sets Chla concentrations at 10, 12, 20, 24, 40, and 60 μg/L as control targets, reflecting the various ecological risk levels or reference-based targets.

3. Results

3.1. Limnological background

Significant differences were found in mean WT ($P < 0.001$), with summer months averaging 28.87 ± 0.91 °C, higher than the annual average of 20.91 ± 0.59 °C. WD also showed a significant increase in summer, averaging 34.57 ± 17.39 m, compared to the annual average of 32.55 ± 17.23 m ($P < 0.001$). Nutrient levels varied significantly as TN between summer, at 0.75 ± 0.20 mg/L, and the full year, at 0.86 ± 0.22 mg/L ($P < 0.001$). TP concentrations were significantly higher in summer, averaging 25.79 ± 10.00 μg/L, than the annual average of 21.06 ± 9.87 μg/L ($P < 0.001$). The temporal patterns of TDN and TDP followed the same trend as TN and TP, respectively. The summer mean N:P was 31.9 ± 5.98 , which was significantly lower than the annual ratio of 53.2 ± 12.3 ($P < 0.001$). For turbidity-related variables, Chla, ISS, and OSS all had significantly higher mean values in summer than the full year. This resulted in a significantly lower mean SD and higher SS during summer (Fig. 2).

3.2. Phytoplankton response to nutrient enrichment

3.2.1. Maximal response of chlorophyll a

In Lake Qiandaohu, Chla has a critical threshold beyond which N limitation is observed. Below a TN concentration of 0.89 mg/L, the maximum lnChla does not significantly increase with further TN enrichment. Above this threshold, however, the maximum lnChla shows a linear response to an increase in lnTN (Fig. 3a). For P, the maximum lnChla consistently increases linearly with lnTP enrichment across the entire P range, indicating potential P limitation in entire Lake Qiandaohu (Fig. 3b).

3.2.2. Nutrient enrichment bioassay experiment

In spring, Chla concentrations in N addition alone treatment did not significantly increase compared to the control ($P > 0.05$). However, P addition—whether alone or with N—resulted in significantly higher Chla concentrations than the control across all four sites ($P < 0.001$) (Fig. 4). In summer, Chla concentrations in N addition alone treatment significantly increased compared to the control in JK ($P = 0.009$), but this effect was not observed at the other three locations (XJS, STD, and DB) ($P > 0.05$). P addition, alone or combined with N, consistently led to significantly higher Chla concentrations than the control at all sites ($P < 0.001$). Notably, at locations JK and XJS, Chla levels in treatments with both N and P were significantly higher than those with P alone ($P < 0.001$).

4. Discussion

4.1. Drivers and mechanisms of nutrient limitation of phytoplankton

Our results indicate that phytoplankton biomass in Lake Qiandaohu is potentially P-limited. The constraint line regression showed a linear increase across the entire TP gradient (Fig. 3b), supports this potentially P-limited status. Nutrient addition experiments conducted in spring and summer confirmed this, with significant increases in Chla concentrations following P addition at all four sites ($P < 0.05$), spanning a gradient of P concentrations from the riverine zone to the dam (Fig. 4). This is consistent with limnological theories that deep lakes and reservoirs typically exhibit potential P limitation, which is largely because P is

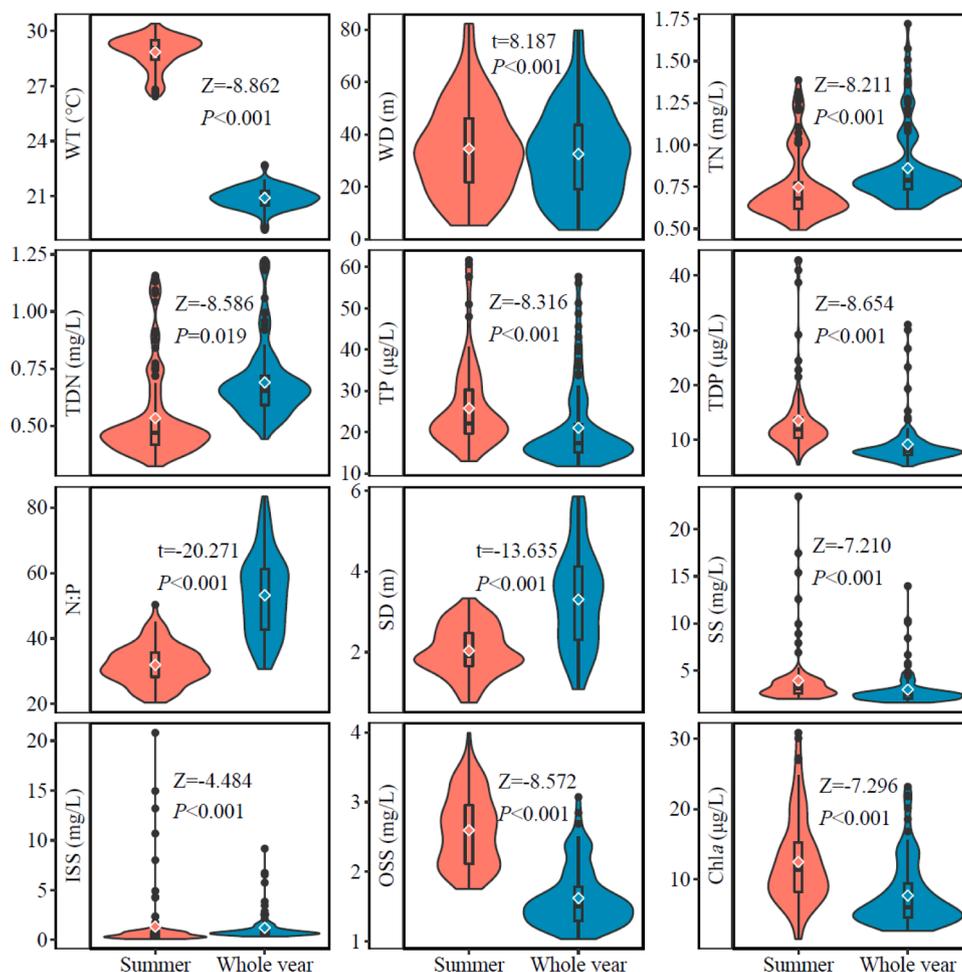


Fig. 2. Violin plots and the difference analysis of water temperature (WT), water depth (WD), total nitrogen (TN), total dissolved nitrogen (TDN), total phosphorus (TP), total dissolved phosphorus (TDP), the mass ratio of nitrogen to phosphorus (N: P), Secchi disk depth (SD), suspended solids (SS), inorganic suspended solids (ISS), organic suspended solids (OSS), and chlorophyll *a* (Chla) in the summer months and in the entire year. The violin plots of these variables in each month from May 2020 to April 2021 were provided in Fig. S1-S3.

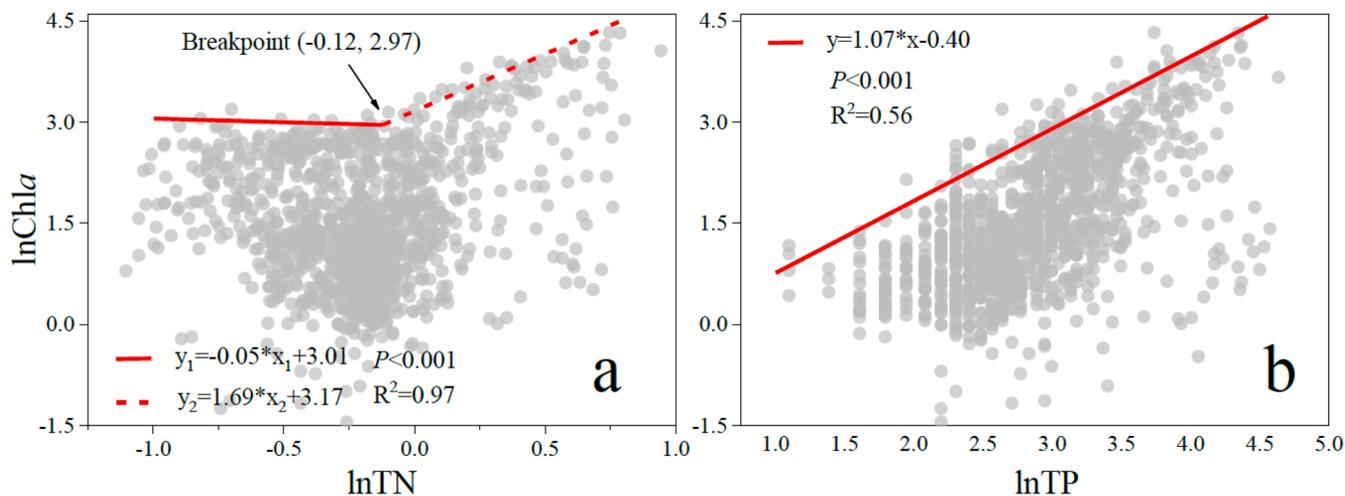


Fig. 3. Scatter diagrams and constraint lines illustrating the relationship between nutrients (i.e., natural-logarithmic total nitrogen, lnTN, mg/L; and natural-logarithmic total phosphorus, lnTP, µg/L)—and natural-logarithmic chlorophyll *a* (lnChla, µg/L) in Lake Qiandaohu.

“trapped” in the hypolimnion in strongly stratified deep lakes (Schindler, 1974; Qin et al. 2020). During the study, the N:P ratio from river input and atmospheric deposition was about 30 and 52,

respectively (Fig. 5), with river input being the primary source of nutrients, contributing 97% of TN and 95% of TP loading. The N:P ratio in sedimented particulate matter, ranging from 2.6 to 7.1 (Shi et al., 2020),

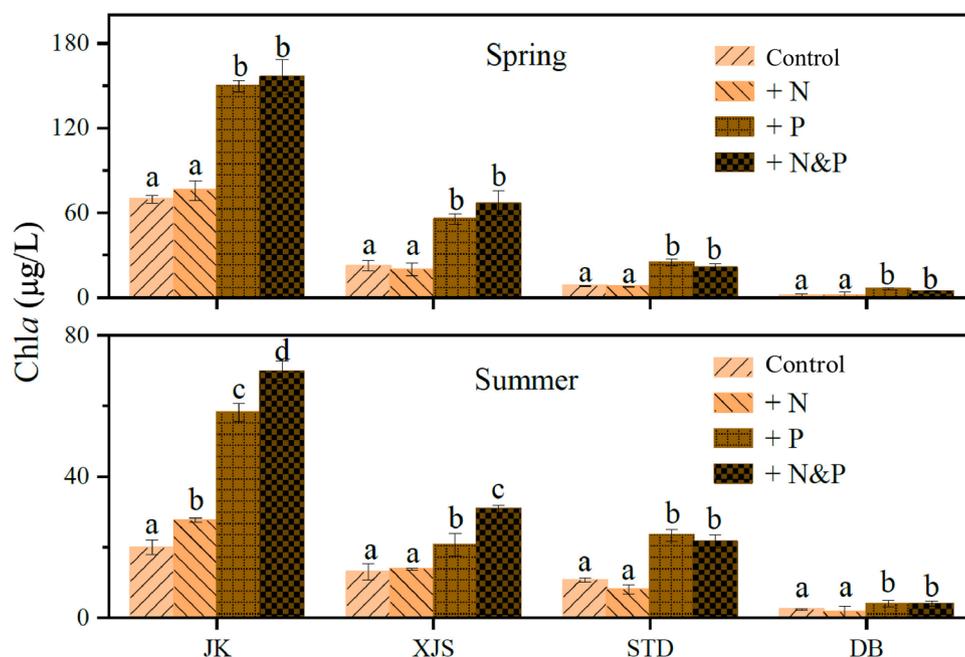


Fig. 4. Chlorophyll *a* (Chla) concentration of the treatments with nitrogen addition (+N), phosphorus addition (+P), and nitrogen and phosphorus additions (+N&P) in the end of bioassays conducted in May and August 2018. Error bars represent standard deviation of triplicate samples. Differences between treatments are shown on the basis of ANOVA post hoc tests ($a < b < c < d$; $P < 0.05$).

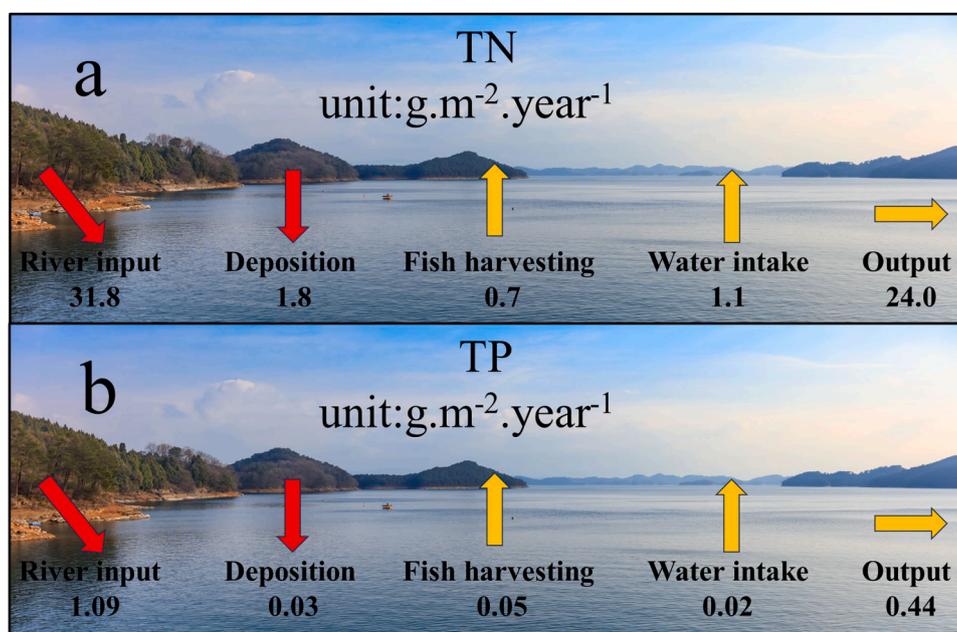


Fig. 5. a: Diagrammatic presentation of total nitrogen (TN), and b: total phosphorus (TP; panel) budgets for Lake Qiandaohu.

was significantly lower than input ratios, suggesting that sedimentation further reduces the N:P ratio in the water column. Consequently, the N:P ratio in most of Lake Qiandaohu exceeds 30, peaking near the dam (Fig. 6). According to Guildford and Hecky (2000), an N:P ratio above 22.6 suggests P limitation, corroborating our findings.

Notably, our nutrient addition experiments suggest potential N&P co-limitation for algal growth at location JK. Statistically, we observed that when TN is below 0.89 mg/L, the increase in maximum potential Chla with TN enrichment is very limited (Fig. 3). Areas with a TN concentration above this threshold are primarily in the northwestern part of the reservoir (Fig. 6), indicating that specific areas within deep reservoirs may experience potential N&P co-limitation. Theoretically,

potential N&P co-limitation is probable at JK, situated at the riverine zone and receiving direct river inputs, where the N:P ratio is often lower due to unsettled suspended solids. Evidence from Lake Qiandaohu supports this hypothesis. The SS concentration decreases exponentially with increasing distance (D) from the riverine zone, expressed as $SS = 8.09 \cdot e^{-0.03 \cdot D}$, R^2 of 0.84, indicating a strong correlation (Shi et al. 2020). As distance from the riverine zone grows, the settling of particulate matter persists, and our study found a significant negative association between SS and the N:P ratio (Fig. 7), consistent with regional patterns in the Chinese Eastern Plain ecoregion reported by (Zou et al. 2022). The negative association between N:P and SS is explained by the differential sedimentation efficiency of N and P, with P settling more readily than N,

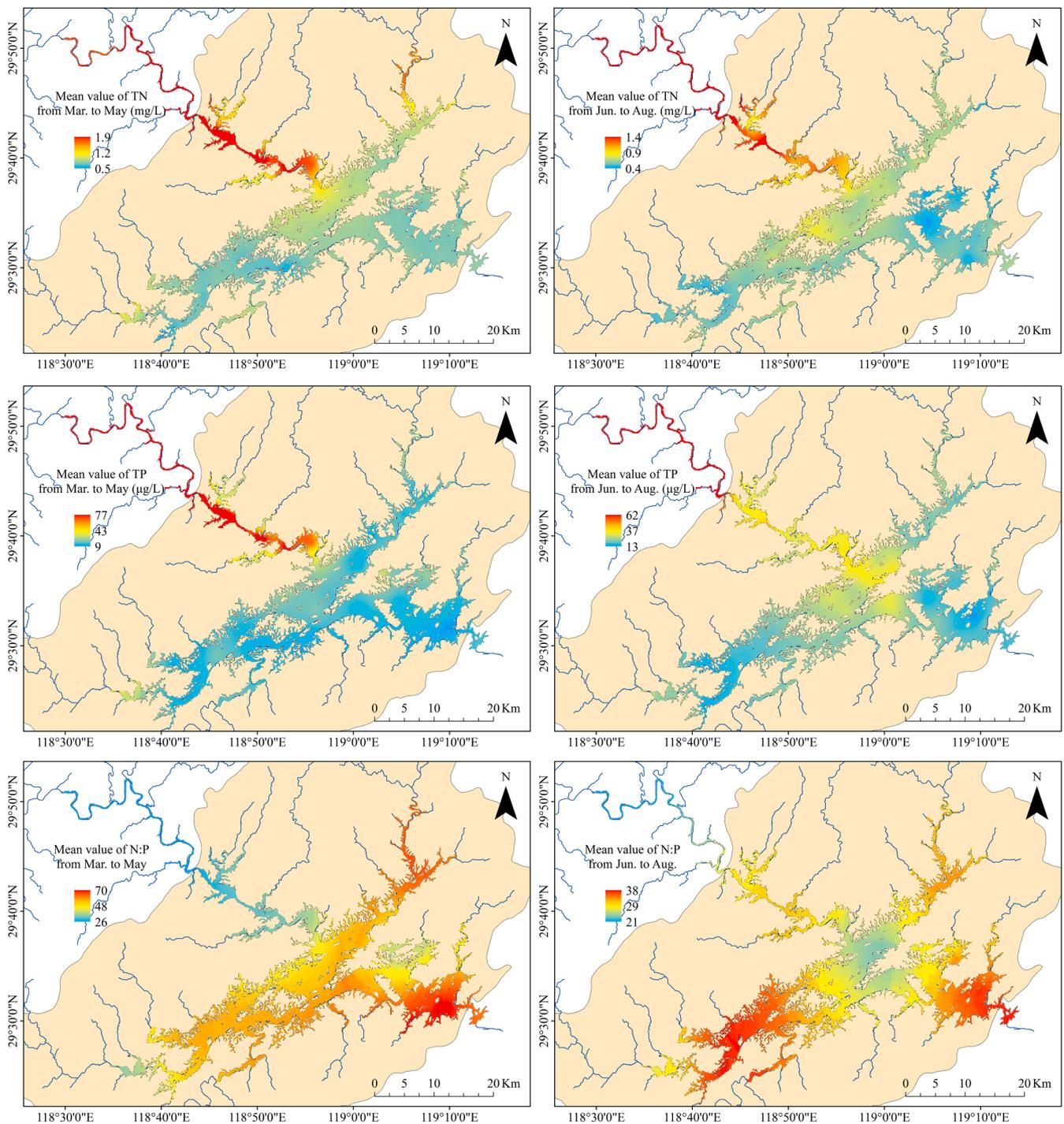


Fig. 6. Spatial interpolation map of average total nitrogen (TN) and total phosphorus (TP), as well as the mass ratio of nitrogen to phosphorus (N:P) in Lake Qiandao for spring (Mar. to May) and summer seasons (Jun. to Aug.).

which often remains in dissolved forms (Qin et al. 2020). Moreover, despite its potential minimal impact, denitrification is likely occurring in the surface sediments and possibly within the water column, which could contribute to the observed lower N:P ratios to some extent in the riverine zone of Lake Qiandao.

We noted that the study identifies phytoplankton limiting nutrients using statistical methods (constrained line regression) and experimental approaches (nutrient addition experiments). These nutrients are associated with potential limitation, affecting the final yield of phytoplankton biomass rather than their growth based on absolute nutrient concentration. Typically, phosphorus limitation is suggested when

dissolved reactive phosphorus concentrations fall below 10 μg/L, and nitrogen limitation when dissolved inorganic nitrogen concentrations are below 0.1 mg/L (Maberly et al., 2020). Fig. 2 illustrates that TDP concentrations surpass 10 μg/L for most summer sampling occasions, and all TDN concentrations exceed 0.1 mg/L. Furthermore, Chorus & Spijkerman (2021) indicate that when soluble phosphorus levels are above 3–10 μg/L and dissolved nitrogen levels above 1.0–1.3 mg/L, TP and TN may not limit phytoplankton growth, as algal self-shading may cause light limitation. The four sites where controlled experiments were conducted displayed TDN concentrations ranging from 0.66 to 1.15 mg/L (Table 1), which confirms that N is not a limiting factor when

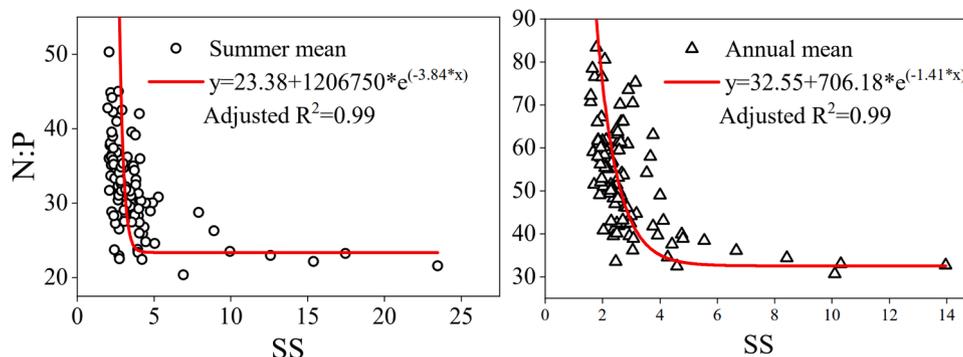


Fig. 7. Displays scatter plots illustrating the mass ratio of nitrogen to phosphorus (N:P) and the concentration of suspended solids (SS, mg/L) in Lake Qiandaohu during the summer months (June to August) and throughout the year (January to December).

Table 1

The concentrations of total nitrogen (TN), total dissolved nitrogen (TDN), total phosphorus (TP), total dissolved phosphorus (TDP), and chlorophyll *a* (Chla) in the water column at the JK, XJS, STD, and DB sites during spring (29 May 2018) and summer (6 August 2018).

Season	Location	TN (mg/L)	TDN (mg/L)	TP (μg/L)	TDP (μg/L)	Chla (μg/L)
Spring	JK	1.39	1.15	63.9	12.4	28.4
	XJS	1.39	0.93	67.9	14.9	20.3
	STD	0.91	0.77	35.8	8.2	6.5
	DB	0.90	0.84	25.6	5.2	1.2
Summer	JK	2.072	0.701	58.0	8.8	23.1
	XJS	1.018	0.848	42.8	6.4	15.1
	STD	0.891	0.660	29.8	4.8	6.9
	DB	0.857	0.856	9.4	3.5	1.6

considering the absolute concentration of nutrients that limiting phytoplankton growth. In a similar vein, DIP concentrations, all of which were above 3.5 μg/L, with at least two sites surpassing 10 μg/L in spring (Table 1), indicate that phosphorus does not serve as a limiting factor during this season. While N and P are not the primary limiting factors for phytoplankton growth in Lake Qiandaohu when considering absolute concentration, they do largely control the maximum potential of phytoplankton biomass. As algae uptake N and P, the dissolved concentrations of these nutrients decrease, which may slow phytoplankton growth rates until an equilibrium is established between the production of new algal cells and their loss. This process ultimately defines the maximum potential of phytoplankton biomass, or the final yield that is limited by P or N&P.

In summary, Chla levels in Lake Qiandaohu appear to be potentially P-limited due to the high N:P ratio in the source materials and the dam-induced deep conditions, favoring P sedimentation over N. However, in the riverine zone, particularly at location JK, phytoplankton growth may be potentially co-limited by both N and P. This is mainly because the riverine zone, being relatively shallow and directly influenced by upstream inputs from the Xin'an River, which has a lower N:P ratio.

4.2. Implications for management

Statistical and experimental findings indicate that phytoplankton biomass throughout Lake Qiandaohu is potentially P-limited. Moreover, the maximum response of lnChla levels to lnTP closes a 1:1 ratio, a pattern observed not only in the Chinese Eastern Plains ecoregion (Zou et al. 2022) but also in lakes and reservoirs worldwide (Chorus and Spijkerman, 2021). This suggests a globally applicable pattern under potentially P-limited conditions, highlighting the importance of P control in mitigating algal blooms in Lake Qiandaohu. However, the seasonal variation in Chla concentration per unit of nutrient is largely

temperature-dependent. As temperature increases, the production of Chla per unit of N or P tends to be higher (Fig. S4 a and c). This suggests that temperature differences due to seasonal changes lead to significant variations in Chla concentration per unit of N or P. Additionally, for a few sites with an N:P ratio higher than 200, lnChla and lnTN consistently plot far from the upper scatter plots (Fig. S4 b), which are generally located far from the inflowing rivers or in areas with high water depth (Fig. 6). In contrast, the N:P ratio appears to have little influence on the relationship between lnChla and lnTP. On the other hand, the absence of algal blooms during low-temperature months, despite high nutrient levels, does not negate the need for controlling N and P. Instead, it is more logical to set preventive thresholds based on the upper boundary constraint line of relationships between Chla and nutrients, which is typically in late spring and summer months in Lake Qiandaohu.

To maintain Chla concentration below specific thresholds, the targets are as follows: below 10 μg/L, 12 μg/L, 20 μg/L, 24 μg/L, 40 μg/L, and 60 μg/L, respectively. The constraint line for TP against Chla in Fig. 3 helps determine these TP thresholds at 12.5 μg/L, 14.8 μg/L, 23.9 μg/L, 28.3 μg/L, 45.7 μg/L, and 66.7 μg/L. Importantly, these TP thresholds are based on peak P utilization efficiency by phytoplankton, typically observed in summer, and thus are more relevant to that season. Utilizing the empirical relationship between annual mean and summer mean TP levels in Lake Qiandaohu (Fig.8), we propose target control levels for annual mean TP concentration below 8.9 μg/L, 11.0 μg/L, 19.3 μg/L, 23.4 μg/L, 39.3 μg/L, and 58.5 μg/L, aligned with maintaining annual peak Chla levels beneath the respective thresholds. By examining the TP thresholds, we can deduce that if the annual average TP in Lake Qiandaohu complies with the Class I standard set by the Ministry of Ecology and Environment of the People's Republic of China (2002), where TP is less than 10 μg/L, the risk of algal blooms can be nearly eliminated (i.e., Chla < 10–12 μg/L). Conversely, if TP exceeds 25 μg/L, aligning with the Class II standard as stipulated by the same ministry (2002), phytoplankton may proliferate abnormally, with Chla levels ranging from 20 to 24 μg/L, potentially impairing the water body's functionality. We should note that for lakes or reservoirs where ecosystem-specific Chla control targets available, it is recommended that they adopt their own tailored Chla control targets to establish more appropriate N and P thresholds.

We further applied classic Vollenweider's loading-concentration response patterns to establish TP loading targets for Lake Qiandaohu. Specifically, the formula is $TP = TP_{in} / (1 + t_w^{0.5})$, where TP represents the annual mean TP concentration (μg/L) in the lake, TP_{in} is the discharge-weighted annual mean inflow concentration (μg/L), and t_w is the hydraulic retention time in years (Vollenweider, 1968). Based on our knowledge, the average annual inflow of Lake Qiandaohu is approximately 10 billion m³ during normal flow years, around 8 billion m³ during dry years, and typically about 14 billion m³ during wet years. The storage volume of Lake Qiandaohu has remained relatively stable in recent years, averaging approximately 14.5 billion m³ (Wang et al.

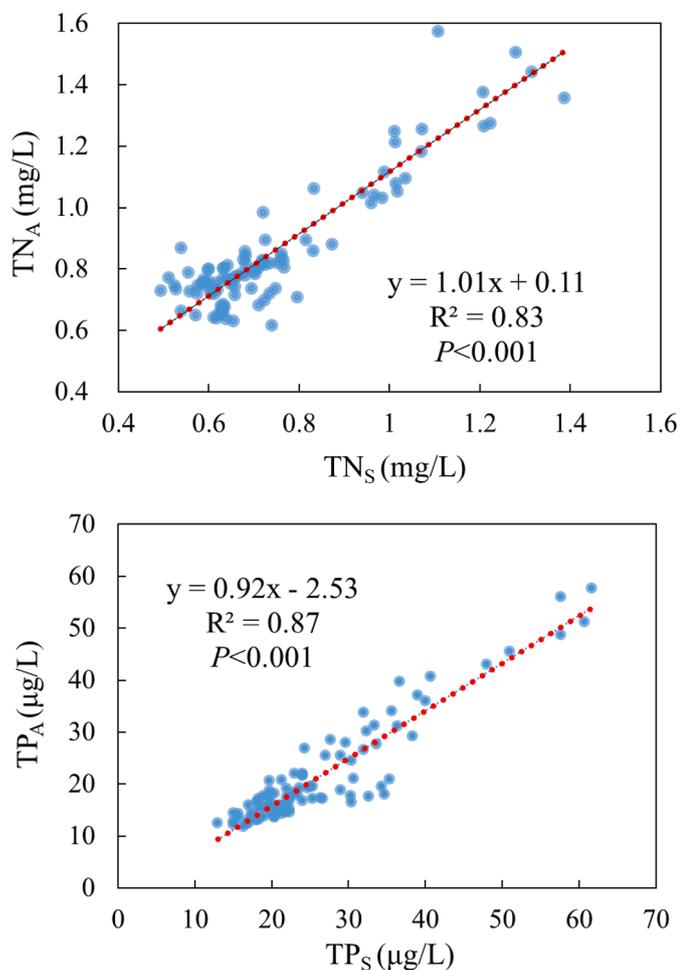


Fig. 8. The relationships between annual mean total nitrogen (TN_A) and its summer mean (TN_S), as well as between annual mean total phosphorus (TP_A) and its summer mean (TP_S), were examined across 100 sampling sites in Lake Qiandaohu.

2024). Utilizing these data and Vollenweider’s model, we have set control targets for TP loading to ensure that the annual peak Chla levels are maintained below 10 µg/L, 12 µg/L, 20 µg/L, 24 µg/L, 40 µg/L, and 60 µg/L for average, relatively dry and wet years, respectively. These P loading targets are outlined in Table 2.

Lake Qiandaohu is also subject to potential N&P-co-limitation. As depicted in Fig. 6, areas with TN concentrations exceeding 0.89 mg/L

Table 2

Thresholds for nitrogen and phosphorus, which includes mean total nitrogen concentration in summer (TN_S), annual mean TN concentration (TN_A), mean total phosphorus concentration in summer (TP_S), annual mean total phosphorus concentration (TP_A) and TP loading in normal (P_N, approximately 10 billion m³), wet (P_W, about 14 billion m³) and dry (P_D, about 8 billion m³) flow years for maintaining xchlorophylla (Chla) is lower than 10 µg/L, 12 µg/L, 20 µg/L, 24 µg/L, 40 µg/L and 60 µg/L. "NA" indicates that reducing TN to control the corresponding Chla evels in Lake Qiandaohu is not feasible due to P limitation

Chla targets (µg/L)	TN _S (mg/L)	TN _A (mg/L)	TP _S (µg/L)	TP _A (µg/L)	P _N loading (t)	P _W loading (t)	P _D loading (t)
10	NA	NA	12.5	8.9	163	247	124
12	NA	NA	14.8	11.0	202	306	154
20	0.89	1.01	23.9	19.3	354	537	270
24	1.00	1.12	28.3	23.4	428	649	326
40	1.36	1.48	45.7	39.3	719	1090	547
60	1.73	1.85	66.7	58.5	1071	1624	816

are predominantly found in the northwestern part of the lake. This suggests that an increase in N levels in these regions could potentially lead to a rise in Chla levels due to a relatively lower N:P ratio. The constraint line equation for TN on Chla demonstrates that maintaining Chla levels below the threshold of 10 µg/L and 12 µg/L is impractical when algal growth is primarily P-limited. To achieve Chla levels below 20 µg/L, 24 µg/L, 40 µg/L, and 60 µg/L, the corresponding TN concentrations required are 0.89 mg/L, 1.00 mg/L, 1.36 mg/L, and 1.73 mg/L, respectively. By applying the empirical relationship between annual mean and summer mean TN levels, as shown in Fig. 8, we suggest target control levels for annual mean TN concentration below 1.01 mg/L, 1.12 mg/L, 1.48 mg/L, and 1.85 mg/L to keep annual peak Chla levels below 20 µg/L, 24 µg/L, 40 µg/L, and 60 µg/L, respectively. This study does not recommend N input control targets for the lake, as most existing empirical models are tailored to the average TN concentration across the entire lake and the external N loading (Jones and Lee 1982; Jeppesen et al. 2005 and 2024). The co-limitation of N and P of phytoplankton biomass is mainly observed in the riverine zone of Lake Qiandaohu, making these models potentially unsuitable for this particular case. Furthermore, the study’s limited data span is inadequate for developing an empirical model that is specific to the unique conditions of Lake Qiandaohu.

Further consideration is necessary regarding implementing a dual N and P control strategy in the catchment of Lake Qiandaohu, where most areas are P-limited, and some areas, such as the riverine zone, exhibit N&P-co-limitation. As Fig. 3 suggests, N control alone is insufficient to achieve low Chla targets in Lake Qiandaohu; P reduction is also necessary to reach below 20 µg/L. Clearly, dual nutrients control could be useful for algal blooms control in the northwest area of Lake Qiandaohu and positively impact downstream areas like the Fuchunjiang Reservoir, which, being less deep and prone to N&P-co-limitation, may support N playing a key role in phytoplankton growth (He et al. 2024). However, if economic resource is limited, more localized control measures could serve as alternative strategies. The spatial interpolation map indicates that areas with annual average Chla exceeding 20 µg/L and annual peak Chla surpassing 40 µg/L are mainly in the northwestern regions of Lake Qiandaohu (Fig. 9). In these relatively higher Chla areas, *in-situ* technologies like floating macrophytes beds may offer a more cost-effective solution for controlling algal blooms. Although floating beds are typically used in nutrient-rich waters (Samal et al. 2019), they can also thrive in parts of Lake Qiandaohu with relatively lower N and P concentrations, such as common macrophytes like *Ipomoea aquatica* and *water celery*, as well as ornamental macrophytes like the floating-leaved *Jussiaea stipulacea*, the submerged *Myriophyllum aquaticum*, and the emergent *Acorus calamus* (Tang et al. 2022; Ni et al. 2024). Two studies have demonstrated that ecological floating beds can markedly enhance the denitrification and N removal capabilities of Lake Qiandaohu, thereby facilitating N reduction. Furthermore, the presence of these floating beds supports a dense macrophyte growth on the water surface, which effectively suppresses algae growth through shading, allelopathy, and by promoting increased zooplankton grazing (Pakdel et al. 2013; Cao et al. 2018).

5. Conclusion

This study sheds light on the impact of N and P on phytoplankton growth in deep subtropical Lake Qiandaohu, China. Empirical and experimental results underscore P as the key potential limiting nutrient, evidenced by a near 1:1 ratio between Chla production and TP levels. This relationship has been instrumental in establishing TP thresholds to regulate Chla concentrations at levels indicative of algal bloom severity—10, 12, 20, 24, 40, and 60 µg/L. Using these thresholds, the study has leveraged Vollenweider’s models to set TP loading targets that align with diverse hydrological conditions, from normal to wet and dry years, ensuring nutrient balanced phytoplankton growth.

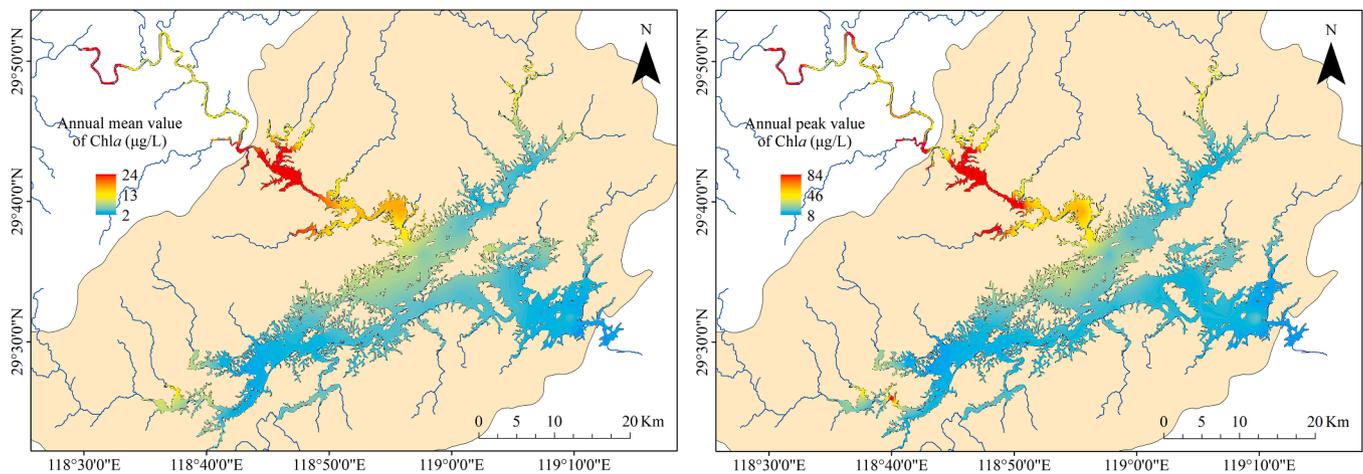


Fig. 9. Spatial interpolation map of annual average and peak chlorophyll a (Chla) in Lake Qiandaohu from May 2020 to April 2021.

The predominance of potential P limitation in large, deep reservoirs like Lake Qiandaohu is attributed to the elevated N:P ratio in the hilly basin's source materials, which, combined with a stratified water column, promotes more P sedimentation and retention over N. However, the riverine zone exhibits potentially N and P co-limitation due to unsettled particulate matter that elevates the N:P ratio, thus affecting nutrient availability for phytoplankton. To counteract this, the study introduces TN thresholds and proposes localized control measures, such as floating macrophytes beds, as alternatives.

In the context of China's "one-size-fits-all" water quality management policies, including the Environmental Quality Standards for Surface Water (GB3838–2022), this research offers a tailored, scientifically informed strategy for managing eutrophication in large, deep subtropical lakes and reservoirs. The study also calls for further research to refine localized models for Lake Qiandaohu and similar water bodies, with the goal of developing more precise eutrophication management policies. It emphasizes the need for future studies to consider the response of phytoplankton to climate change, especially the impact of increasingly extreme rainfall events on the dynamics between nutrient loads, concentrations, and algal growth.

CRediT authorship contribution statement

Hai Xu: Writing – review & editing, Data curation, Conceptualization. **Wei Zou:** Writing – review & editing, Writing – original draft, Data curation, Conceptualization. **Guangwei Zhu:** Writing – review & editing, Resources, Data curation. **Yu Qiu:** Investigation. **Huiyun Li:** Visualization, Software, Formal analysis, Data curation. **Mengyuan Zhu:** Writing – review & editing, Investigation, Data curation. **Hans W. Paerl:** Writing – review & editing, Conceptualization. **Zhixu Wu:** Supervision, Resources. **Boqiang Qin:** Supervision, Resources, Conceptualization. **Yunlin Zhang:** Validation, Supervision.

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.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.watres.2024.122787](https://doi.org/10.1016/j.watres.2024.122787).

Data availability

Data will be made available on request.

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