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Contributions of external nutrient loading and internal cycling to cyanobacterial bloom dynamics in Lake Taihu, China: Implications for nutrient management

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Abstract

Harmful cyanobacterial blooms (CyanoHABs) are linked to increasing anthropogenic nitrogen (N) and phosphorus (P) inputs. However, CyanoHABs in many large lakes continue despite extensive abatement efforts, mostly focused on external P loading. Internal nutrient cycling can modify nutrient availability and limitation; thus, understanding the relative importance of external vs. internal nutrient loading is essential for developing effective mitigation strategies for CyanoHABs. We estimated long-term nutrient budgets for Lake Taihu, China, from mass balance models using extensive monitoring of input and output nutrient data from 2005 to 2018 to quantify contributions from internal nutrient loading. The nutrient mass balance showed that 9% and 63% of annual external N and P inputs, respectively, were retained in the lake. Denitrification removed 54% of external N loading and can thus help explain rapid decreases in lake N concentrations and summer N limitation. Water column NH_4^+ regeneration can help sustain CyanoHABs over the short term and contributed 38–58% of potential NH_4^+ demand for summer-fall, *Microcystis*-dominated blooms. Internal P release contributed 23–90% of CyanoHABs P demand, although Taihu was a net P sink on an annual scale. Our results show that internal nutrient cycling helps sustain CyanoHABs in Taihu, despite reductions in external nutrient inputs. Furthermore, N is leaving the lake faster than P, thereby creating persistent N limitation. Therefore, parallel reductions in external N loading, along with P, will be most effective in reducing CyanoHABs and accelerate the recovery process in this and other large, shallow lakes.

Cultural eutrophication is a significant threat facing freshwater ecosystems globally (Scheffer et al. 1993; Jeppesen et al. 2017). Cyanobacterial harmful algal blooms (CyanoHABs) are a troubling indicator of accelerating eutrophication (Brookes and Carey 2011; Paerl and Otten 2013) and adversely affect water and habitat quality, drinking water supplies, food webs, and overall sustainability of impacted systems (Gubelit and Berezina 2010; Paerl et al. 2011; Paerl and Otten 2013). Nitrogen (N) and phosphorus (P) are the key nutrients linked to CyanoHAB proliferation in freshwater lakes (Lewis et al. 2011; Paerl et al. 2014*b*, 2016*a*). For effective management of lake eutrophication, it is therefore essential to determine the extent to which both nutrients (N and P) should be controlled.

Phosphorus input restrictions were implemented widely for lake eutrophication management during previous decades (Paerl et al. 2016*b*). This approach was based on the premise that P is the ultimate limiting nutrient, whereas N-limitation is only temporary, and ecosystem N requirements can be met by cyanobacterial N_2 fixation (Scott and McCarthy 2010). Therefore, reducing N inputs from external sources was

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Additional Supporting Information may be found in the online version of this article.

questioned as a useful management strategy. Phosphorus reductions have decreased eutrophication rates and reduced algal bloom potentials in some cases (Carpenter 2008; Schindler et al. 2016). However, eutrophication control strategies based only on P reductions have failed in many other waterbodies, especially large, shallow lakes, such as Lakes Apopka, George, and Okeechobee, Florida, U.S.A. (Havens et al. 2001), Lake Kasumigaura, Japan (Conley et al. 2009; Paerl et al. 2011, 2016*b*), and Lake Erie, Canada/U.S.A. (Newell et al. 2019).

Anthropogenic activities have increased N loading to freshwaters relative to P in many instances (Conley et al. 2009; Peñuelas et al. 2013). Excessive N loads have promoted non-N_2 fixing CyanoHABs, especially the toxin producing, colonial, scum forming (buoyant) cyanoHAB *Microcystis* (Paerl 2008; Paerl et al. 2016*a*). Moreover, N_2 fixation in lakes only satisfies a small proportion of annual N requirements, even in the presence of N_2 fixers (Ferber et al. 2004; Dolman et al. 2012; Gobler et al. 2016), and thus N_2 fixation is generally not sufficient to offset managed reductions of external N loading (Scott and McCarthy 2010; Paerl et al. 2014*b*, 2016*b*; Shatwell and Köhler 2019). Results of nutrient enrichment experiments at a range of scales, from bottle bioassay to whole lake experiments, showed that growth of phytoplankton and formation of CyanoHABs are most frequently controlled by combined N and P inputs (Lewis et al. 2011; Paerl et al. 2014*b*, 2016*b*; Xu et al. 2015; Shatwell and Köhler 2019). Furthermore, the limiting roles of N and P vary temporally across seasons, geographically with regions, and even spatially within a lake (Chaffin et al. 2013; Xu et al. 2015; Bullerjahn et al. 2016; Janssen et al. 2017).

Nutrient limitation patterns depend on external loading and internal nutrient cycling and loading. Nutrients entering lakes undergo different cycling dynamics and fates, including, but not limited to: assimilation and regeneration by organisms (e.g., bacteria, phytoplankton, periphyton and benthic microalgae, and macrophytes); sedimentation and burial; N loss to the atmosphere via denitrification; and release from sediment by resuspension, diffusion, decomposition of organic matter, and hypoxic/anoxic events (Egemose et al. 2011; Palmer-Felgate et al. 2011; Søndergaard et al. 2013; McCarthy et al. 2016). If external N and/or P inputs are reduced, then cyanoHABs may still occur due to legacy N and P loading, particularly for P, which does not have a gaseous form that can escape from the system.

Internal sediment P loading is well studied (Janssen et al. 2017; Lepori and Roberts 2017; Paytan et al. 2017), and rates of sediment P release vary seasonally, with increases often observed in warm seasons (Spears et al. 2012; Yang et al. 2013). Sediment P release can equal or exceed external P loading in some lakes (Søndergaard et al. 2013; Nürnberg and LaZerte 2016; Wu et al. 2017). Reducing external P inputs may thus be counterbalanced by internal loading from the "legacy" P pool in sediments (Jeppesen et al. 2005; Søndergaard et al. 2013). This internal loading is frequently implicated in lake recovery delays after external P loading reductions (Phillips et al. 2005; Søndergaard et al. 2005, 2013; Watson et al. 2016).

N is "lost" to the atmosphere via denitrification (Seitzinger et al. 2006; McCarthy et al. 2007; Paerl et al. 2016*b*), and denitrification increases with eutrophication due to organic matter availability and hypoxic/anoxic zones conducive to this process (Finlay et al. 2013; Small et al. 2014; Olsen et al. 2015; Ding et al. 2018). Denitrification often dominates N removal pathways in eutrophic, shallow lakes and may drive aquatic systems toward N limitation (Seitzinger et al. 2006; Harrison et al. 2009; McCarthy et al. 2016). However, this removal mechanism is offset, to varying degrees, by internal N regeneration of legacy N inputs from the watershed or accumulated in lake sediments and in biomass, which help sustain phytoplankton growth during low nutrient/high biomass periods (McCarthy et al. 2016; Van Meter et al. 2018). In large, shallow lakes with long hydraulic retention times, internal nutrient cycling may modify lake nutrient dynamics and induce seasonal changes in N and P availability, which affects phytoplankton growth and bloom patterns (Kilinc and Moss 2002; McCarthy et al. 2007, 2016).

Lake Taihu is a large, shallow lake, where non N_2-fixing CyanoHABs (*Microcystis* spp.) cause serious water supply and economic disruptions (Qin et al. 2010). Nutrient inputs have increased since the 1980s, leading to accelerated eutrophication and increasingly frequent and spatially expanding toxic CyanoHABs (Qin et al. 2007; Duan et al. 2009). After a drinking water crisis in 2007, the Chinese government adopted a series of measures to control eutrophication and CyanoHABs in Lake Taihu (Wu and Hu 2008; Yang and Liu 2010). However, CyanoHABs have not decreased in size and frequency as expected from abatement efforts (Qin et al. 2015, 2019; Yang et al. 2016). Considerable research focusing on abiotic factors has been conducted in Taihu to improve the understanding of mechanisms supporting and sustaining CyanoHABs. These factors include nutrient supply rates and ratios, external nutrient loading, and temperature and wind conditions, all influenced by climate change (Liu et al. 2011; Xu et al. 2015; Yang et al. 2016; Zhang et al. 2016; Janssen et al. 2017; Deng et al. 2018). While the role of internal nutrient cycling in Lake Taihu eutrophication is recognized (McCarthy et al. 2007; Paerl et al. 2011, 2014*b*, 2016*a*,*b*; Hampel et al. 2018; Wang et al. 2019), its quantitative importance in supporting and sustaining CyanoHABs in large lake systems like Taihu is not well established.

The aim of our study was to utilize a large, long-term, intensive water quality monitoring data set of nutrient concentrations and fluxes into and out of Lake Taihu to quantify the relative importance of internal cycling processes vs. external nutrient inputs in determining magnitudes and duration of CyanoHABs. We hypothesized that: (1) internal N and P loads represent a large nutrient source driving summer

CyanoHABs; (2) denitrification removes a large proportion of external N loads and contributes to seasonal N deficiency; (3) N_2 fixation does not exceed denitrification and thus does not alleviate long-term summer N deficiency; and (4) ammonium regeneration in the water column helps sustain cyanoHAB biomass during N deficiency.

Methods

Lake description

Lake Taihu is the third largest freshwater lake in China and is the primary drinking water source for ~ 20 million people (Qin et al. 2010). Taihu is located in the southeastern region of the Yangtze River delta (latitude 30°55′40″–31°32′58″N; longitude 119°52′32″–120°36′10″E). It is a large, shallow (mean depth ~ 2 m), polymictic lake, with a surface area of 2338 km^2, a catchment area of 36,500 km^2, and a volume of 4.4 billion m^3 (Qin et al. 2007, 2010). In the Taihu basin, the greatest amount of rainfall occurs in summer and the least in winter. Annual freshwater input to the lake averages $88 \times 10^8\ \mathrm{m}^3$, and the average water retention time is approximately 180 d (Qin et al. 2007). The Taihu basin is characterized by a complex set of river networks, with 172 rivers, tributaries, and channels draining into the lake (Qin et al. 2007). Inflow is largely from surface runoff during rainfall events. Generally, freshwater inputs enter the lake from the southwest and western mountainous watershed, and the main outflow is through the Taipu River in East Taihu, which flows through Shanghai into the East China Sea (Fig. 1).

Water quality and sediment data

A long-term water quality monitoring program was implemented from 2005 to 2018 by the Taihu Laboratory for Lake Ecosystem Research (TLLER), Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences. Of the 32 total monitoring sites, 15 sites were monitored monthly, and 17 sites were monitored quarterly. In this study, extensive water quality data for the lake were obtained from TLLER to reveal in-lake nutrient and CyanoHABs dynamics during 2005–2018. Monitored water quality parameters included total nitrogen (TN; unfiltered), total dissolved nitrogen, total particulate nitrogen, ammonium (NH_4-N), nitrate (NO_3-N), nitrite (NO_2-N), total phosphorus (TP; unfiltered), total dissolved phosphorus, total particulate phosphorus, soluble reactive phosphorus (SRP), and chlorophyll *a* (Chl *a*). Detailed analytical methods for water quality parameters are described in Xu et al. (2010). Sediment TN and TP content data were obtained from TLLER to calculate TN : TP ratios in surface sediments. Sediment monitoring at 32 sites was conducted in May of each year. Sediment cores were collected using a modified gravity corer, and fresh surface sediment (0–2 cm) subsamples were collected from the cores for TN and TP analysis as described in the "Method S1" section in Supporting Information.

Quarterly nutrient and Chl *a* data for 32 sites in the lake were divided into eight regions to best capture spatial variation in cyanoHABs and nutrients in Taihu. The eight regions included Meiliang Bay, Zhushan Bay, Gonghu Bay, West Lake, South Lake, Central Lake, Xukou Bay, and East Lake (Fig. 1).

Inventory calculations of in-lake nutrients and Chl *a*

The depth-integrated nutrient and Chl *a* inventories were calculated based on quarterly data from 32 sampling sites from 2005 to 2018. Using the Thiessen polygon method (Zhao et al. 2013), the lake was divided into 32 polygons whose water quality was represented by a sampling station. Water level and bottom topography data were obtained from TLLER and the Taihu Basin Authority (2012) and used to calculate water depth. Average water depth of each polygonal area was calculated as the difference between average polygon bottom surface elevation and mean water level. Volumes under each polygon were calculated as the polygonal area times average water depth. Nutrient and Chl *a* inventories for each polygon were calculated by multiplying concentration by volume of the polygonal solid, and inventories for the whole lake were calculated as the sum of all 32 polygonal areas.

Nutrient budget calculation

We quantified N and P inputs and outputs for Lake Taihu to determine nutrient mass balances. Total inputs were considered as riverine inputs plus atmospheric deposition onto the lake surface and N_2 fixation. Total outputs were considered as riverine outflows, removal by resource extraction (e.g., fisheries, cyanoHAB biomass collection, drinking water intake, etc.) and loss by denitrification for N.

Annual nutrient inputs and outputs, as well as water flux data during the calendar years 2005–2018, were obtained from Zhang (2014) and the Taihu Health Report of the Taihu Basin Authority (2013–2018). Tributary inputs and outputs were estimated by measuring flow volume and nutrient concentrations (Wang et al. 2017; *see* "Method S2" section in Supporting Information). Atmospheric deposition of TP and TN directly onto the lake were determined by Zhai et al. (2009), Yu et al. (2011), and Zhang et al. (2014) and estimated from bulk deposition measurements made at six to ten stations around the lake. N_2 fixation rates in Taihu sediments and water column were measured monthly using acetylene reduction assays (Zhang et al. 2016; Yao et al. 2018). N inputs by N_2 fixation were estimated by extrapolating area-weighted N_2 fixation rates to the whole lake. Fish catch data from 2005 to 2018 were provided by Q. Zeng (pers. comm.; Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences; Supporting Information Table S1) to estimate nutrient outputs by fish harvesting as fish catch multiplied by the average nutrient content of fish (0.31% for P and 4.65% for N; Taihu Basin Authority 2014). Water consumption by drinking water plants was obtained from S. Xue (pers. comm.; Wuxi Water Group Co.) to estimate N and P losses via water consumption

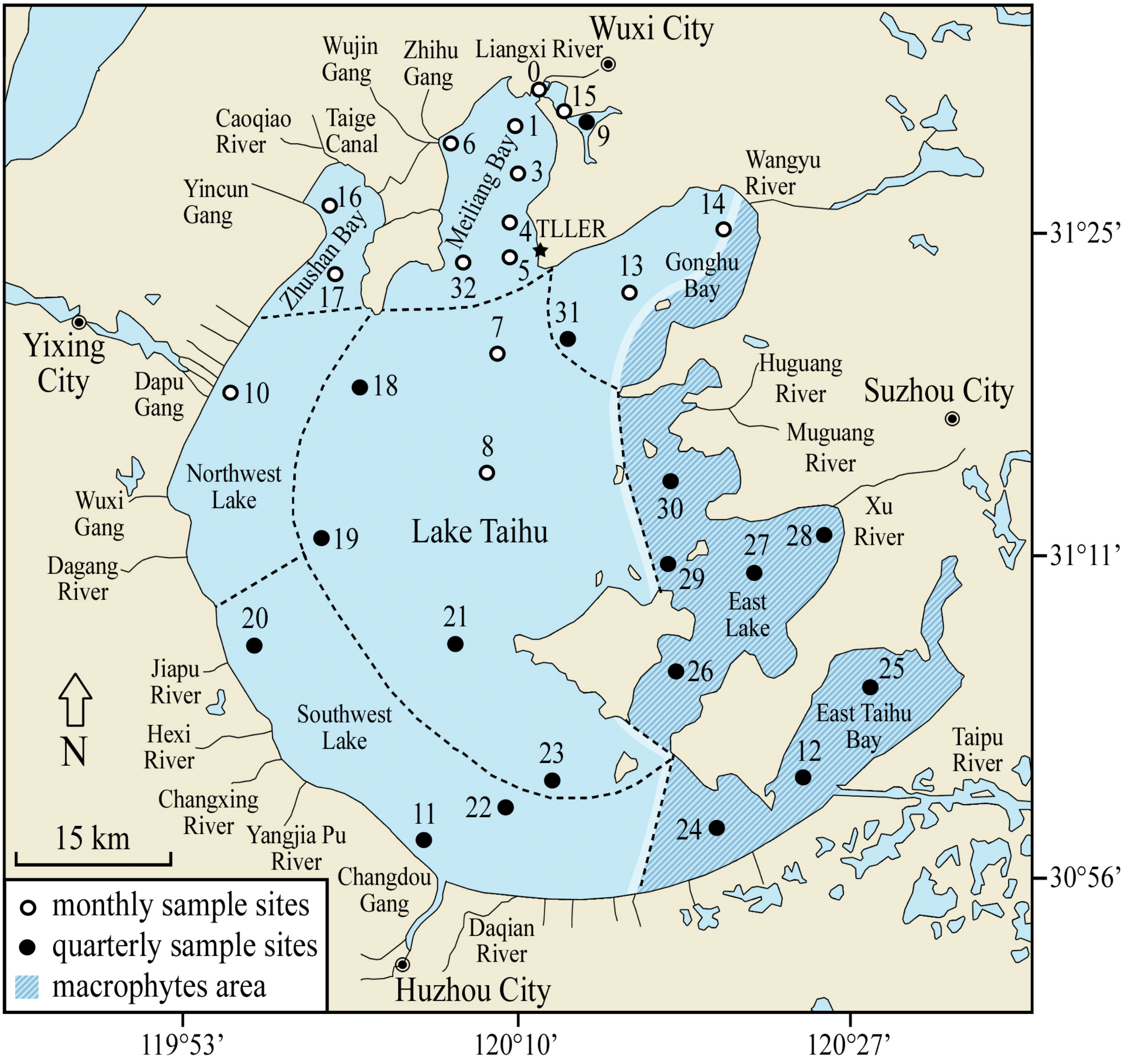

Fig 1. Monitoring sites on Lake Taihu: 15 sites (white circles) for monthly monitoring and 17 sites (black circles) for quarterly monitoring.

(as extracted water volume multiplied by ambient nutrient concentrations measured by TLLER). CyanoHAB biomass was harvested manually from the lake since 2007. Data on biomass of cyanobacteria harvested between 2007 and 2018 was provided by Z. Zhang (pers. comm.; Cyanobacteria management office of Wuxi Resources Bureau) to estimate nutrient removal from algal harvesting as cyanobacterial biomass multiplied by average nutrient content of cyanobacterial dry biomass (0.68% for P and 6.70% for N; Taihu Basin Authority 2014).

Annual N and P retention (R) in the lake was calculated as the difference between the mass (M) inputs and outputs from the lake:

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

where M_{in} is the input from rivers, M_{atmos} is the input from atmosphere, M_{fixation} is the input from N_2 fixation, M_{out} is output from rivers, M_{intake} is output from drinking water intake consumption, M_{algal} is output from algal harvesting, M_{fish} is output from fish catch, and M_{dnf} is output by denitrification.

Estimation of N loss by burial and denitrification

It is difficult to measure N burial rates in Lake Taihu directly due to frequent wind-driven resuspension events and removal of N by denitrification. Thus, N burial rate was estimated based on net TP retention and surficial sediment TN to TP ratios (Molot and Dillon 1993; Nõges et al. 1998). This method assumes that all net retained P is stored in the sediments, and the sediment N to P ratio, when multiplied by the P flux to sediment, yields an estimate of N burial.

$$N_{\text{burial}} = \left(P_{\text{R}} - \Delta P_{\text{storage}}\right) \times N:P_{\text{sediment}} \tag{2}$$

where P_{R} is P retention, $\Delta P_{\text{storage}}$ is the change in water column P inventory between the beginning and end of the season or year, and $N{:}P_{\text{sediment}}$ is surficial sediment TN to TP ratio.

Loss of N via denitrification was calculated as the residual (unmeasured) in the mass balance; that is, denitrification is equal to total internal N loss less N burial to sediment.

$$\begin{aligned} N_{\text{denitrification}} = (&M_{\text{in}} + M_{\text{atmos}} + M_{\text{fixation}} - M_{\text{out}} - M_{\text{intake}} \\ &- M_{\text{algal}} - M_{\text{fish}} - \Delta N_{\text{storage}}) - N_{\text{burial}} \end{aligned} \tag{3}$$

where $\Delta N_{\text{storage}}$ is the change in water column N inventory between the beginning and end of the season or year, and N_{burial} is N loss to sediment per season or year.

Water column NH_4^+ regeneration and potential uptake

NH_4^+ regeneration and potential uptake rates were obtained from McCarthy et al. (2007), Paerl et al. (2011), and Hampel et al. (2018). The methodology for determining N regeneration and potential uptake has been described in detail by Hampel et al. (2018).

To scale regeneration rates for comparison with external loads (Hampel et al. 2018), the lake area (2338 km^2) was divided into four sections varying in habitat and biogeochemical properties: (1) three northern bays (361.8 km^2) most affected by CyanoHABs; (2) the main lake (1524 km^2); (3) the east Taihu Lake (ELT) region, dominated by rooted and floating macrophytes (357.5 km^2); and (4) shorelines < 1 m deep (94.8 km^2). After regrouping the sampling sites, volumetric regeneration rates were converted to areal rates using water depth and extrapolated based on surface area of the appropriate lake region (Hampel et al. 2018).

Estimation of internal P loading

The mass balance-derived internal P load was quantified from annual and seasonal nutrient mass balances. Changes in water column nutrient storage during a specific time interval, compared with seasonal retention estimates, can be used to estimate internal P flux:

$$\text{Internal P flux} = \Delta P_{\text{storage}} - P_R \tag{4}$$

where $\Delta P_{\text{storage}}$ is the change in water column P inventory between the beginning and end of the season or year, and P_R is P retention per season or year. Positive values indicate net P release, and negative values indicate net P burial.

Internal P release processes are complex in shallow lakes. Wind-induced sediment resuspension occurs frequently, especially during storms (thunderstorms, typhoons), which are common in the region (Zhu et al. 2014). Resuspended particulate P will rapidly return to the sediments during calm periods and is generally not bioavailable for CyanoHABs. Therefore, we focused mainly on internal SRP loading. However, algae may rapidly assimilate SRP (Zhu et al. 2014); hence, it is difficult to directly measure internal SRP flux by observing changes in SRP concentrations in the water column. Here, we used changes in phytoplankton biomass (Chl *a*) in the water column to calculate the P demand required to support observed biomass based on known relationships between bioavailable P and Chl *a* (Xu et al. 2015), which remained quite constant during the study period. We estimated internal P flux based on the difference between P demand by phytoplankton and seasonal P retention. We modified Eq. 4 as follows:

$$\text{Internal P flux} = \Delta \text{DP}_{\text{storage}} - P_R \tag{5}$$

where $\Delta \text{DP}_{\text{storage}}$ is the change in water column P stored as phytoplankton biomass between the beginning and end of the season or year, and P_R is P retention per season or year. Positive values indicate net P release, and negative values indicate net P burial.

Data processing and statistical analysis

Monthly nutrient and Chl *a* data at 15 monitoring sites were categorized as mean values for spring (March–May), summer (June–August), autumn (September–November), and winter (December–February), as well as annual mean values for 2005–2018. Nutrient-Chl *a* relationships were derived using linear least squares regression on annual mean values to examine the effects of long-term changes in external nutrients loading on phytoplankton biomass. Uncertainty of annual N and P budgets used to calculate rates of internal loading and denitrification were estimated based on propagating the errors associated with each term in the budget using the root mean square error propagation method (Topping 1972; "Method S3" section in Supporting Information).

Results

External nutrient loading and retention

External loading of TN and TP to Taihu from tributaries during 2005–2018 varied from 16.6 to 24.1 g TN $\text{m}^{-2}\ \text{yr}^{-1}$ (average 19.3 g TN $\text{m}^{-2}\ \text{yr}^{-1}$) and from 0.73 to 1.20 g TP $\text{m}^{-2}\ \text{yr}^{-1}$ (average 0.89 g TP $\text{m}^{-2}\ \text{yr}^{-1}$; Table 1; all areal rates are by lake surface area). These tributary loads of TN and TP comprised 83% and 91% of total annual TN and TP inputs, respectively. Annual atmospheric deposition of TN and TP to Taihu were

Table 1. Mass loads of TN and TP from 2005 to 2018, and associated uncertainty (± standard error). Units are g m^{-2} yr^{-1}. NA and - indicates not assessed and not applicable, respectively. Uncertainty was assumed negligible for nutrient fluxes due to N_2 fixation (M_{fixation}), algal (M_{algal}) and fish (M_{fish}) harvesting, and drinking water intake consumption (M_{intake}).

		Input Loads			Output Loads					Retention	
Year	**Nutrient**	M_{in}	M_{atmos}	$\mathrm{M}_{\text{fixation}}$	M_{out}	M_{algal}	M_{intake}	M_{fish}	M_{dnf}	**Loads**	**% of inputs**
2005	TN	17.92 (9.0)	2.49 (0.23)	0.09	5.23 (2.6)	NA	1.63	0.69	11.67 (5.6)	1.27 (0.4)	6
	TP	0.74 (0.55)	0.09 (0.008)	-	0.19 (0.14)	NA	0.05	0.05		0.54 (0.24)	66
2006	TN	17.84 (8.9)	3.80 (0.34)	0.09	5.57 (2.6)	NA	1.02	0.70	12.19 (5.7)	2.25 (0.7)	10
	TP	0.73 (0.55)	0.09 (0.008)	-	0.19 (0.14)	NA	0.06	0.05		0.53 (0.24)	64
2007	TN	18.24 (9.1)	3.51 (0.32)	0.09	6.30 (3.2)	NA	0.99	0.63	12.96 (5.9)	0.95 (0.8)	4
	TP	0.78 (0.59)	0.09 (0.008)	-	0.24 (0.18)	NA	0.03	0.04		0.56 (0.26)	64
2008	TN	20.28 (10.1)	3.56 (0.32)	0.09	6.85 (3.5)	0.11	0.97	0.63	11.57 (6.6)	3.78 (1.5)	16
	TP	0.94 (0.71)	0.09 (0.008)	-	0.23 (0.17)	0.01	0.03	0.04		0.72 (0.30)	70
2009	TN	21.12 (10.6)	3.88 (0.35)	0.09	7.10 (3.6)	0.12	0.92	0.85	13.37 (6.8)	2.73 (1.4)	11
	TP	0.92 (0.70)	0.09 (0.008)	-	0.23 (0.17)	0.01	0.03	0.06		0.69 (0.30)	68
2010	TN	24.14 (12.1)	4.16 (0.38)	0.09	10.71 (5.4)	0.13	0.93	0.89	12.04 (8.1)	3.68 (1.5)	13
	TP	1.20 (0.90)	0.09 (0.008)	-	0.29 (0.22)	0.01	0.02	0.06		0.90 (0.39)	70
2011	TN	20.28 (10.2)	4.19 (0.38)	0.09	7.26 (3.7)	0.22	0.86	1.00	13.83 (6.6)	1.39 (1.1)	6
	TP	1.08 (0.81)	0.09 (0.008)	-	0.22 (0.17)	0.02	0.02	0.07		0.84 (0.34)	72
2012	TN	20.23 (10.1)	3.85 (0.35)	0.09	7.43 (3.7)	0.25	0.86	1.00	12.01 (6.6)	2.61 (1.2)	11
	TP	0.85 (0.64)	0.09 (0.008)	-	0.24 (0.18)	0.02	0.02	0.07		0.60 (0.28)	63
2013	TN	16.55 (8.3)	2.96. (0.27)	0.09	6.11 (3.1)	0.24	0.82	1.00	9.92 (5.4)	1.49 (1.1)	8
	TP	0.77 (0.58)	0.09 (0.008)	-	0.26 (0.19)	0.02	0.02	0.07		0.50 (0.26)	58
2014	TN	17.97 (9.0)	4.71 (0.42)	0.09	5.56 (2.8)	0.24	0.78	1.02	12.86 (5.8)	2.28 (1.1)	10
	TP	0.74 (0.56)	0.09 (0.008)	-	0.23 (0.17)	0.02	0.02	0.07		0.50 (0.24)	59
2015	TN	18.82 (9.4)	4.36 (0.39)	0.09	6.46 (3.3)	0.38	0.80	1.18	12.31 (5.1)	2.13 (0.9)	9
	TP	0.87 (0.66)	0.08 (0.007)		0.28 (0.21)	0.04	0.03	0.08		0.53 (0.29)	56
2016	TN	23.14 (11.6)	5.22 (0.47)	0.09	10.31 (5.2)	0.29	0.98	1.34	12.98 (7.9)	2.56 (2.2)	9
	TP	1.11 (0.84)	0.09 (0.009)	-	0.38 (0.29)	0.03	0.03	0.09		0.68 (0.37)	56
2017	TN	16.85 (8.4)	3.30 (0.30)	0.09	5.47 (2.8)	0.56	0.98	1.29	12.59 (5.4)	-0.66 (0.81)	
	TP	0.86 (0.64)	0.09 (0.008)	-	0.30 (0.23)	0.06	0.03	0.09		0.48 (0.28)	56
2018	TN	16.94 (8.5)	3.27 (0.30	0.09	4.70 (2.4)	0.35	0.98	0.97	13.49 (5.4)	-0.20 (1.0)	
	TP	0.81 (0.61)	0.13 (0.012)	-	0.21 (0.16)	0.04	0.03	0.06		0.61 (0.26)	64
Mean	TN	19.31 (9.7)	3.80 (0.34)	0.09	6.79 (3.5)	0.26	0.97	0.94	12.41 (6.3)	2.26 (1.21)	9
	TP	0.89 (0.68)	0.09 (0.008)	-	0.25 (0.19)	0.03	0.03	0.06		0.62 (0.28)	63

3.8 g TN m^{-2} yr^{-1} and 0.09 g TP m^{-2} yr^{-1}, which comprised 16% and 9% of total annual TN and TP inputs, respectively. Annual N inputs by N_2 fixation were very low (0.09 g TN m^{-2} yr^{-1}) and only contributed 0.38% of total TN inputs. External TN and TP loading, including tributary inputs, atmospheric deposition, and N_2 fixation, increased after the 2007 drinking water crisis until 2010, then decreased until 2013 (Fig. 2B,C). External TN and TP loading increased again from 2013 until 2016. Variability of annual external nutrient loading to Taihu followed changes in inflow water discharge (Fig. 2A).

Nutrient exports from the lake included river outflow, removal by resource extraction (drinking water intake, algae harvesting, and fish catches) and loss by denitrification for N (see below). TN and TP outflow through rivers ranged from 4.7 to 10.7 g TN m^{-2} yr^{-1} (average 6.8 g TN m^{-2} yr^{-1}) and from 0.19 to 0.39 g TP m^{-2} yr^{-1} (average 0.25 g TP m−2 yr −1) during 2005-2018, contributing 32% of total TN output and 70% of total TP output. TN and TP outputs by drinking water intakes contributed 5% and 8% of total TN and TP output, respectively, which ranged from 0.8 to 1.6 g TN m^{-2} yr^{-1} (average 1.0 g TN m^{-2} yr^{-1}) and 0.02 to 0.06 g TP m^{-2} yr^{-1} (average 0.03 g TP m^{-2} yr^{-1}). Fish were harvested from September to December each year, with corresponding outputs of 0.9 g TN m^{-2} yr^{-1} and 0.06 g TP m^{-2} yr^{-1}, contributing 4% and 17% of total TN and

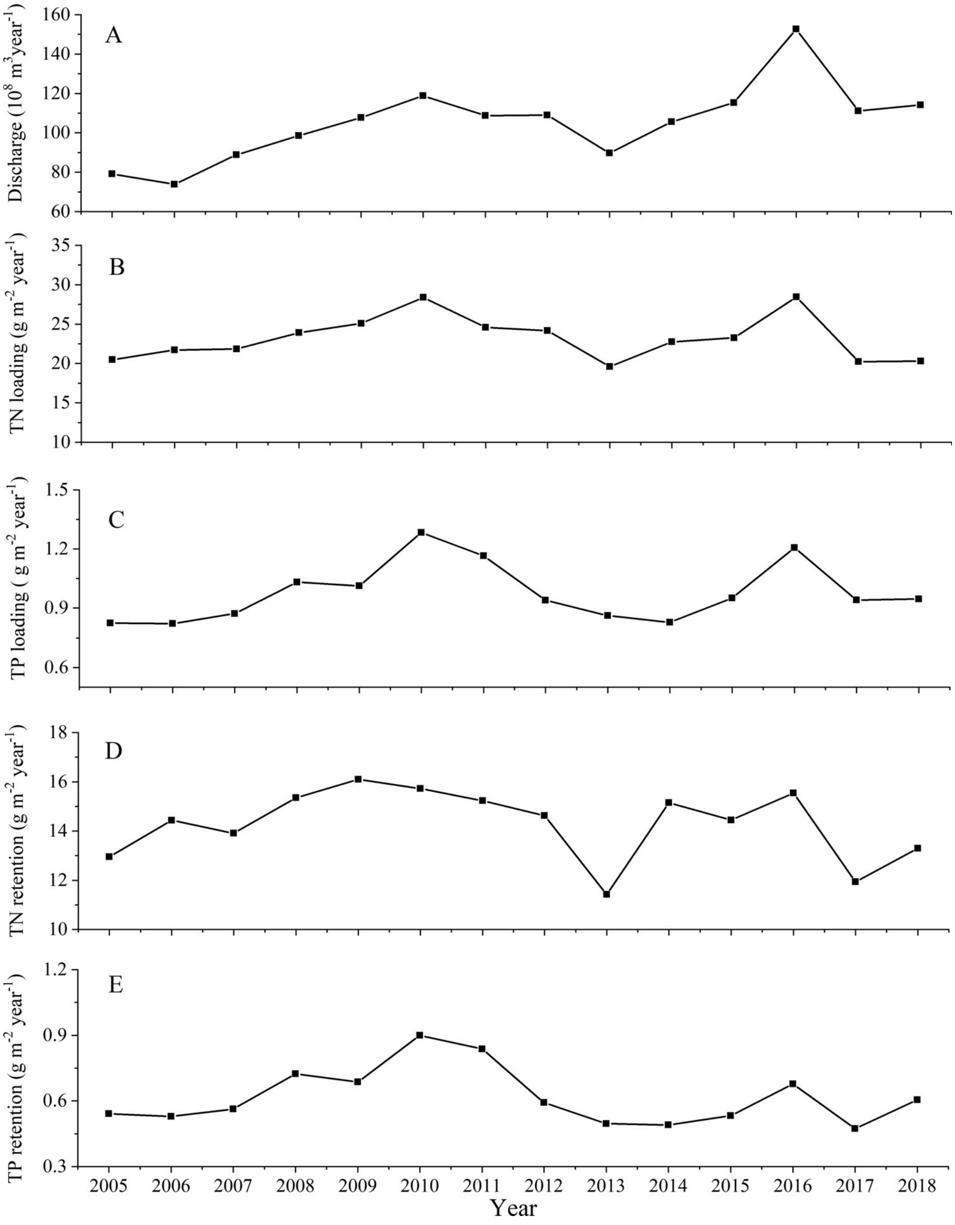

Fig 2. Variations in discharge (**A**), TN (**B**) and TP (**C**) loading, and TN (**D**) and TP (**E**) retention for 2005–2018.

TP output, respectively. Nutrient outputs through cyanobacterial biomass harvesting averaged 0.3 g TN m^{-2} yr^{-1} and 0.03 g TP m^{-2}yr^{-1}, contributing 1% and 7% of total TN and TP output, respectively.

Annual nutrient retention was calculated by subtracting nutrient exports from nutrient inputs. TP retention ranged from 0.47 to 0.90 g TP m^{-2} yr^{-1} (mean 0.62 g TP m^{-2} yr^{-1}) (Table 1), accounting for 50–72% (mean 63%) of external TP loading. Annual variability of TP retention showed similar patterns as external loading (Fig. 2E), and the fraction of TP retained declined with increasing discharge.

Based on net TP retention and surficial sediment TN:TP ratios, we estimated N burial (including temporary incorporation into unharvested biomass) and N loss by denitrification. Annual N burial ranged from 0.9 to 3.9 g TN m^{-2} yr^{-1} (mean 2.3 g TN m^{-2} yr^{-1}; Fig. 3). Annual N losses via denitrification ranged from 9.9 to 13.4 g TN m^{-2} year^{-1} (mean 12.4 g TN m^{-2} yr^{-1}; Fig. 3). These denitrification estimates accounted for 49 -66 % (mean 59%) of total TN output and 43 - 68% (mean 54%) of external TN loading. Denitrification rates were highest during summer (33% of annual denitrification), lowest during fall (18% of annual denitrification), and spring and winter averaged 25% and 23%, respectively, of annual denitrification.

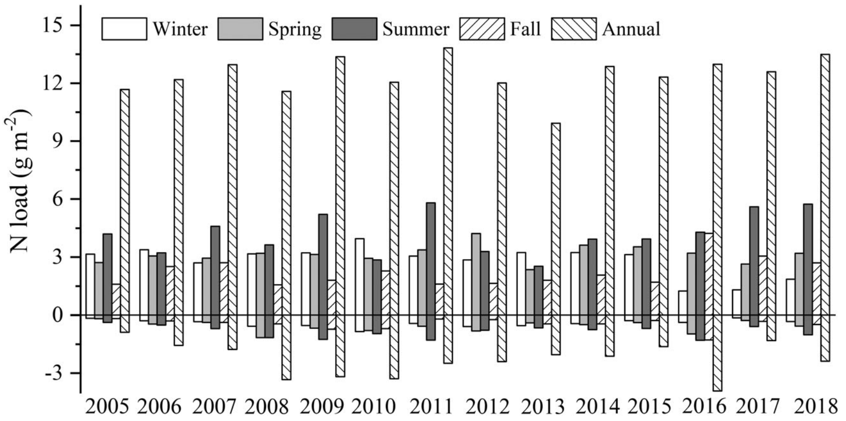

Fig 3. Seasonal and annual N loss and burial for 2005–2018. Positive values indicate N loss by denitrification. Negative values indicate net burial.

Annual TN retention was calculated by subtracting exports (including denitrification) from inputs, which ranged from 0.95 to 3.68 g TN m^{-2} yr^{-1} (mean 2.26 g TN m^{-2} yr^{-1}), accounting for 4 - 16% (mean 9%) of external TN loading (Table 1). The TN exports were higher than inputs in 2017 and 2018.

Annual trends for nutrient and Chl *a* concentrations and inventories

During the past 14 yr, annual mean area-weighted TN concentrations in the lake have decreased by 40% ($p < 0.01$; Fig. 4A). Considering that nutrient concentrations may be affected by fluctuating water levels, we calculated depth-integrated TN inventories. Annual mean area-weighted TN inventories for the entire lake also decreased, similar to decreases in TN concentrations (Supporting Information Fig. S1). However, annual mean area-weighted TP concentrations did not decline (Fig. 4B). Annual mean area-weighted Chl *a* concentrations increased slightly from 2005 to 2018, which peaked at 44 μg L^{-1} during 2017 (Fig. 4C).

Seasonal dynamics of nutrients and cyanobacterial blooms

Lake-wide average TN concentrations were higher (mean 3.27 mg L^{-1}) in winter and spring, with lower values ($\sim$ 1.89 mg L^{-1}) in summer and fall (Fig. 5A). NO_3-N concentrations were highest in spring ($\sim$ 1.95 mg L^{-1}) and lowest during summer and fall ($\sim$ 0.11 mg L^{-1}; Fig. 5B). In winter, NH_4-N concentrations ($\sim$ 0.76 mg L^{-1}) were approximately double the average concentration during other seasons (0.28–0.35 mg L^{-1}). The seasonality of NO_3-N and NH_4-N concentrations help explain the seasonal patterns of TN concentrations. Depth-integrated N inventories showed similar seasonal patterns to N concentrations (Supporting Information Fig. S2A–C).

TP concentrations for the whole lake were about 10% higher in summer ($\sim$ 0.12 mg L^{-1}) than spring and fall ($\sim$ 0.11 mg L^{-1}; Fig. 5D). Depth-integrated TP inventories exhibited more seasonality than TP concentrations, with higher values in summer (Supporting Information Fig. S2D). SRP concentrations and inventories were also higher in summer and fall (Fig. 5E, Supporting Information Fig. S2E). TN to TP mass ratios in Lake Taihu showed strong seasonal patterns, with values higher than 30 during spring and lower than 20 during summer and fall (Fig. 5G). Median Chl *a* concentrations exhibited an approximately threefold variation, with highest levels in summer (mean 22.0 μg L^{-1}) and lowest levels (mean 7.0 μg L^{-1}) in winter (Fig. 5F).

Long-term monthly monitoring revealed a more detailed assessment of seasonal dynamics in concentrations and inventories of N, P, and Chl *a* in the main cyanoHAB area (West Lake, Zhushan Bay, Meiliang Bay, Gonghu Bay, and the central lake; Supporting Information Figs. S3–S5). Generally, TN concentrations and inventories increased from late November to May, followed by a large decrease from late July into early November. TP concentrations remained stable from January to April and then sharply increased from May to July, reaching high values during August–October, with the largest increases observed in the northern bays (e.g., Meiliang Bay; Supporting Information Fig. S4). CyanoHAB biomass (as Chl *a*) in different regions showed strong recurring seasonality, with blooms starting in April or May, peaking from July to October, and lasting well into November (Supporting Information Fig. S5).

Water column NH_4^+ regeneration and potential uptake

NH_4^+ regeneration rates ranged from 3.0 to 33.0 μg L^{-1} h^{-1} and averaged 5.0 μg L^{-1} h^{-1} in Taihu (Hampel et al. 2018). Potential NH_4^+ uptake rates ranged from 2.0 to 95.0 μg L^{-1} h^{-1} and averaged 12.3 μg L^{-1} h^{-1} (Hampel et al. 2018). NH_4^+ regeneration contributed 38–58% of potential NH_4^+ demand for summer-fall, *Microcystis*-dominated blooms (Hampel et al. 2018).

Since Taihu is shallow and well mixed, NH_4^+ regeneration rates were extrapolated to the whole water column to estimate

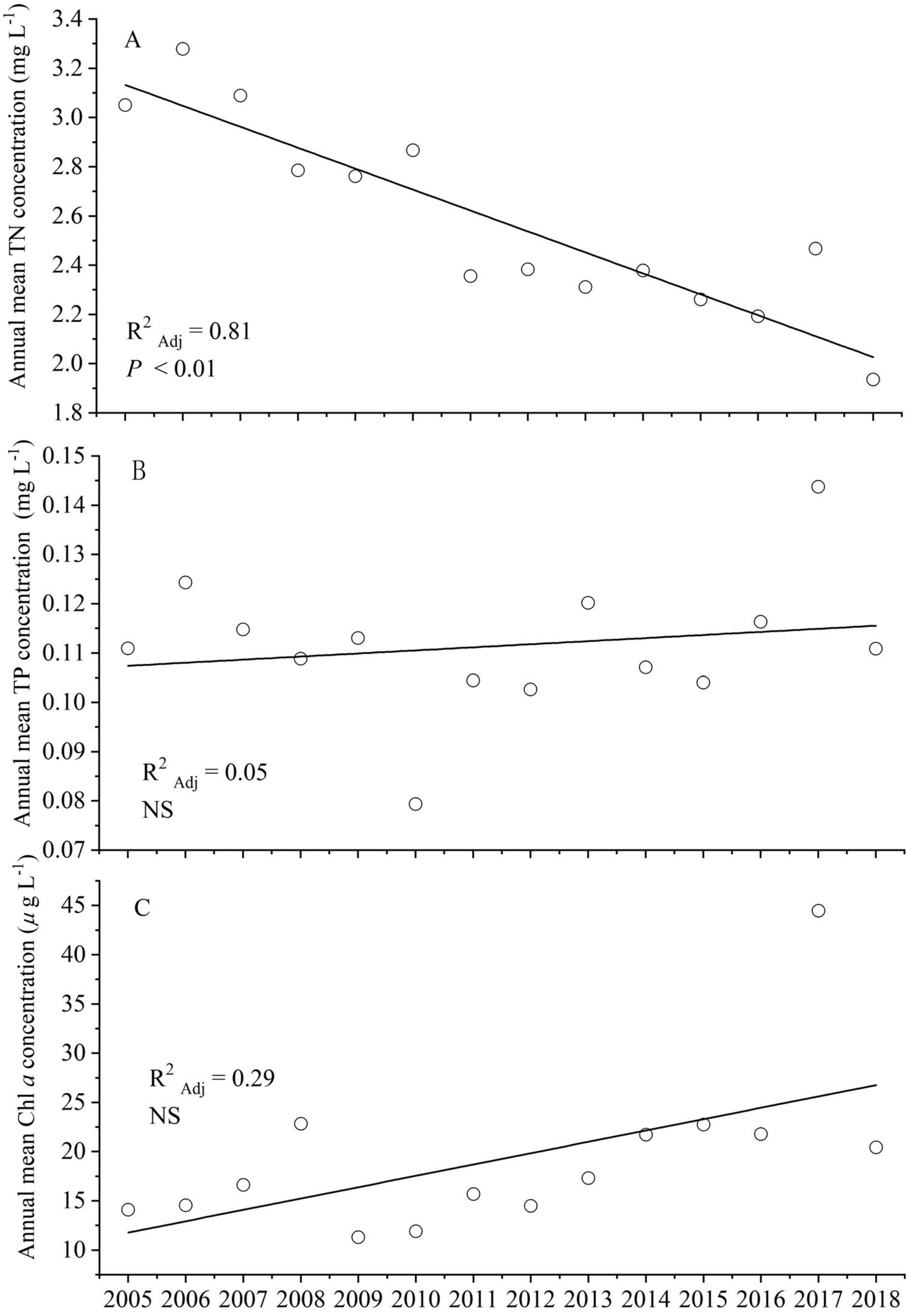

Fig 4. Trends in nutrient and Chl *a* levels averaged for Lake Taihu from 2005 to 2018 (**A**: TN concentration; **B**: TP concentration; **C**: Chl *a* concentration).

a total internal NH_4^+ load from water column recycling. Annual water column NH_4^+ regeneration provided bioavailable NH_4^+ at about 200% of total external TN loading (Hampel et al. 2018). Seasonal fluctuations in external loads and remineralization showed that, during winter, water column NH_4^+ regeneration was equivalent to about 60% of the TN loading. However, during summer and fall, NH_4^+ regeneration was 260–340% of external TN loading (Fig. 6).

Internal P loading dynamics

Internal TP loading was quantified from nutrient balances based on seasonal changes in Chl *a* and P retention. Annual

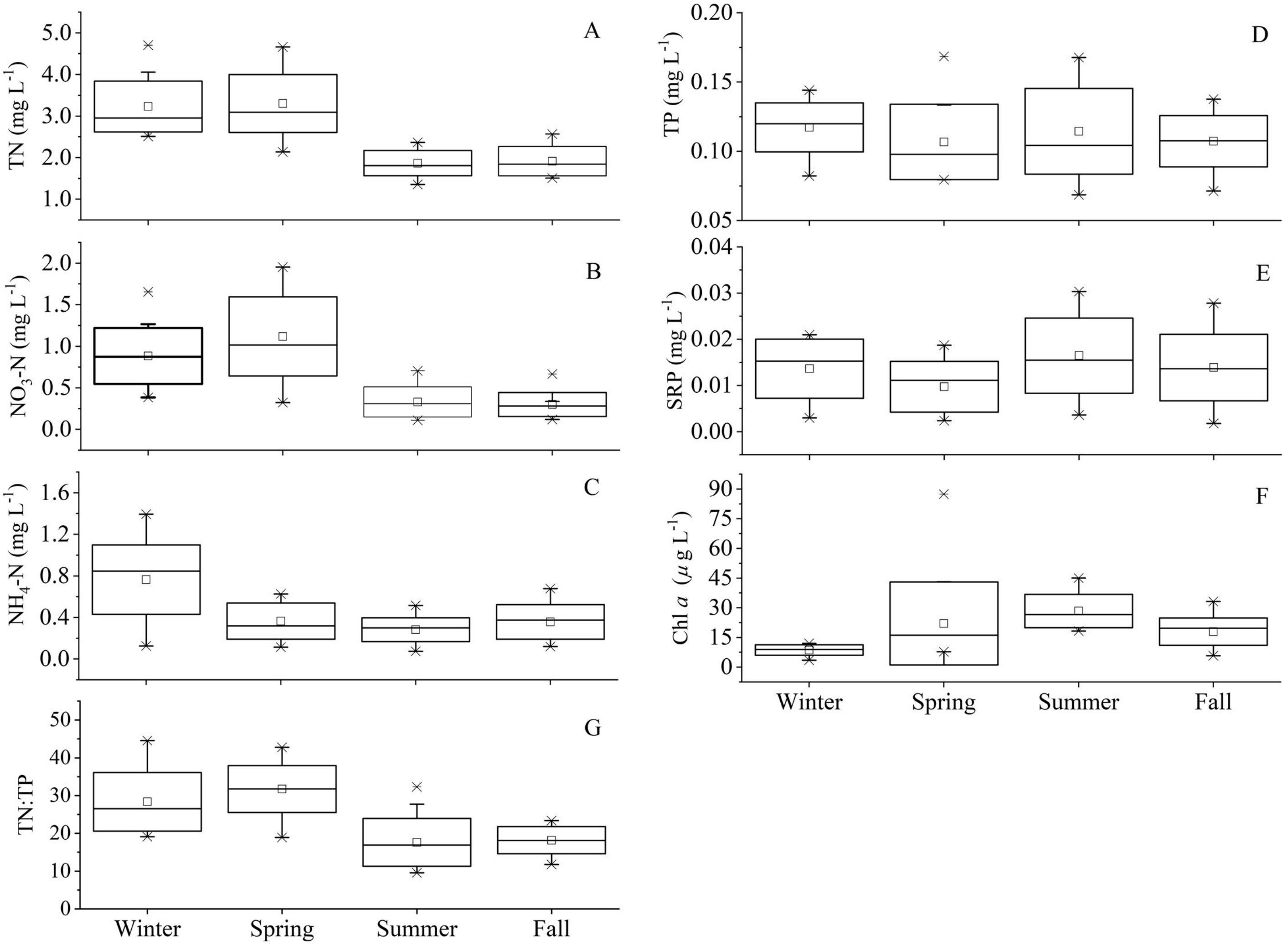

Fig 5. Seasonal changes in area-weighted TN (**A**), NO3-N (**B**), NH4-N (**C**), TP (D), SRP (**E**), and Chl a (**F**) concentrations in Lake Taihu. Center horizontal lines show the medians, center squares show the means, box limits indicate the 25th and 75th percentiles as determined by Origin software, whiskers extend to minimum and maximum values.

internal TP loading ranged from 0.03 g TP m^{-2} yr^{-1} in 2007 to 0.89 g TP m^{-2} yr^{-1} in 2017 (mean 0.16 g TP m^{-2} yr^{-1}; Fig. 7). Sediment P release mainly occurred during spring and summer. TP released from sediments contributed 23 % in spring 2007 to 90% in spring 2017 (mean 40%) of TP required to support cyanoHAB biomass. No net P release was observed in 2010, 2011, or 2016 due to very high external loadings.

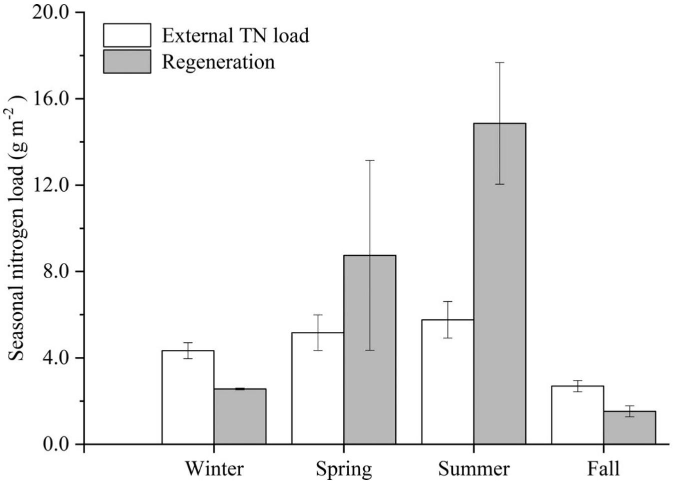

Fig 6. Mean seasonal TN loading and extrapolated internal whole-lake NH$_4^+$ regeneration load in Lake Taihu.

Discussion

Responses of lake nutrient concentrations to variations in external loading

Nutrient management strategies for N and P pollution control were implemented in the Taihu watershed after the 2007 drinking water crisis (Qin et al. 2019). In response to these measures, TN and TP concentrations decreased in rivers around the lake after 2007 (Yi et al. 2016). However, annual

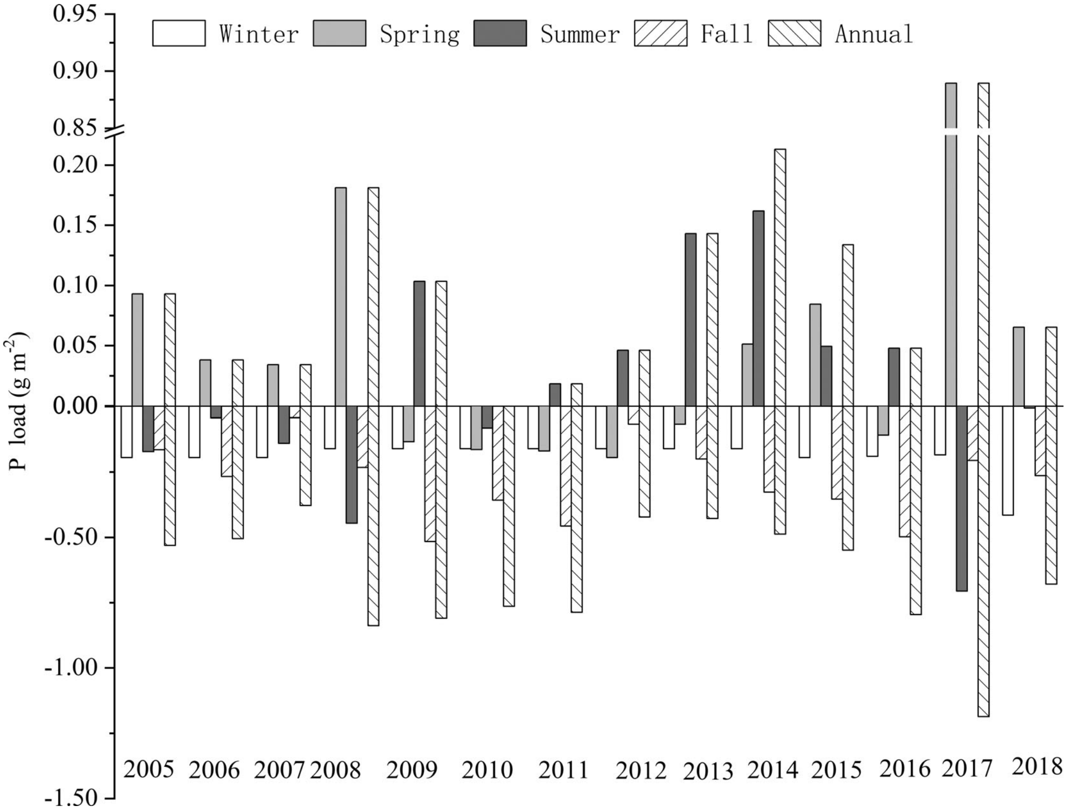

Fig 7. Seasonal and annual P release and burial for 2005–2018. Positive values indicate net P release. Negative values indicate net burial.

TN and TP loading increased until 2010 and then decreased for several years (Fig. 2B,C). Annual nutrient loading reached a peak again in 2016. Annual nutrient loads to Taihu displayed high variability that closely followed discharges in inflow (Fig. 2A), suggesting that changes in loads are also driven by climate-induced variability in precipitation, in addition to nutrient management interventions.

Annual average TN concentrations in the lake decreased since 2007 (Fig. 4; Supporting Information Figs. S6, S7). This observation indicates that TN can respond quickly to nutrient management in the watershed. However, TP has remained stable in the water column and even increased in 2017 (Fig. 4), indicating a slow response to reductions in external P loading.

Sediment legacy nutrients can impede lake responses to external loading reductions (Søndergaard et al. 2005; Jarvie et al. 2013; Van Meter et al. 2018). Phosphorus has a particularly long residence time in lakes because it is only lost via outflows, since it lacks a gaseous phase. A water residence time of > 180 d in Lake Taihu minimizes P losses by flushing and maximizes P retention. As a result, 63% of total external P loading was retained annually by Taihu. Of long-term sediment legacy P, the biologically available P pool in surface sediments of Taihu was estimated at 5,168 tonnes using a sequential extraction method (Zhu et al. 2013). Net internal P release in Taihu was estimated previously, based on suspension-sedimentation experiments and wind speed data, and amounted to 0.12 g m^{-2} yr^{-1} (Pang et al. 2008). Our study estimated internal P loading of 0.16 g m^{-2} yr^{-1} based on the difference between P demand by phytoplankton and seasonal P retention. Our internal P loading estimate was similar to that extrapolated from direct experiments. Internal P loads varied interannually, with higher values during more recent years due to increasing magnitudes of CyanoHABs, perhaps stimulated by long-term increases in mean lake temperature (Deng et al. 2014; Qin et al. 2019). Relatively large CyanoHABs occurred during the unusually warm early spring of 2017, with P release rates up to 0.89 g TP m^{-2} yr^{-1}. Therefore, lake warming may result in strong seasonal fluctuations of internal P loading and present a challenge for controlling TP concentrations.

While P must be flushed from the system to remove legacy nutrients, denitrification offers a potentially important N removal mechanism (McCarthy et al. 2007). Losses of N via denitrification were calculated here as the residual in the mass balance; that is, denitrification was assumed to be equal to the total of all inputs less losses via outflows, removal by resource extraction, and burial (mean = 12.4 g N m^{-2} yr^{-1}; Fig. 8A). As is often the case (Seitzinger 1988), the accumulation of errors

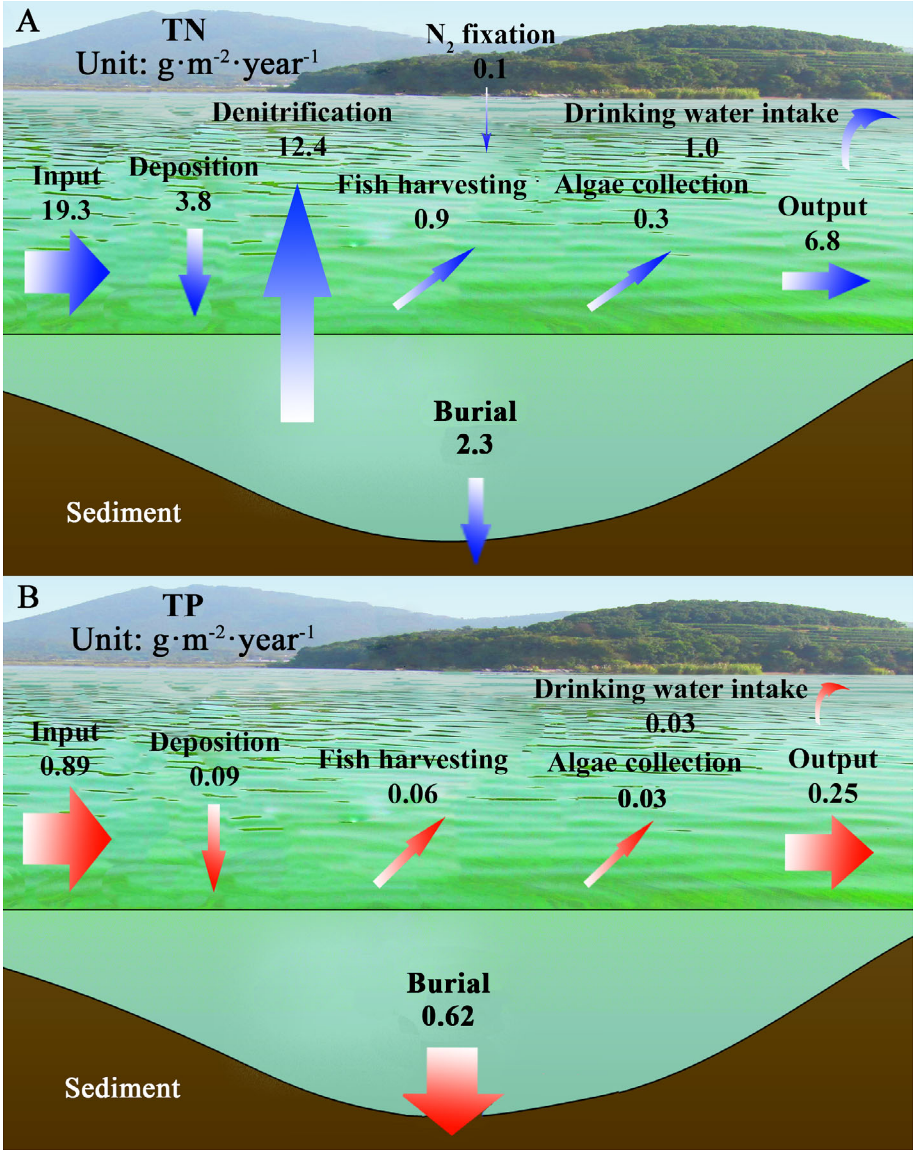

Fig 8. Diagrammatic presentation of TN (total nitrogen; panel A) and TP (total phosphorus; panel B) budgets for Lake Taihu.

in the mass balance produced a relatively high (~ 40% of the mean) degree of uncertainty for annual estimates of denitrification (Table 1). Previous direct measurements of denitrification rates in Taihu ranged from 1.6 to 18.4 g N m^{-2} yr^{-1}, with an average of 15.3 g N m^{-2} yr^{-1} (McCarthy et al. 2007). Our whole lake estimate of denitrification was thus remarkably similar to denitrification rates extrapolated from direct measurements in Taihu. The relatively low variability of denitrification rates between years (< 20% of study mean), and consistency with prior studies of denitrification in Lake Taihu, provide confidence in the reported magnitude of the denitrification estimates from mass balance.

Based on our mass balance estimates, only 9% of external TN loading were retained annually in Taihu, and denitrification removed 54% of annual external TN loading to Taihu and accounted for 85% of total internal N losses. In other shallow lakes, denitrification removed 30–60% of annual external N loading (David et al. 2006; Bruesewitz et al. 2012; Zhao et al. 2015; McCarthy et al. 2016). These results support observations showing that denitrification is a mechanism by which TN concentrations in shallow, eutrophic lakes can respond rapidly after external N loads are reduced (e.g., Jeppesen et al. 2005; Mulholland et al. 2008; Gardner and McCarthy 2009).

Role of internal nutrient cycling in cyanoHAB dynamics

The impacts of internal N and P cycling processes on seasonal patterns of nutrient concentration and limitation have been hypothesized previously (Xu et al. 2010), but quantitative evidence regarding these impacts is limited. In similarly eutrophic Lake Dianchi, China, internal nutrient cycling, not external loading, largely determined nutrient limitation status (Wu et al. 2017). Internal N and P cycling imposed different impacts in different seasons on nutrient concentrations in Taihu. Sediment P release can increase TP and decrease TN to TP ratios in the water column, especially when external P inputs have decreased. Net P release from sediments may cause higher TP concentrations in summer vs winter in shallow eutrophic lakes (Søndergaard et al. 2013). Models of the diffusive flux of SRP across the sediment-water interface in Taihu increased from February to July and remained elevated until August (Ding et al. 2018). Results from a nutrient-driven, dynamic eutrophication model showed that internal processes have potential impacts on nutrient concentrations and seasonal nutrient limitation in Taihu (Wang et al. 2019).

Our lake-wide estimates showed that internal P loading contributed from 23% to 90% (mean 40%) of CyanoHABs P demand. Thus, although sediment P exchange was a net sink on an annual scale, seasonal sediment P release remained important in supporting spring-summer CyanoHABs. Sediment P release mainly occurred during spring and summer in Taihu (Fig. 7). Increases in microbial activity during summer lowers the redox potential in surface sediments, which may induce release of Fe-bound P (Ding et al. 2018). Furthermore, cyanoHAB-induced high pH in the water column, and low oxygen within the benthic boundary layer, enhance internal P loading (Xie et al. 2003; Xu et al. 2010). Such conditions are also becoming more common in spring, as large CyanoHABs are proliferating earlier (and even through winter; Ma et al. 2016) in response to rapid increases in water temperature (Deng et al. 2014).

In Taihu, denitrification removed 54% of external N loading, which dominates N removal pathways and drives aquatic systems toward N limitation. Denitrification rates in Taihu previously showed clear seasonal trends, with higher rates in spring and lower rates in summer and autumn, depending on N substrate concentrations (Zhong et al. 2010). However, our results showed that N losses via denitrification were highest during summer, contributing 33 % of total N loss (Fig. 5). From spring to early summer, denitrification is favored by rapidly rising temperatures (Herrman et al. 2008; Veraart et al. 2011). Uptake by phytoplankton and sediment denitrification compete for N during the spring high DIN period. Earlier warming during spring provides a growth advantage for CyanoHABs (Paerl and Huisman 2009), allowing them to obtain more N to support growth and possibly disrupting benthic/pelagic coupling (Boedecker et al. 2020). This possibility may help explain the generally poor relationship between annual average Chl *a* and nutrient concentrations. During summer, CyanoHABs may accelerate N removal and N limitation because bloom biomass can sink and increase organic matter delivery to the sediment surface, which may benefit heterotrophic denitrification (Chen et al. 2012, 2016).

Compared to N loss via denitrification, significant rates of N_2 fixation were not observed in Taihu during summer (Paerl et al. 2014*b*; Yao et al. 2018), despite N limitation during summer and fall (McCarthy et al. 2007; Xu et al. 2010; Paerl et al. 2011, 2014*a*), indicating that N_2 fixation did not compensate N loss via denitrification in Taihu. This phenomenon in many cases is attributed to physical control by temperature, irradiance, and hydrology (Paerl and Otten 2016) or limitation by micronutrients (Wurtsbaugh 1988). The non-N_2 fixer *Microcystis* exhibits persistent blooms during summer, and rapid regeneration and NH_4^+ turnover can fuel and sustain CyanoHABs, despite low in situ NH_4^+ concentrations (McCarthy et al. 2007; Hampel et al. 2019). In shallow Lake Balaton, Hungary, for example, external N loading only supplied about 10% of the N assimilated by the phytoplankton community, with most of the remainder supplied by internally regenerated NH_4^+ (Présing et al. 2001, 2008). In Taihu, about 38–58% of potential NH_4^+ uptake was supported by regeneration during summer. In cyanobacteria-dominated Sandusky Bay (Lake Erie) during summer (June–August), water column NH_4^+ regeneration provided bioavailable N equivalent to $\sim 77\%$ of the annual N load (Hampel et al. 2019). A similar pattern occurred in eutrophic Missisquoi Bay, Lake Champlain (U.S.A./Canada), where sediment and water column NH_4^+ regeneration exceeded external N loads but could not fully support community N assimilation (McCarthy et al. 2013, 2016). In Taihu, water column NH_4^+ regeneration, driven initially by external nutrient inputs, reached about 260–340% of external TN loading in summer and fall (Fig. 6), which can offset N losses.

Implications for nutrient management

Despite considerable investment in external nutrient load reductions, cyanoHABs continue to persist in Taihu (Qin et al. 2019). Annual TN and TP loading showed no relationship with Chl *a* during 2005–2018 (Supporting Information Fig. S7). This observation indicates that there is sufficient N and P available to support blooms on an annual basis. Our results indicate that legacy internal N and P supplies will contribute to nutrient demands of CyanoHABs in Taihu; therefore, we should expect a lag between reduction in external loading and decreases in bloom magnitude and areal extent. Nutrient reductions must also consider climate change-induced increases in extreme weather events, including heavier rainfall and protracted heat waves and droughts, which can extend the magnitudes and duration of CyanoHABs (Paerl and Huisman 2009; Paerl et al. 2016*a*; Yang et al. 2016). For example, earlier and warmer spring temperatures have extended the period for cyanobacterial growth when high N concentrations prevail (Deng et al. 2014). Climate warming, which continues to affect the region (Qin et al. 2019), will further enhance cyanoHAB potential and persistence in Taihu. Warming also affects (lowers) nutrient thresholds at which blooms occur (Paerl and Huisman 2009), potentially extending the restoration time and putting additional pressure on reducing external nutrient loads.

Our results indicate that further reduction in external N loading will cause a relatively rapid response of in-lake TN concentrations, because N loss by denitrification reduces internal N loading. Furthermore, recent work has shown that N_2 fixation does not compensate for N losses in Taihu (Paerl et al. 2014*b*; Yao et al. 2018) and other eutrophic lakes (Scott and McCarthy 2010; Shatwell and Köhler 2019). Therefore, reducing N inputs, along with P, will yield a more rapid and sustainable reversal of eutrophication and bloom potentials than reducing P inputs alone.

Taken together, these results confirm that large reductions in external N and P loading will be necessary to achieve biomass reductions in Taihu, and in other large lakes affected by toxin-producing CyanoHABs. These nutrient reductions from large lake watersheds can best be achieved by advanced wastewater treatment, establishing riparian buffers around agricultural lands, artificial wetlands, agronomic use of fertilizers, treatment and recycling of animal waste, improved stormwater management (retention ponds), reductions in atmospheric emissions, and many other strategies aimed at reducing external nutrient loads to surface waters.

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Conflict of Interest

None declared.

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