

Spatial and temporal variations in algal phosphorus in Taihu Lake

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ABSTRACT

Phosphorus circulation in Taihu Lake has attracted extensive attention, but the contribution of *Microcystis* to phosphorus circulation in this area is unknown. In this study, the phosphorus concentrations in algal samples collected from the lake in 2015–2016 were determined in the laboratory. From the concentration data, the total quantity of algal phosphorus was calculated and the seasonal variations in algal phosphorus were examined. The results indicated that the intracellular phosphorus content of *Microcystis* in Taihu varied from 0.044 to 0.130 pg/cell and tended to be high in spring and low in summer. The total amount of algal phosphorus in Taihu Lake ranged between 7.78 and 97.32 t over the study period. Algal phosphorus only accounted for between 1.5 and 18.5% of the phosphorus stock in the water. Because *Microcystis* accumulated downwind, there was a tendency for the total phosphorus concentrations to be low in the east of the lake and high in the west of the lake. This new information about the spatial and temporal distribution of algal phosphorus contributes to our understanding of how phosphorus in *Microcystis* contributes to phosphorus circulation in Taihu Lake.

Key words: algal phosphorus, intracellular phosphorus content, *Microcystis*, phosphorus circulation, Taihu Lake

HIGHLIGHTS

- The total quantity of algal phosphorus in Taihu Lake was estimated ranging from 7.78 to 97.32 t, reaching a peak in summer.
- Compared with the total quantity of TP and DTP in Taihu Lake, the total amount of algal phosphorus and its impact on water quality were limited in general but significant in specific lake areas.
- Efforts to control the phosphorus in Taihu Lake should focus on decreasing the exogenous phosphorus inputs.

INTRODUCTION

Taihu Lake is one of the most eutrophic lakes worldwide. In recent years, because of heavy investment and relentless persistence of all levels of government, the water quality of Taihu Lake has improved, but the large-scale *Microcystis* blooms remain (Zhu & Zhu 2019). The concentrations of total nitrogen (TN) and phosphorus (TP) in Taihu Lake had been declining since 2007, but the TP concentration rebounded in 2016 (Wang *et al.* 2019), and now remediation efforts are directed at TP. Taihu Lake is a large shallow lake that covers a huge area and has an average water depth of only 2 m. Because of the large area it covers, the southeast monsoon has a long fetch range and the flow is driven by strong winds. The shallow depth means that the water layers are well mixed and sediments and water interact frequently. Under these environmental conditions, researchers have observed unique patterns in the migration and transformation of substances and organisms in Taihu Lake. For example, Zhu *et al.* (2021) reported that the phosphorus in the lake was distributed unevenly, with high concentrations in the west and low concentrations in the east. There are rarely large differences in the TP concentrations among different areas of a lake. In Taihu Lake, this characteristic is related to the bloom-forming *Microcystis* that proliferates and accumulates frequently in the northwestern part of the lake. Therefore, information is needed about the spatial and temporal variations in the TP concentrations in the lake, and the quantity of phosphorus taken up by, and accumulated in, *Microcystis* (algal phosphorus).

The relationship between *Microcystis* and phosphorus in the water may be classified into three different groups: (1) *Microcystis* obtains nutrients from the water for growth, leading to decreases in dissolved phosphorus in the

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water (Morel 1987; Grover 2010). (2) The uptake of phosphorus by *Microcystis* may induce phosphorus release from sediment to the water body, thereby re-establishing the adsorption/desorption balance (Fan *et al.* 2006; Cottingham *et al.* 2015). (3) Uptake of carbonate ions by algae for growth may cause the pH of the water to gradually increase, and thereby promote the release of phosphorus from the sediment to the water body (Seitzinger 1991; Xie *et al.* 2003). These processes that promote the release of phosphorus from sediment to water as phytoplankton grow have also been termed as the pumping effect.

Microcystis itself may also affect the transformations between phosphorus forms. Algal phosphorus, a type of organic phosphorus that is produced in large quantities during algal bloom outbreaks, could be considered a special sink of phosphorus. Inorganic orthophosphate is the only form of phosphorus that can be directly absorbed and used by algae (Robarts & Zohary 1987). However, in natural aquatic environments, the amount of orthophosphate that can be directly used is limited. As algae proliferate rapidly across large areas, they consume inorganic phosphorus from water, meaning that the supply of phosphorus is limited. Algae may then secrete alkaline phosphatase, which may promote the release of soluble organic phosphorus into the water (Mhamdi *et al.* 2007). In addition, the mass death of *Microcystis* in autumn may lead to a dramatic increase in the supply of this fraction of organic phosphorus to the water body such that algal phosphorus may be regarded as a unique source of phosphorus in this season. Li *et al.* (2011) studied the decomposition of cyanobacterial debris and illustrated that the concentrations of soluble inorganic phosphorus and soluble organic phosphorus in water increased as cyanobacterial debris decreased, but followed slightly different time scales and patterns. Zhang *et al.* (2018) conducted experiments in an enclosed part of Taihu Lake during the winter of 2016 and found that the phosphorus released as the cyanobacteria decayed was mainly orthophosphate. Therefore, because of its scale, algal phosphorus may strongly affect the phosphorus stock in water.

Previous studies have detected a strong correlation between cyanobacteria biomass (represented by chlorophyll concentration, for example) and the phosphorus concentration in water (Zhu *et al.* 2018). However, those studies did not estimate the scale of algal phosphorus, nor did they investigate the spatial and temporal changes in algal phosphorus in Taihu Lake. The density of cyanobacteria in Taihu Lake has remained at a high level over the years, and its biomass there is extremely large (The Health Status Report of Taihu Lake 2015, 2016, 2017, 2018). Cyanobacteria contain phosphorus, but it is unknown whether they significantly contribute to the phosphorus level in Taihu Lake. In addition, cyanobacteria can accumulate due to wind-induced currents (Zhu *et al.* 2019), so it is possible that their accumulation in some areas of the lake will affect regional phosphorus levels. To address these unknowns, it is of great value to estimate the scale and influence of algal phosphorus in Taihu Lake.

At present, the scale and spatial-temporal distribution of algal phosphorus in Taihu Lake is unknown. Analyses of samples collected from different areas of the lake and over a period of time are required to determine the impact of algal phosphorus on the overall and regional water quality of Taihu Lake. Information about the scale and distribution of algal phosphorus will shed light on its contribution to total phosphorus circulation in this lake. In this study, the cell density and the biomass quantity of *Microcystis* in Taihu Lake were monitored over a period of 2 years (2015–2016). The total quantity, distribution, and concentrations of algal phosphorus were also studied and compared with the corresponding properties of TP in Taihu Lake, to support estimations of the scale of algal phosphorus. Seasonal variations in the distribution of phosphorus and algae in different areas of the lake were also considered.

MATERIALS AND METHODS

Study site description

Microcystis blooms frequently occur in Meiliang Bay and Gonghu Bay in Taihu Lake. For this study, six sampling sites were established in these two bays (Figure 1), and samples were collected twice a month. The samples were analysed for TP, dissolved total phosphorus (DTP), the *Microcystis* biomass, and the intracellular phosphorus content of *Microcystis*. The concentrations of TP and DTP, and *Microcystis* biomass data for Zhushan Bay; the western, eastern, and southern coastal areas; the centre of the lake, and the eastern part of the lake were obtained from the Taihu Basin Authority of the Ministry of Water Resources (The Health Status Report of Taihu Lake 2015, 2016).

Sample collection

Water samples were collected using a plexiglass water collector, then mixed evenly and put into 500-mL plastic bottles. They were sealed and stored as soon as possible and then transported back to the laboratory. All the samples were then stored in a refrigerator at 4 °C until the phosphorus concentrations were determined.

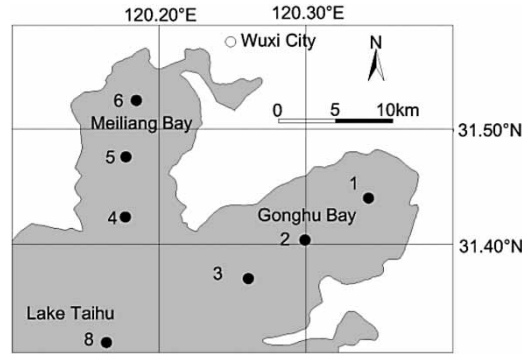


Figure 1 | Sampling sites in Taihu Lake.

Additional water samples (10 L) to be analysed for the algal properties were collected with a plexiglass water collector. The algae samples were concentrated through a phytoplankton net with an aperture of 63 μm . The highly concentrated algal slurries were put into 50-mL plastic bottles and transported back to the laboratory immediately. To avoid deterioration of the samples and subsequent large errors in the results, the algal samples were analysed for the cell density and intracellular phosphorus content within 24 h.

Analysis methods

Water sample analysis

The phosphorus concentrations of the water samples were determined by colorimetry using a UV-Visible spectrophotometer (Shimadzu, UV-2450) after digestion in a solution of $\text{K}_2\text{S}_2\text{O}_8$ and NaOH. We determined the TP concentrations of unfiltered lake water and the DTP concentrations of lake water filtered through a 0.45- μm membrane. The concentrations of total particle phosphorus (PTP) were obtained by subtracting the TP and DTP concentrations.

Acquisition of algal samples

Fresh *Microcystis* slurry (5-mL) collected from Taihu Lake was pumped and filtered through a 0.45- μm membrane. The algae on the membrane were gently washed into the centrifuge tube with distilled water and centrifuged in a refrigerated centrifuge (3-18R, TOMOS, Shanghai, China) at 1,500 rpm for 10 min. The clear liquid was discarded. The algal cells were separated, distilled water was added, and the mixture was centrifuged again. The washing process was repeated three times to remove other phosphorus from the water and any loose-bound EPS of algae.

Cell counting and calculation of the intracellular phosphorus content

A glomerular counter and a microscope (Olympus CX31, with magnification 400 \times) were used for the cell counting. Each sample was counted three times. If the difference among the three counts was <10%, the mean value was taken as the final algal cell density, otherwise it was recounted. The cell density was recorded as C_n (10^4 cells/mL). After digestion with potassium persulfate, the total algal phosphorus content C_p (mg/L) was determined by UV spectrophotometry, and the intracellular phosphorus content was calculated in Equation (1):

$$C_i \text{ (pg/cell)} = C_p / C_n * 100 \quad (1)$$

Phosphorus stock calculation

The phosphorus stock (W_{ip} , t) in each lake area was calculated from the phosphorus concentration (W_i , mg/L) and water quantity (V_i , km^3) in that lake area, using the following formula:

$$W_{ip} = W_i * V_i / 1,000 \quad (2)$$

The algal phosphorus stock (C_{ip} , t) in each lake area could be calculated by algal phosphorus content (C_i , pg/cell), algal density (C_{in} , 10^8 cells/L) and water quantity (V_i , km^3) in each lake area, and the calculation

formula was given as follows:

$$C_{ip} = C_i * C_{in} * V_i / 100 \quad (3)$$

Correlation analysis

The correlations between the algal phosphorus and TP/DTP were determined with the Spearman, Kendall, and Pearson correlation tests in SPSS 19.0. For the analysis, we used data for these parameters from each area of Taihu Lake for the period of the *Microcystis* bloom outbreak in 2015 and 2016. All the correlation results were tested for significance.

RESULTS AND DISCUSSION

Variations in the phosphorus concentrations in Taihu Lake

The seasonal DTP and PTP concentrations in the different areas of Taihu Lake from 2015 to 2016 are presented in Figures 2 and 3. The average concentration of DTP in Taihu Lake for 2015 and 2016 was approximately 0.028 mg/L, and the average concentrations of PTP in 2015 and 2016 were approximately 0.054 and 0.056 mg/L, respectively. Particulate phosphorus, accounting for about two-thirds of TP, dominates the phosphorus forms in Taihu Lake. The phosphorus concentrations in each lake area were slightly higher in 2016 than in 2015; in particular, the TP concentration in Zhushan Bay increased sharply between 2015 and 2016 and fluctuated widely, and varied by up to 88.5% of the average value. The DTP and PTP concentrations were 0.042–0.337 and 0.020–0.348 mg/L, respectively. The phosphorus concentration was higher in the northwest of the lake than elsewhere, and the TP concentration in the northwest of the lake was three times the concentration in the southeast, where the concentration was low (in line with the pattern of low concentrations in the east and high concentrations in the west reported elsewhere). The spatial differences in the phosphorus concentration in Taihu Lake were particularly significant in summer and autumn.

The TP concentration, calculated by adding the DTP and PTP concentrations, indicates that the lake was in a hypereutrophic state during the algal bloom outbreaks in 2015–2016 ($TP > 0.09$ mg/L). The high nutrient concentrations may reflect the transport of water from eutrophic water bodies via rivers into the lake after floods in 2015–2016. Of the 22 rivers that flow into Taihu Lake, 12 flow into the northwest, so the northwest receives more exogenous phosphorus inputs than the other lake areas. The main flows in the lake are generally from west to east and from north to south. The southeastern part of the lake is downstream from the northwestern area. Taihu Lake has a certain self-purification capacity. Therefore, the relatively low and stable concentrations of DTP and PTP in the eastern part of Taihu Lake and the eastern coastal area downstream of the northwestern area reflect this internal self-purification.

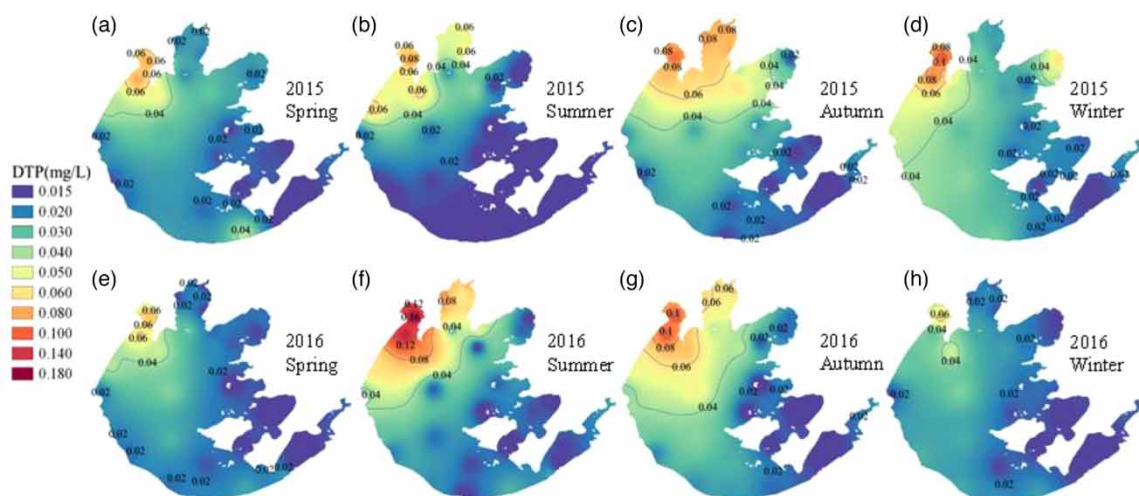


Figure 2 | Seasonal variation of DTP concentration in Taihu Lake in 2015–2016.

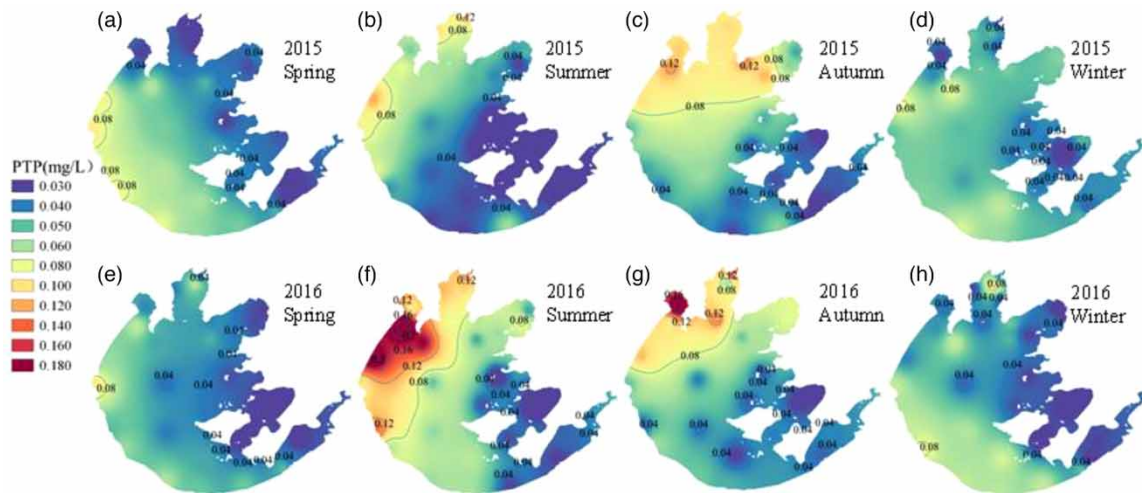


Figure 3 | Seasonal variation of PTP concentration in Taihu Lake in 2015–2016.

Density and variation of *Microcystis* in Taihu Lake

The *Microcystis* densities in the different areas of Taihu Lake from 2015 to 2016 are presented in Figure 4. The graph shows that the cell densities of *Microcystis* in Taihu Lake increased dramatically from 2015 to 2016, and the maximum average cell density in the whole lake in 2016, at 3.02×10^8 cells/L, was about three times that in 2015. In 2015, there were frequent bloom outbreaks in the summer, in June and July. In 2016, the bloom outbreak persisted from April to September. Data from different parts of the lake for 2015 and 2016 show that the cell densities were higher in several areas in the northwest in 2016 than in 2015, including Meiliang Bay, the western coastal area, and Zhushan Bay. The cell density values in Meiliang Bay, the western coastal area, and Zhushan Bay reached 3.4×10^8 , 6.1×10^8 , and 5.3×10^8 cells/L in 2015, and 9×10^8 , 6.4×10^8 , and 7.9×10^8 cells/L in 2016, respectively.

The algae density varied spatially and was high in the northwest and low in the southeast. The spatial variation in the algae density may be attributable to high nutrient concentrations and wind-driven flow caused by the stable wind field. The 12 rivers that flow into the northwest of the lake transport water with high nutrient concentrations into the lake. The stable wind field is mainly in the southeast. During the *Microcystis* bloom outbreak, the wind speed was mainly 1–2 m/s. Algae cells may have migrated to the northwestern part of the lake in the surface water flow driven by the wind.

Intracellular phosphorus concentrations and algal phosphorus in *Microcystis*

The amount of phosphorus in *Microcystis* was assessed from data for intracellular phosphorus, derived from samples collected twice a month at six sites. The average content of phosphorus was obtained from the average

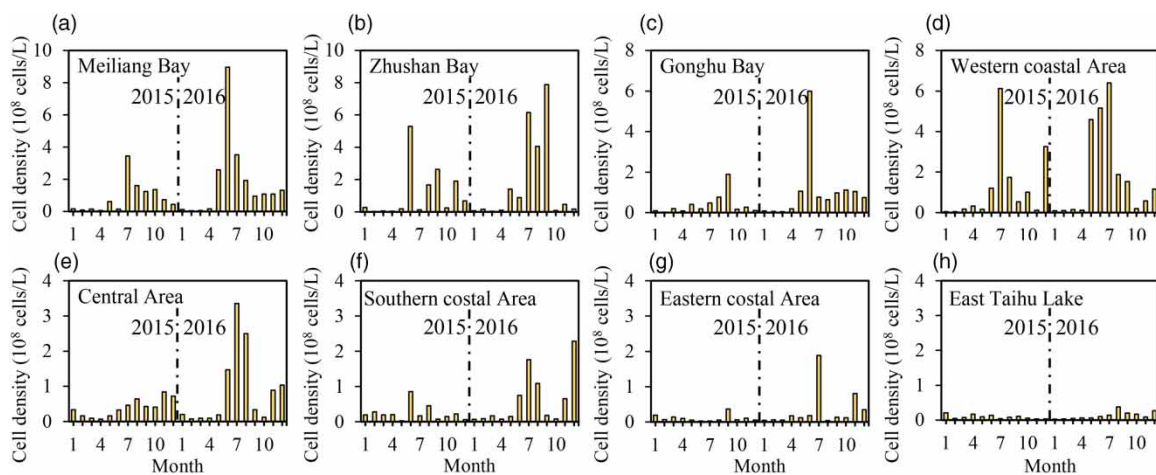


Figure 4 | Density and variation of *Microcystis* in various lake areas of Taihu Lake.

intracellular phosphorus content for each month (Figure 5). The intracellular phosphorus content varied from 0.044 to 0.130 pg, and the peak concentration was as much as three times greater than the lowest concentration over the year. The intracellular phosphorus content of *Microcystis* varied seasonally and was highest in April (0.130 pg/cell) and lowest in July (0.044 pg/cell), and so followed a pattern of being low in summer and high in spring.

The intracellular phosphorus content of *Microcystis* is regulated by the phosphorus concentration in the environment and the growth stage. Saxton *et al.* (2012) determined that the intracellular phosphorus content of *M. aeruginosa* (PCC 7806) in a medium with a phosphorus concentration of 0.24 P mg/L was 0.04 pg/cell. When the concentration of the medium was increased to 2.4 mg/L, the intracellular phosphorus content increased to 0.145 pg/cell, which indicates that the content was related to the phosphorus concentration of the medium. The TP concentration used in the experiment of Saxton *et al.* (2012) is much higher than the concentration in Taihu Lake, but the gap between the intracellular phosphorus content and the measured value in this paper is similar. Han *et al.* (2004) cultured *M. aeruginosa* isolated from Taihu Lake in phosphorus concentrations between 0 and 6.2 mg/L, and recorded intracellular phosphorus concentrations of 2–30 mg/g DW, which are similar to those obtained in this study. Chen *et al.* (2011) measured the intracellular phosphorus content of *Microcystis* in Meiliang Bay and Gonghu Bay in 2011. They found that the intracellular phosphorus concentrations ranged from 0.28 to 0.86×10^{-2} pg/cell, and that they were low during the bloom outbreaks and high in the settled period. Wang (2017) collected samples at Caohai in Dianchi Lake and estimated that *Microcystis* had total phosphorus concentrations of 1.5536 and 3.0799 mg/mg chl in the summer and winter of 2016, respectively. The above discussion confirms that the intracellular phosphorus concentrations of *Microcystis* measured in this paper are reliable. The concentrations of phosphorus in *Microcystis* cells generally vary seasonally, and tend to be high in spring and low in summer. However, even with changes in the quality of the water, the highest concentration of phosphorus in single cells remains, at most, three times greater than the lowest concentration.

The algal phosphorus concentrations are strongly influenced by the environment and the growth stage and biomass, with the environment having the least influence on the concentrations. Therefore, biomass has a strong influence on the total amount of algal phosphorus. The cyanobacteria biomass in Taihu was high in 2017 (The Health Status Report of Taihu Lake 2017). According to the phosphorus content per cell, the maximum amount of algal phosphorus in Taihu Lake may have been more than 100 t. The overall balance of phosphorus (Zhu *et al.* 2020) showed that the annual TP flux into the lake was 2,569.3 t, the flux out was 886.3 t, the net flux into the lake was about 1,683 t, and the average annual TP stock in the water body was 525 t. A large amount of phosphorus is transformed within the lake and can enter the sediment or be taken up by aquatic animals and plants. However, between 7.78 and 97.32 t of the TP stock in the water body exists in the form of algal phosphorus. This accounts for only 1.5–18.5% of the TP flux and is equivalent to 3.7–45.9% of the DTP. The DTP stock (105–317 t) is larger than the algal phosphorus stock and accounts for 20–60.4% of TP. The *Microcystis* therefore only use a small proportion of the available supply of DTP, and so the lake remains enriched in phosphorus.

Algal phosphorus quantity and relationships with DTP and PTP in Taihu Lake

The total amount of phosphorus in Taihu Lake and its distribution in the different lake areas were calculated from the phosphorus concentrations of *Microcystis* (Figure 5), measured data of the biomass of *Microcystis* in Meiliang Bay and Gonghu Bay, and data of the *Microcystis* biomass in other lake areas from the Taihu Basin Authority of

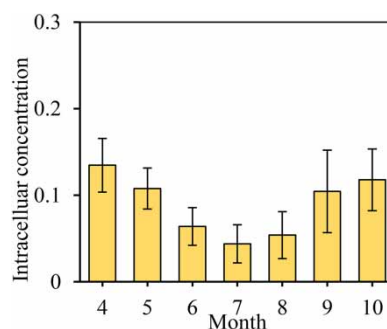


Figure 5 | Seasonal variation of intracellular phosphorus content in *Microcystis*.

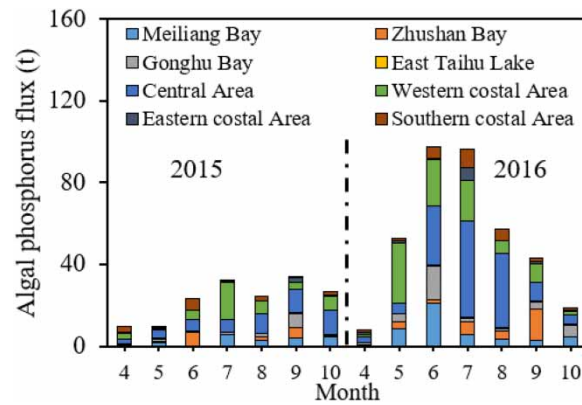


Figure 6 | Algal phosphorus flux in Taihu Lake in 2015–2016.

Ministry of Water Resources. The total amounts of phosphorus in *Microcystis* in Taihu Lake in 2015 and 2016 were 9.48–32.37 t and 7.78–97.32 t, respectively, and the quantity of phosphorus used by *Microcystis* varied from 8 to 97 t/a over the 2 years (Figure 6). The maximum amount of algal phosphorus in 2016 was three times that in 2015, mainly because of the difference in the maximum biomass between the years. While the intracellular phosphorus content of *Microcystis* was low in summer and high in spring, the total quantity of phosphorus in algae was obviously high in summer and low in spring. Compared with 2015, the flux of phosphorus in algae changed with the biomass, so the proportion of phosphorus in algae was highest in the central part of the lake, as it had the largest water surface area and water storage capacity.

Because the water storage amounts varied widely among the lake areas, it is difficult to understand the differences caused by the *Microcystis* biomass only from the total amount. Therefore, to account for the differences in the volume of water in each lake area, the content of algal phosphorus in the water body (APIW), namely the algal phosphorus concentration, was obtained by combining the intracellular phosphorus content with the cell density (Figure 7). Using this measure, we can clearly see the variations in the algal phosphorus contents among the lake areas. The maximum algal phosphorus contents varied across the lake and were between 60 and 80 $\mu\text{g/L}$ in Zhushan Bay and Meiliang Bay, approximately 40 $\mu\text{g/L}$ in Gonghu Bay and the western coastal area, approximately 40 $\mu\text{g/L}$ in the central lake, less than 10 $\mu\text{g/L}$ in the southern coastal area, and less than 5 $\mu\text{g/L}$ in the eastern part of the lake. The spatial pattern in algal phosphorus was consistent with the high TP concentrations in the west and low TP concentrations in the east. There was obvious seasonal variation in the phosphorus concentrations, with maximum values observed in July and August. The results suggest that, in spring and summer, *Microcystis* continuously absorbed and used phosphorus from water. The amount of phosphorus used and stored by *Microcystis* gradually decreased after autumn and was released back into the water.

The water body and phosphorus stocks in different areas of the lake may be calculated from the data of water quality and water quantity for the different lake areas (Figure 8). To better understand the relationship between

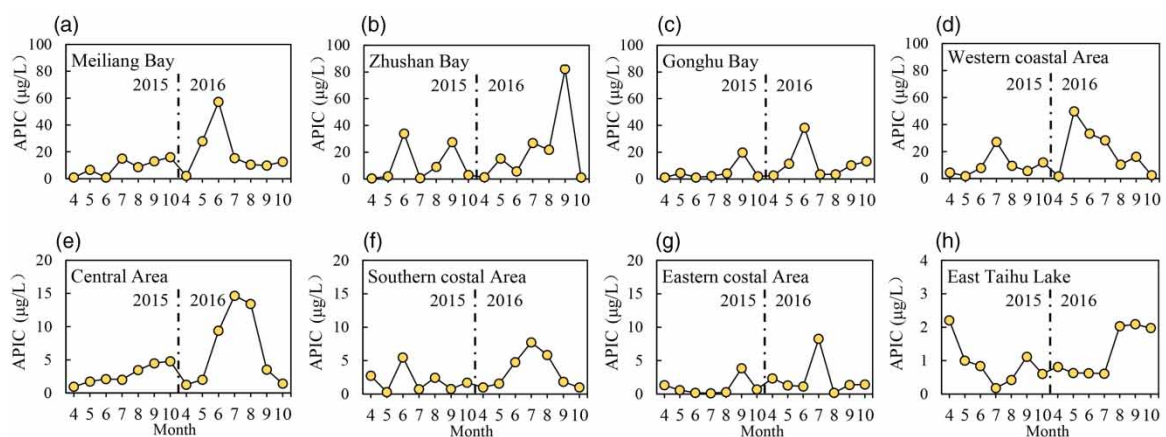


Figure 7 | Variation of algal phosphorus concentration in Taihu Lake.

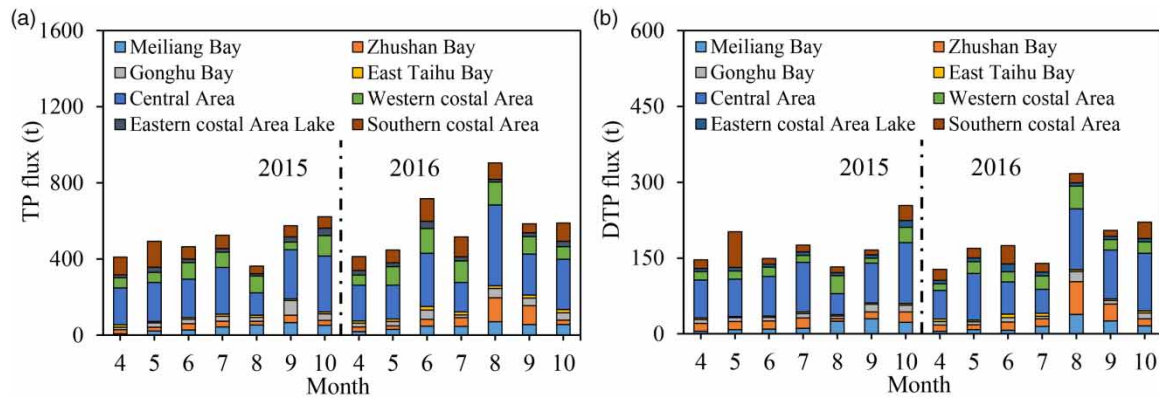


Figure 8 | TP (a) and DTP (b) fluxes in Taihu Lake during *Microcystis* blooms in 2015–2016.

the phosphorus flux and phosphorus concentrations, we examined the correlations between the algal phosphorus and the DTP and PTP. Apart from the period before and during the 2016 floods, the algal phosphorus was significantly and positively correlated with DTP and PTP throughout the whole process of the long-term water flood (Table 1). We then examined the correlations before, during, and after the floods, to determine the impacts of the major floods in 2015. Algal phosphorus is part of PTP and was always significantly and positively correlated with PTP, and the correlation became stronger from before to during and after the flood, which shows that algal phosphorus accounted for a large proportion of the particle phosphorus transported by external floods. Algal phosphorus and DTP were only significantly and positively correlated after the flood, which suggests that the algal growth may have been promoted by the large amounts of phosphorus transported by the floods.

Theoretically, there was a balance between the phosphorus concentrations and amounts among the algae, water, and sediment in the lake. *Microcystis* absorbs DTP from water as it grows and then becomes a part of PTP. During the decay process, DTP is released as the cells decompose. Therefore, the stocks of algal phosphorus and DTP should be negatively correlated. However, we found that they were still significantly and positively correlated (Table 1).

There are two possible reasons for this. While DTP is consumed by the algae through the growth process, phosphorus may also be released from the sediment because of changes in environmental conditions. For example, Zhu *et al.* (2018) reported that the pH in the water increased, and the dissolved oxygen decreased, as algae proliferated, giving anaerobic conditions, which may promote the release of phosphorus from sediment to the water and cause increases in the TP concentrations in water. Additionally, to meet the phosphorus demand from algae

Table 1 | Correlation between algal phosphorus flux/concentration and DTP and PTP

	Phosphorus flux			Phosphorus concentration in column		
	Spearman	Kendall	Pearson	Spearman	Kendall	Pearson
Before flood						
DTP	0.596**	0.441**	0.191	0.238	0.176	0.248
PTP	0.691**	0.487**	0.349*	0.471**	0.333**	0.604**
During flood						
DTP	0.463**	0.31*	0.258	0.182	0.123	-0.004
PTP	0.758**	0.577**	0.596**	0.746**	0.569**	0.742**
After flood						
DTP	0.798**	0.605**	0.766**	0.748**	0.558**	0.574**
PTP	0.893**	0.733**	0.918**	0.913**	0.767**	0.858**
Whole process						
DTP	0.611**	0.437**	0.393**	0.432**	0.302**	0.369**
PTP	0.780**	0.578**	0.642**	0.727**	0.541**	0.738**

* $p < 0.05$, ** $p < 0.01$.

during the bloom season, that is, the pumping effect, phosphorus may also be released from the sediment to the overlying water. The combination of these factors may lead to the massive growth of algae during the water bloom period, leading to significant increases in DTP in Taihu Lake. It may be that the amount of algal phosphorus is small compared with the stock and concentrations of DTP, meaning that it has a very limited influence on DTP. Meanwhile, the large supply of exogenous DTP then becomes the main stimulus for the growth of algal phosphorus (Table 1). If, in the most extreme case, we assume that all the phosphorus in *Microcystis* was released into the water body during the bloom outbreak, it would account for only 0.006 and 0.016 mg/L of the TP concentrations in the water body. The influence of the algal phosphorus on DTP is negligible compared with the influence of the exogenous inputs. Alternatively, Taihu Lake is a shallow lake that is hypertrophic and has high phosphorus concentrations. Because of ongoing hydrodynamic processes, there is ongoing phosphorus exchange between the sediment and water, which obscures the relatively small impact of *Microcystis* on phosphorus in the lake water.

Of these two possibilities, the latter is the more suitable. The adverse effects of algae on the water DTP may not be as serious as reported in previous studies; on the whole, the nutrients in water rely on algae growth, and the algae have minimal adverse effects on the concentrations in the water.

The overall influence of algae phosphorus is limited and makes a minimal contribution to water DTP or TP. However, the accumulation of *Microcystis* in the northwestern part of the lake, easily transported on the water surface by the relatively stable southeastern monsoon, does contribute to the uneven distribution of phosphorus through the lake. An examination of the regional distribution of algal phosphorus through the lake by Zhu *et al.* (2019) showed that the algal phosphorus in the central area of the lake accounted for about half of the algal phosphorus in the whole lake (Figure 8); Zhu *et al.* (2019) reported that *Microcystis* produced in other lake areas dominated by the central area would gather in the bays downwind of the central area under appropriate wind speeds, such as Zhushan Bay, Meiliang Bay, and the western coastal area, and form *Microcystis* blooms. In this way, algal phosphorus in the lake migrates to the northwestern part of the lake, such that the east of the lake is less polluted than the west. The amounts of algal phosphorus in 2015 and 2016 were high in the west and the north, and low in the south and the east. In the bay areas where *Microcystis* blooms occur frequently, algal phosphorus accounted for as much as 30.12 and 44.68% of the total phosphorus in 2015 and 2016, respectively, and these proportions were relatively high compared with other lake areas.

The results of this study, therefore, show that algal phosphorus in the lake accounted for a very small proportion of the total phosphorus stock, and that it had a minimal impact on the phosphorus circulation. While algae, through the pumping effect or other effects, may promote the release of phosphorus from sediment, the impact on the phosphorus concentrations in Taihu Lake is minimal. Even though algal phosphorus has a very limited impact on the overall phosphorus circulation, it contributes to regional differences in the water quality, because of its tendency to migrate to, and aggregate in, downwind areas with wind-driven flow.

CONCLUSION

1. The intracellular phosphorus concentrations of *Microcystis* in Taihu Lake were between 0.044 and 0.130 pg/cell. The concentrations varied seasonally and were high in spring and autumn and low in summer. In 2015 and 2016, the total amount of algal phosphorus ranged from 7.78 to 97.32 t. The summer had the highest number of *Microcystis* bloom outbreaks. There was spatial variation in the distribution of algal phosphorus across the lake, with the largest amounts of algal phosphorus in the western coastal area, the central lake area, and Meiliang Bay, and the lowest amount in the eastern part of the lake.
2. Data for the proportion of phosphorus that is algal phosphorus, and the correlations between algal phosphorus and dissolved phosphorus, demonstrate that algal phosphorus has a minimal impact on the overall phosphorus cycle in Taihu Lake and its effects are very small relative to the scale and impact of the exogenous phosphorus inputs. However, because *Microcystis* is transported by wind and aggregates in downwind areas, algal phosphorus contributes to the regional differences in the TP concentrations in Taihu Lake.
3. Algal phosphorus only accounts for between 1.5 and 18.5% of the TP stock in water and represents between 3.7 and 45.9% of DTP, reflecting the hypertrophic state of Taihu Lake. Efforts to control the phosphorus and remediate the trophic status of the lake should focus on decreasing the exogenous phosphorus inputs, particularly the DTP inputs.

ACKNOWLEDGEMENTS

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DATA AVAILABILITY STATEMENT

All relevant data are included in the paper or its Supplementary Information.

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