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Impacts of algal community structure on algae-derived phosphorus concentrations in Lake Taihu, China, from 2021 to 2025

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Abstract

Phosphorus control remains a critical challenge for managing eutrophication in Lake Taihu, yet quantitative assessments of algae-derived phosphorus (ADP) and its response to community shifts remain scarce. Based on monthly data from 20 entire-lake stations during 2021–2025 and an experimentally determined cellular phosphorus content for *Microcystis* spp. (1.46×10^{-10} mg/cell), we estimated cell-specific phosphorus for 113 algal species by cell-volume conversion and quantified ADP and phylum-level contributions. Annual mean total algal density decreased from 1.2×10^{8} cells/L in 2021 to 6.9×10^{7} cells/L in 2025, with marked turnover: *Microcystis* spp. fell from 83.6% to 32.4% of total density, while diatoms, cryptophytes and chlorophytes rose significantly. Annual mean ADP ranged from 0.015 to 0.022 mg/L (33.4% of TP) and was dominated by cyanobacteria, diatoms and chlorophytes. Cyanobacteria supplied over 65% of ADP during 2021–2022, declining markedly after 2023, while diatom and chlorophyte contributions rose. Notably, an algal rebound in December 2024 (density up 79.3% year-on-year) coincided with a 25.0% ADP decrease, because a large gain in small-celled cyanobacteria was outweighed by a much smaller loss of large-celled diatoms containing seven to eight times more phosphorus per cell. These findings show that ADP is a key component of TP in Lake Taihu and is governed by two mechanistically distinct controls: algal biomass (quantity) and the community-weighted cell-specific phosphorus content set by the assemblage cell-size structure (quality), which can act in opposite directions. Algal community structure thus acts as an active regulator of lake phosphorus and must be considered alongside algal density in phosphorus management.

1 Introduction

As the third-largest lake in China and the core of the aquatic ecosystem within its basin, Lake Taihu's eutrophication has garnered widespread attention from various sectors of society (Li et al., 2025; Paerl and Otten, 2013; Wang et al., 2025; Yan et al., 2024). As a large shallow lake, the issue of phosphorus fluctuations in Lake Taihu poses challenges for controlling and meeting surface water phosphorus concentrations standards (Martin et al., 2014; Qin et al., 2020; Singh et al., 2015; Zhang et al., 2016). Through a series of management measures, the intensity of cyanobacterial blooms in Lake Taihu has decreased in recent years; however, total phosphorus (TP) still exhibits fluctuations, and phosphorus control and reduction remain critically important topics in Lake Taihu's management (Han et al., 2013; Qin et al., 2019; Yin et al., 2024; Yuan et al., 2023).

Years of research indicate that phosphorus pollution in Lake Taihu is primarily caused by both external and internal phosphorus pollution as in many lakes (Qin et al., 2019; Qin et al., 2020; Yin et al., 2022; Yuan et al., 2026). Externally sourced phosphorus input remains the most significant source of phosphorus pollution in Lake Taihu (Yuan et al., 2023). This external phosphorus input arises from the phosphorus load transported by inflowing rivers entering the lake. Despite continuous intensification of efforts to reduce external phosphorus input in recent years, the phosphorus flux entering the lake remains in a state of net increase (Wang et al., 2025). Internal phosphorus pollution originates mainly from physical, chemical, and biological cycles within the lake, predominantly comprising sediment-released

phosphorus and biotic particulate phosphorus (BPP) (Ding et al., 2015; Yu et al., 2015). Sediment-released phosphorus is caused by changes in the lake's natural climatic and chemical environment, coupled with the metabolic activities of benthic microorganisms and phytoplankton, which collectively facilitate the gradual transformation of bound phosphorus in the sediment into soluble phosphorus released into the water column, thereby increasing the water phosphorus concentrations (Dhiman et al., 2026; Hu et al., 2011; Kang et al., 2023; Xu et al., 2015; Zhang et al., 2007). As biological entities, algal cells can be considered a form of BPP (Jiang et al., 2025; Shinohara et al., 2016). Typically, in eutrophic water bodies with high algal biomass, its contribution to total particulate phosphorus (TPP) and even TP cannot be ignored, especially when algal aggregation and blooms can cause anomalous fluctuations in TP at some monitoring sites (Han et al., 2022; Jiang et al., 2025; Shinohara et al., 2016). Although existing research has established the importance of ADP's contribution to lake TP (Jiang et al., 2025), reports quantitatively assessing the ADP concentrations and its proportion to lake TP in Lake Taihu are lacking, and systematic studies on the impact of algal community structure changes on ADP concentrations are absent.

Mechanistically, ADP should not be regarded as a passive by-product of eutrophication but as an actively cycling intermediate of the internal phosphorus pool. Phytoplankton assimilate dissolved inorganic phosphorus into nucleic acids, phospholipids, polyphosphate and ATP, so the phosphorus held in algal biomass represents the fraction of the lake phosphorus pool that is temporarily immobilised in living cells (Elser et al., 2000). Importantly, the cell-specific phosphorus content q is not a fixed trait but a physiologically regulated quota: cells can take up phosphorus in excess of their immediate requirement, storing it as polyphosphate, so that q varies between a minimum quota and an upper storage capacity as a function of ambient phosphorus supply and growth rate (Droop, 1973). ADP is therefore governed by two mechanistically distinct channels, namely the quantity of algae (total biomass) and the quality of the assemblage, expressed as its community-weighted mean cell-specific phosphorus content.

The second channel is ultimately set by cell size and taxonomy. Cell-specific phosphorus content scales allometrically with cell volume, with reported exponents of about 0.7 to 1.0 for phytoplankton, so that a single diatom, cryptophyte or dinoflagellate cell contains roughly one to three orders of magnitude more phosphorus than a single *Microcystis* cell (Finkel et al., 2010). Numerical dominance and phosphorus dominance therefore need not coincide, and a compositional shift can move ADP in the opposite direction to total cell density. In addition, ADP is recycled rather than permanently removed: enzymatic hydrolysis of particulate organic phosphorus and the lysis of senescent cells return phosphorus to the dissolved pool, whereas sedimentation of negatively buoyant cells, notably diatoms, transfers phosphorus to the sediment and wind-driven resuspension in this shallow lake returns part of it to the water column. Resolving how community structure regulates ADP is thus necessary both to close the phosphorus budget of Lake Taihu and to explain the episodic TP fluctuations that persist despite declining external loads.

This study focused on the entire water body of Lake Taihu. Based on entire-lake algal monitoring data from 2021 to 2025 in conjunction with synchronous water quality measurements, we investigated the

effects of declining algal density and algal community succession on the concentration of ADP and its fraction of TP in the lake. This work aims to quantitatively assess entire-lake ADP levels and elucidate the dynamic impacts of changes in algal density and community structure on TP dynamics in Lake Taihu.

2 Materials and methods

2.1 Sampling and data sources

The aquatic ecological and water quality data used in this study were obtained from long-term ecological monitoring data collected for Lake Taihu from 2021 to 2025. The distribution of the 20 lake monitoring sites in Lake Taihu is presented in Fig. 1. The monitoring frequency was monthly. Water samples were collected at a depth of 0.5 m below the water surface using a plexiglass water sampler for phytoplankton and water quality analyses. For the pretreatment of algal samples, 1 L of each water sample was measured with a graduated cylinder and transferred into brown narrow-mouth glass bottles. Lugol's solution was added as a fixative at a volume ratio of 1.5%. All samples were then stored in an insulated cooler with ice packs and transported back to the laboratory for analysis within 4 hours after sampling.

2.2 Determination of cellular phosphorus content in *Microcystis* spp.

Water samples were collected from algae-accumulating waters of Lake Taihu. Microscopic observation and enumeration were performed on the collected samples to analyze algal species composition and algal density. Analysis confirmed that *Microcystis* spp. was the dominant species with a dominance index above 99% (Thus, the water sample may be approximated as a pure culture of *Microcystis* spp.). Subsequently, the water samples were filtered through a 25# plankton net (mesh aperture 64 μm) to harvest algal particles. The retained algal particles were carefully rinsed multiple times with ultrapure water. The rinse-water from each washing step was collected for dissolved phosphorus analysis. Rinsing was terminated when no dissolved phosphorus could be detected in the eluate. The washed algal particles were then transferred into a 50 mL colorimetric tubes to prepare concentrated algal suspensions. After thorough homogenization of the concentrated suspension, 25 mL of algal suspension was immediately mixed with an equal volume of ultrapure water to obtain a 1:1 diluted algal suspension. Then, 25 mL of the diluted suspension was further mixed with an equal volume of ultrapure water. This dilution procedure was repeated three times to yield a total of five serially-diluted algal suspensions (with theoretically halved algal density for each successive dilution), and parallel samples were prepared. Algal density, dissolved phosphorus and total phosphorus concentrations were determined for each dilution series. The filtrate obtained after sample filtration through a 0.45 μm aqueous-phase membrane filter was used for dissolved-phosphorus measurement, while unfiltered aliquots of the samples were used for total-phosphorus determination.

It is well-known that TP mainly consists of total dissolved phosphorus (TDP) and TPP. TPP can be further divided into ADP and non-algal-derived phosphorus (NADP). Accordingly, the mass concentration of total phosphorus in water can be calculated by Eq. (1):

TP = TDP + ADP + NADP (1)

In this experiment, TDP was not detected in any sample. In addition, microscopic observation of serially-diluted samples revealed no other non-algal microorganisms or impurity particles, indicating that TDP and particulate impurities in the raw water sample had been removed through sieving and rinsing during pretreatment. Consequently, TDP and NADP in the diluted algal suspensions could be neglected. Therefore, the equation for TP mass concentration of the gradient algal suspensions in this study was simplified to Eq. (2):

TP = ADP (2)

Since the gradient algal suspensions were almost exclusively composed of *Microcystis* spp., the total mass concentration of ADP was contributed solely by *Microcystis* spp.. Eq. (2) can thus be rewritten as Eq. (3):

TP = C_M×N (3)

C_M : the average phosphorus content of a single *Microcystis* spp. cell (mg/cell); N: the *Microcystis* spp. cell density (cell/L).

Based on Eq. (3), linear-regression analysis was performed between algal density and TP mass concentration for the serially-diluted samples. C_M was determined to be 1.46×10^{-10} mg/cell ($p < 0.001$). The cellular phosphorus contents of other algae were estimated based on their cell-volume ratios relative to *Microcystis* spp..

2.3 Laboratory analysis

0.1 mL of fully homogenized water sample was pipetted into a glass plankton-counting chamberand an alyzed for algal density and community structure with an AI-based algae analyzer (AH-20S, Hongzhong Baide, China). A biological optical microscope (E1000, Nikon, Japan) was used for cross-checking to guarantee a data error belo 5 %. Concentrations of phosphorus was determined using the ammonium molybdate spectrophotometric method at 880 nm (TU-1900, Persee, China). For TP analysis, samples were subjected to potassium persulfate digestion prior to measurement.

Data sorting was performed using WPS 2026 (Kingsoft, China). Statistical analyses, correlation analysis and graph plotting were carried out with Origin 2019 (OriginLab, USA). Pearson correlation coefficient (p) was adopted for correlation judgement, and $p < 0.001$ was regarded as an extremely significant difference.

3 Results and discussion

3.1 Changes in algal conditions in Lake Taihu

The annual-mean total algal density and the density of *Microcystis* spp. (the major cyanobacterial bloom-risk genus) in Lake Taihu both exhibited fluctuating changes from 2021 to 2025 (Fig. 2). The annual mean total algal density decreased from 1.2×10^8 cells/L in 2021 to 6.9×10^7 cells/L in 2025, while *Microcystis* spp. density declined from 1.0×10^8 cells/L in 2021 to 2.2×10^7 cells/L in 2025, corresponding to reductions of 49.1% and 78.0%, respectively.

However, notable algal rebounds occurred during the onset of summer in both 2024 and 2025. Algal density increased year-on-year after July, with particularly pronounced rises in August. The total algal density in August 2024 registered a year-on-year increase of 129.1%. From August to October 2025, the total algal density continued to rise compared to the same period in the previous year, leading to an increase in the mean total algal density from 5.4×10^7 cells/L in 2023 to 6.6×10^7 cells/L in 2024 and 6.9×10^7 cells/L in 2025, respectively.

Inter-annual changes in the algal community structure across Lake Taihu from 2021 to 2025 are shown in Fig. 3. Since 2021, the algal community structure in Lake Taihu has undergone changes. The density and proportion of cyanobacterial continuously declined, while the densities and proportions of cryptophytes, chlorophytes, and diatoms showed an increasing trend. Compared to 2021, the densities of cryptophytes, chlorophytes, and diatoms in 2025 increased by 68.6%, 675.2%, and 176.9%, respectively, while their proportions relative to total algae increased by 135.6%, 1043.7%, and 196.3%, respectively, with proportion increases being more pronounced.

A mechanistic reading of the compositional shift described above is more informative than a purely descriptive one. As external and internal phosphorus loading declined, the supply rate of dissolved inorganic phosphorus, the resource that most strongly limits phytoplankton growth in Lake Taihu, decreased, which is expected to shift competitive dominance toward taxa with lower half-saturation constants for phosphorus uptake and lower minimum quotas. Diatoms and chlorophytes are efficient competitors under moderate phosphorus limitation because of high maximum uptake rates and a large capacity for luxury polyphosphate storage, and the additional ability of cryptophytes to supplement photosynthesis with phagotrophy and osmotrophy gives them a further advantage when dissolved phosphorus is scarce.

At least three further mechanisms may act in concert, and they are not mutually exclusive. First, the decline of *Microcystis* spp. may be partly a lagged and self-limiting process: *Microcystis* spp. overwinters in the sediment and its summer biomass depends on the size of the recruited inoculum, so successive years of weaker blooms progressively deplete the benthic seed population. Second, changes in nitrogen speciation associated with improved wastewater treatment, in particular the shift from ammonium to nitrate dominance, favour taxa that assimilate nitrate efficiently relative to *Microcystis* spp., which is

strongly adapted to ammonium uptake. Third, the improvement of the underwater light climate that accompanies reduced cyanobacterial biomass benefits taxa that cannot regulate buoyancy, while wind-driven mixing and frequent sediment resuspension in this large shallow lake raise turbidity in a way that affects taxa with different sinking and buoyancy strategies unequally. Because the present dataset contains density and composition but no physiological rate measurements, these mechanisms should be regarded as hypotheses to be tested by nutrient-addition and competition experiments rather than as conclusions drawn from the monitoring record.

3.2 Fluctuation of TP in Lake Taihu

The results showed that the inter-annual TP in Lake Taihu decreased from 2021 to 2025 (**Fig. S2**). The annual average TP concentration declined from 0.058 mg/L in 2021 to 0.048 mg/L in 2025. However, a distinct rebound in TP concentration occurred in July 2025. Compared with July 2024 and July 2023, TP concentrations increased by 29.4% and 31.0%, respectively, reaching the highest value for the same month in the past three years, second only to the five-year peak TP concentration of 0.099 mg/L observed in 2022. Concurrently, the TP concentrations showed significant seasonal fluctuations, with the annual maximum values typically occurring in the summer and autumn seasons after July, demonstrating good temporal overlap with the peak algal density.

Previous research has established that TP in Lake Taihu is mainly composed of total dissolved phosphorus (TDP) and TPP (Lv et al., 2026). Analysis of entire-lake phosphorus speciation from 2021 to 2023 (**Fig. S1**) showed that the annual mean TDP was relatively stable, fluctuating around 0.022 mg/L, with its proportion to TP showing little variation, ranging from 36.9% to 44.3%. TPP concentrations in Lake Taihu fluctuated between 0.029 and 0.037 mg/L. Accounting for over 60% of TP throughout the period, TPP dominated phosphorus speciation in Lake Taihu.

3.3 Contribution of ADP to TP in Lake Taihu

Given that particulate phosphorus (PP) makes the largest contribution to TP in Lake Taihu, TPP in the lake can be further divided into algal-derived particulate phosphorus (ADP) and non-algal particulate phosphorus (Jin et al., 2023). Based on the measurement results from our previous study on the average cellular phosphorus content of *Microcystis* spp. in Lake Taihu (1.46×10^{-10} mg/cell) and the algal community structure monitoring data from 2021 to 2025, the average cellular phosphorus content parameters for all 113 identified algal species in Lake Taihu were derived using the cell volume conversion method based on the *Microcystis* spp. average cellular phosphorus content parameter, thus completing the estimation of ADP concentrations in Lake Taihu.

Analysis of phosphorus speciation from 2021 to 2025 (Fig. 4) demonstrated that ADP is an important contributor to TP in Lake Taihu, and its concentrations and proportion to TP exhibited pronounced monthly fluctuations. Specifically, the monthly mean ADP concentrations in Lake Taihu from 2021 to 2025 ranged from 0.001 to 0.060 mg/L, and its proportion to TP ranged from 1.1% to 77.5%, with an average proportion of 33.4%. During the period from January to June across 2021–2025, the mean ADP concentrations were 0.016 mg/L, 0.013 mg/L, 0.015 mg/L, 0.013 mg/L, and 0.011 mg/L, respectively.

However, in July 2025, the ADP concentrations in Lake Taihu showed a significant rebound (0.023 mg/L, accounting for 42.6% of TP), increasing by 15.8% and 90.0% compared to July 2024 and July 2023, respectively, reaching the highest value for the same period in the past three years. The algal conditions during the same period also showed a similar trend: total algal density in July 2023, 2024, and 2025 showed a year-on-year increasing trend, reaching 6.1×10^7 cells/L, 9.4×10^7 cells/L, and 1.0×10^8 cells/L, respectively. This indicates that the increase in ADP concentrations caused by the increase of algal conditions in July 2025 contributed significantly to the rebound in lake TP concentrations.

Furthermore, the monthly variation in the proportion of ADP to TP showed distinct seasonal fluctuation characteristics. ADP concentrations in Lake Taihu remained at a low level during winter (typically < 15% of TP), rapidly increased in spring and remained high until late summer, during which peak values could account for over 70% of the lake TP, gradually declined in autumn, and dropped back to low levels in winter.

Mechanistically, this seasonal ADP cycle reflects the interaction of temperature-driven growth, physiological regulation of the phosphorus quota and the vertical redistribution of biomass. In spring, rising temperature and irradiance with a still well-mixed water column allow rapid biomass accrual; because cells take up phosphorus in excess of their immediate requirements (luxury uptake) and their quota rises toward the upper storage capacity, ADP increases at least as fast as biomass. As thermal stratification develops in summer, dissolved inorganic phosphorus in the epilimnion is depleted toward the half-saturation concentration for uptake, and the assemblage responds in two ways: alkaline phosphatase activity is up-regulated to hydrolyse dissolved organic phosphorus, and cells retain a high internal quota, so that ADP can account for more than 70% of a TP pool that is itself declining. Conversely, in autumn and winter, low temperature and irradiance reduce growth rates, cells senesce and settle, and their phosphorus is transferred to the sediment and partly returned to the dissolved pool by lysis and enzymatic hydrolysis, which is why the ADP/TP ratio falls below 15%. ADP thus functions as a seasonally reversible phosphorus capacitor: it accumulates rapidly cycling phosphorus during the growing season and releases it during winter, and this buffering capacity explains why TP in Lake Taihu varies seasonally with, but not in strict proportion to, the dissolved phosphorus pool.

3.4 Impact of algal community structure shifts on ADP and TP in Lake Taihu

As shown in **Fig. S2**, the algal conditions in Lake Taihu in December 2024 rebounded both month-on-month and year-on-year, with a total algal density of 4.9×10^7 cells/L compared to 2.7×10^7 cells/L in the same period of 2023, representing a year-on-year increase of 79.3%. However, the ADP concentrations in December 2023 and December 2024 showed an opposite trend, decreasing from 0.012 mg/L in 2023 to 0.009 mg/L in 2024 (Fig. 4), a year-on-year decrease of 25%.

An algal rebound occurred in Lake Taihu in winter 2024, yet the ADP concentrations was lower than that in the same period of 2023. To investigate this anomalous result, the ADP in Lake Taihu over the past five

years was statistically analyzed by algal taxonomic phyla. The results (Fig. 5) indicated that the ADP in Lake Taihu is primarily contributed by three phyla: cyanobacterial, diatoms, and chlorophytes, with cyanobacterial and diatoms together accounting for more than 80% of the ADP. In summary, it can be seen that the ADP concentrations in Lake Taihu is determined by two factors:

First, the baseline algal conditions (total algal density). The ADP rebound in summer and autumn 2025 was caused by a synchronous deterioration in algal conditions and a year-on-year increase in algal density. From July to October across 2023, 2024, and 2025, the total algal density in Lake Taihu was 8.1×10^7 cells/L, 1.2×10^8 cells/L, and 1.4×10^8 cells/L, respectively, corresponding to ADP concentrations of 0.017 mg/L, 0.021 mg/L, and 0.027 mg/L.

Second, the algal community structure. This considers the significant differences in cellular phosphorus content per cell among different algal phyla. In December 2024, although the total algal density in Lake Taihu increased significantly by 79.3% compared to December 2023, the ADP concentrations decreased by 25.0%. This was because the main increment in algal density in December 2024 came from cyanobacterial, whose density increased from 1.4×10^7 cells/L to 3.9×10^7 cells/L, a year-on-year increase of 242.8%, reaching a proportion of 80.4%. Meanwhile, the density and proportion of diatoms dropped sharply from 6.7×10^6 cells/L to 1.6×10^6 cells/L, a year-on-year decrease of 71.6%, accounting for only 3.1% of the total density (yet still contributing nearly 20% of the ADP). The decrease in ADP contributed by diatoms resulting from the decline in diatom density (reduction of 0.006 mg/L) was greater than the increase in ADP contributed by cyanobacterial resulting from the rise in cyanobacterial density (increase of 0.004 mg/L). The ADP contributions from other phyla (cryptophytes, chlorophytes, etc.) were minimal and showed little year-on-year change, resulting in a net reduction in total ADP concentrations for December, a phenomenon opposite to the trend in algal density.

According to the above results, the diatom density in December 2024 decreased by 5.1×10^6 cells/L year-on-year, corresponding to a reduction in its ADP contribution of 0.006 mg/L. In contrast, although the cyanobacterial density increased by 2.5×10^7 cells/L year-on-year, its ADP increment was only 0.004 mg/L. Although the absolute decrease in diatom density was much smaller than the absolute increase in cyanobacterial density, diatoms contributed more significantly to total ADP, largely due to the large differences in cell volume and biomass among algal phyla (Liu et al., 2024; Raven et al., 2019). As shown in **Fig. S3**, common algal species from phyla such as diatoms, cryptophytes, and dinoflagellates in Lake Taihu generally possess larger cell volumes compared to cyanobacterial, implying larger individual biomass and higher phosphorus content per cell (Liu et al., 2024). Therefore, the difference in total biomass between diatoms and cyanobacteria is significantly smaller than the difference in cell density. As also seen from Fig. 5, in the winter of 2024, the diatom density proportion in Lake Taihu was only 3.1%, yet its proportion to total ADP was 16.5%. This demonstrates that when assessing the contribution of ADP to total lake phosphorus, it is essential to consider not only changes in total algal density but also the composition of the algal community structure.

3.5 A mechanistic framework for ADP: density and composition control

The observations above can be condensed into a compact and testable framework. The ADP concentration at any time is the sum, over all taxa *i*, of cell density *N* and cell-specific phosphorus content *q*:

$C_{ADP} = \Sigma N_i \times q_i$ (4)

Differentiating with respect to time separates the two controlling channels:

$dC_{ADP}/dt = \Sigma q_i (dN_i/dt) + \Sigma N_i (dq_i/dt)$ (5)

The first term is the quantity channel, that is, the change in algal biomass at fixed composition, and the second is the quality channel, that is, the change in composition and in cellular phosphorus quotas at fixed biomass. The two channels may reinforce or oppose each other, and the 2024–2025 record contains clear examples of both.

Between July and October the two channels acted in the same direction: total algal density increased while the community shifted toward larger-celled taxa, and ADP rose from 0.017 mg/L (2023) to 0.021 mg/L (2024) and 0.027 mg/L (2025). In December 2024, by contrast, the channels opposed each other. Total density increased by 79.3% year-on-year, yet ADP fell by 25.0%, because the increase was dominated by small-celled cyanobacterial while the large-celled diatoms collapsed; the quality channel thus outweighed the quantity channel and produced a compositional decoupling of ADP from algal abundance.

This decoupling can be quantified directly from the data. The decrease of 5.1×10^{6} cells/L in diatoms was accompanied by a 0.006 mg/L decrease in ADP, implying an apparent cell-specific phosphorus content of about 1.2×10^{-9} mg/cell for the diatom assemblage, whereas the increase of 2.5×10^{7} cells/L in cyanobacteria produced an ADP increase of only 0.004 mg/L, implying about 1.6×10^{-10} mg/cell. The ratio of roughly seven to eight is of the order predicted by allometric scaling of cellular phosphorus with cell volume (Finkel et al., 2010) and is internally consistent with the independently measured value for *Microcystis* spp. (1.46×10^{-10} mg/cell). It explains in a single number why a large numerical gain by cyanobacteria can be more than offset by a much smaller numerical loss of diatoms: ADP is an abundance measure weighted by cell size, and its sensitivity to a given taxon is directly proportional to that taxon's *q*.

The same weighting is visible over the whole record when the share of a phylum in cell density is compared with its share in ADP (Fig. 6a). Pooled over the 60 months of 2021–2025, cyanobacteria contributed 85% of total cell density but only 51% of ADP, whereas diatoms contributed only 6% of cell density but 32% of ADP. The discrepancy is systematic rather than incidental: in 22 of the 60 months,

diatoms accounted for less than 20% of cell density yet more than 30% of ADP, and the ratio of their ADP share to their density share had a median of 3.7 across the 58 months in which diatoms exceeded 0.5% of total density, and reached 33 in extreme summer months. Numerically minor but large-celled taxa therefore exert a disproportionate control on the ADP pool, which is why total algal density alone is an unreliable predictor of algae-derived phosphorus.

Three physiological facts underpin the taxonomic differences in *q*. First, ribosomal RNA accounts for a large and growth-rate-dependent fraction of cellular phosphorus (Elser et al., 2000), so rapidly growing taxa with high ribosome contents carry more phosphorus per cell. Second, diatoms and several cyanobacteria store polyphosphate in vacuoles (Sanz-Luque et al., 2020), which allows phosphorus to accumulate far beyond immediate metabolic needs and makes *q* a regulated rather than a fixed property. Third, cell size sets an upper bound on the phosphorus a cell can contain (Smith and Kalff, 2010), so the cell-size spectrum of the community effectively defines the ceiling of the ADP pool.

An important corollary concerns the fate of this phosphorus. Because diatoms are negatively buoyant and sink rapidly, a diatom-dominated assemblage exports phosphorus to the sediment and thus acts as a biological phosphorus pump (David et al., 2003), whereas buoyant *Microcystis* spp. retains phosphorus in the water column and recycles it in situ (Fig. 6b). The same reasoning applies qualitatively to dinoflagellates, which are numerically rare in Lake Taihu but possess the largest cell volumes, and hence the largest per-cell biomass, among the dominant phyla; because their cell volumes and cellular phosphorus quotas were not measured in this study, their contribution to ADP is not quantified separately here (see Sect. 3.6). A shift toward large-celled, rapidly sinking taxa therefore has two opposing consequences for water-column TP, namely an immediate increase in ADP and a longer-term increase in the sedimentary phosphorus flux, and it is this trade-off, rather than the instantaneous ADP value alone, that should guide the interpretation of community-based phosphorus management.

A convenient diagnostic summarizing these effects is the community-weighted mean cell-specific phosphorus content, CWM-q = $\Sigma\ (N_i \times q_i)\ /\ \Sigma\ N_i$ = C_{ADP} / total algal density, which averaged 2.3×10^{-10} mg/cell over 2021–2025. In December 2024 the lake became numerically denser but, in algal terms, phosphorus-poorer per cell, because CWM-*q* declined while total density increased. Routine monitoring that tracks only total algal density or chlorophyll a would not detect this shift, whereas pairing density with taxonomic composition, as in the present dataset, makes the phosphorus-relevant signal visible. Once taxon-specific q values have been validated experimentally, CWM-*q* can be computed operationally and used to anticipate ADP-driven TP rebounds following community shifts.

4 Conclusion

This study identifies algae-derived phosphorus (ADP) as a key component of total phosphorus (TP) in Lake Taihu, governed jointly by total algal density and community structure, so both must be considered when assessing its contribution to TP. Mechanistically, because ADP is the product of algal abundance and cell-specific phosphorus content—the latter differing by roughly an order of magnitude among the

phyla present—shifts in community composition alone can decouple ADP from total algal abundance, even driving the two in opposite directions (as in December 2024), while the seasonal uptake of dissolved phosphorus into biomass, its retention as an internal quota and its release through senescence, enzymatic hydrolysis and sedimentation form a reversible phosphorus capacitor that modulates TP independently of external loading. Two implications follow: the response of Lake Taihu to phosphorus control should be detectable first in algal community composition—a progressive shift towards smaller-celled, lower-P-quota taxa—and only later in bulk TP; and, because buoyant cyanobacteria retain phosphorus in the water column whereas diatoms export it to the sediment, the trajectory of community structure, not algal density alone, determines whether the internal phosphorus pool is drained or recycled. Consistently, recent ecological improvement, the decline in total algal density and the amelioration of community structure have lowered ADP overall, contributing positively to phosphorus control; yet the algal-dominated habitat has not been fundamentally reversed and the western and southern lake regions remain prone to bloom outbreaks, where fluctuations or rebounds in algal conditions can readily increase ADP, and hence TP, and degrade water quality. Sustained algae control therefore remains essential for continued water quality improvement in Lake Taihu.

Declarations

Conflict of interest

The authors declare no competing interests.

Ethical approval

All authors have read, understood, and have complied as applicable with the statement on “Ethical responsibilities of authors” as found in the Instructions for Authors and are aware that with minor exceptions, no changes can be made to authorship once the paper is, submitted.

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Author Contribution

Zhe Yang, Bingchuan Zhu, Junyi Zhang, Ting Song, Yan Zhuang, Hujun Zhang, and Yanjuan Xu conceived and designed the experiment. Zhe Yang, Ximing Dai, and Yan Zhuang analyzed the data. Zhe Yang wrote and revised the paper. All authors have read and agreed to the published version of the manuscript.

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Data Availability

All data that support the findings of this study are included in the manuscript.The datasets generated and analyzed during the current study are available from the corresponding author upon reasonable request.

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Figures

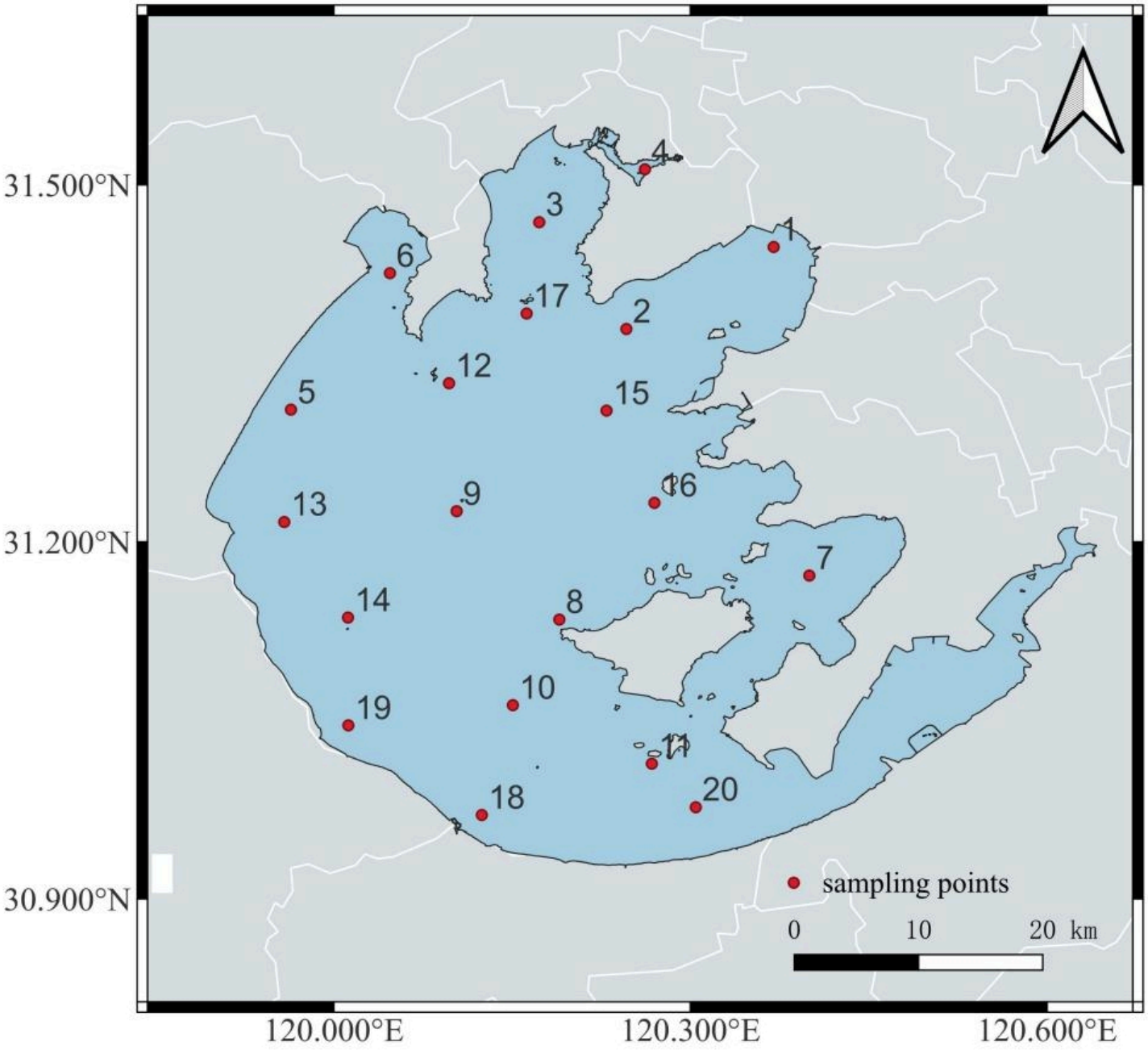


Figure 1

Distribution of monitoring sites in Lake Taihu

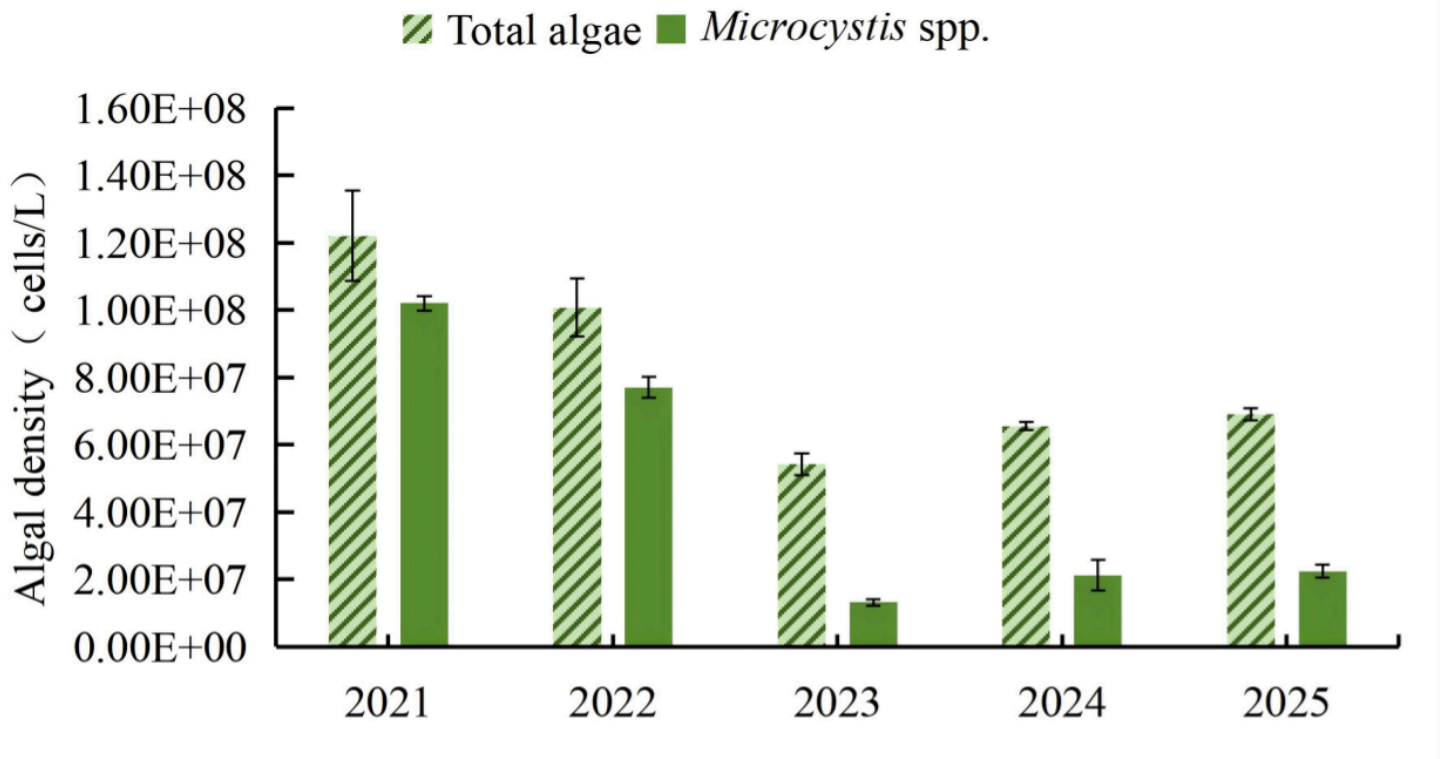


Figure 2

Changes in total algal density and *Microcystis* spp. density in Lake Taihu from 2021 to 2025

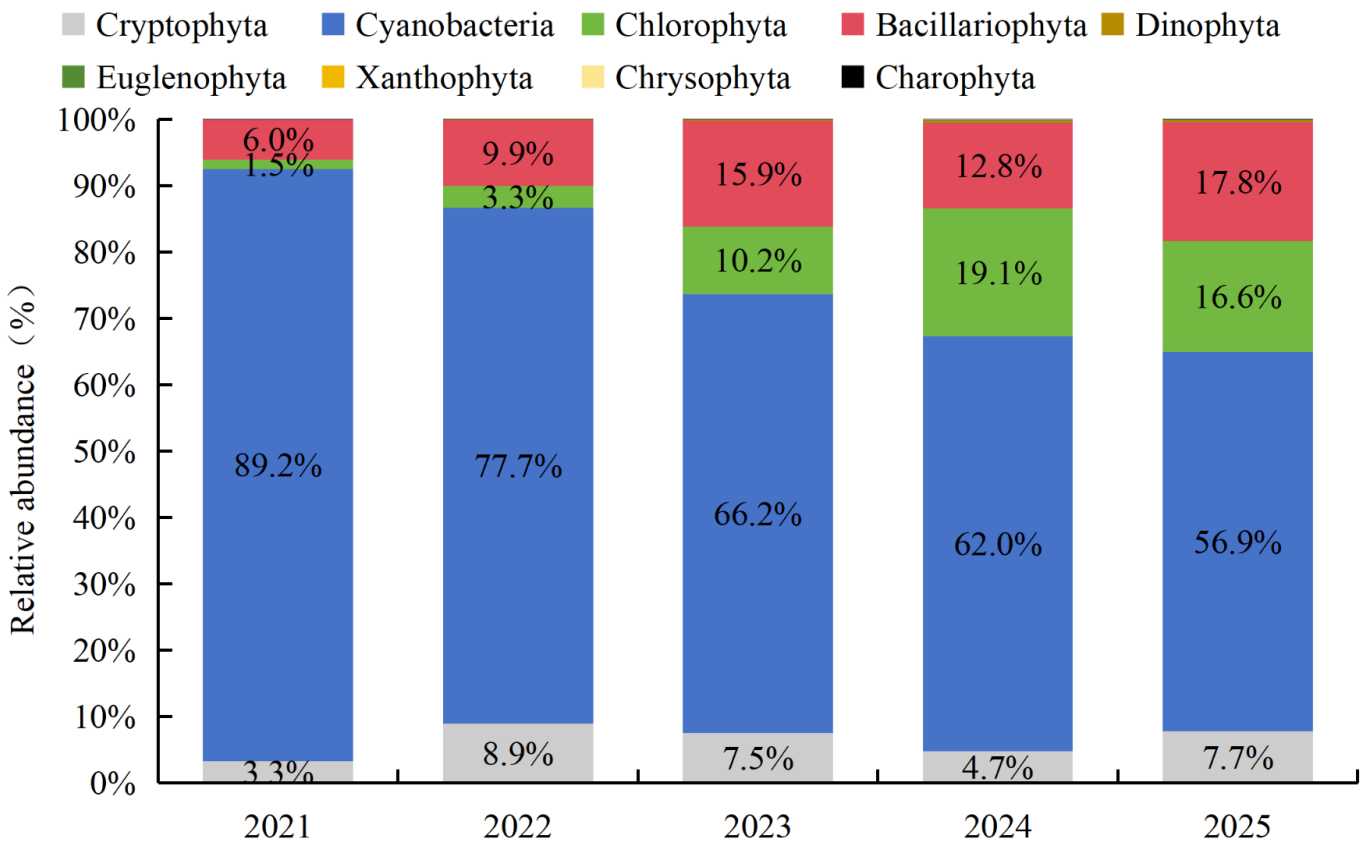


Figure 3

Interannual variations in algal community structure in Lake Taihu from 2021 to 2025

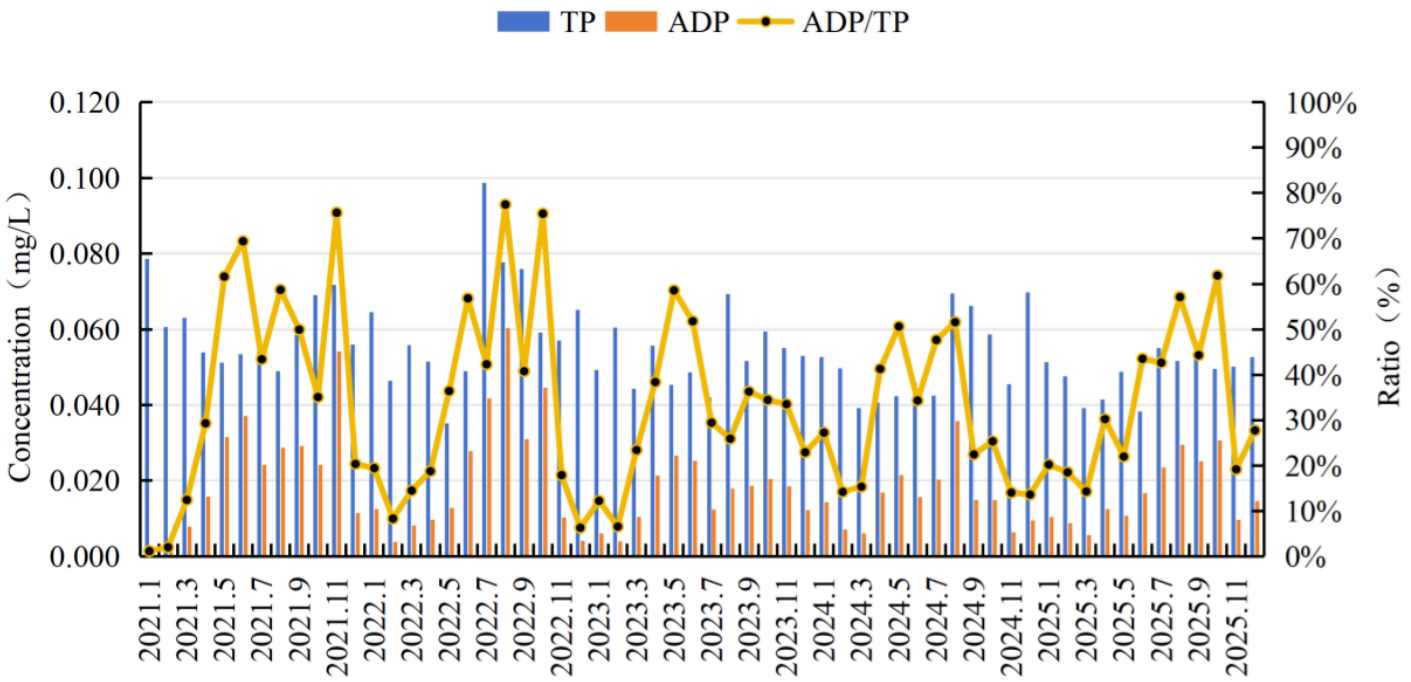


Figure 4

Monthly variations of ADP and TP concentrations in Lake Taihu, 2021-2025

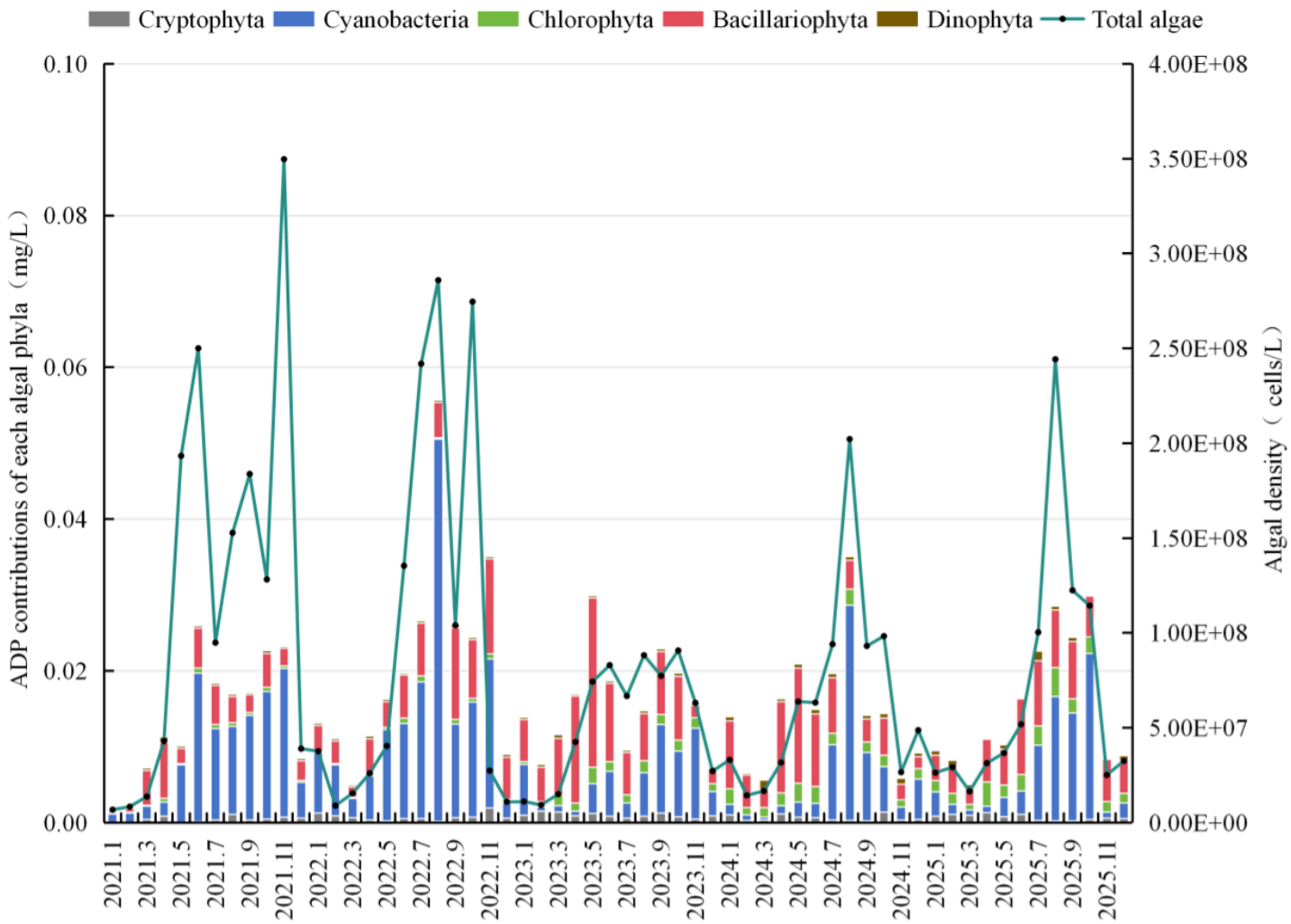
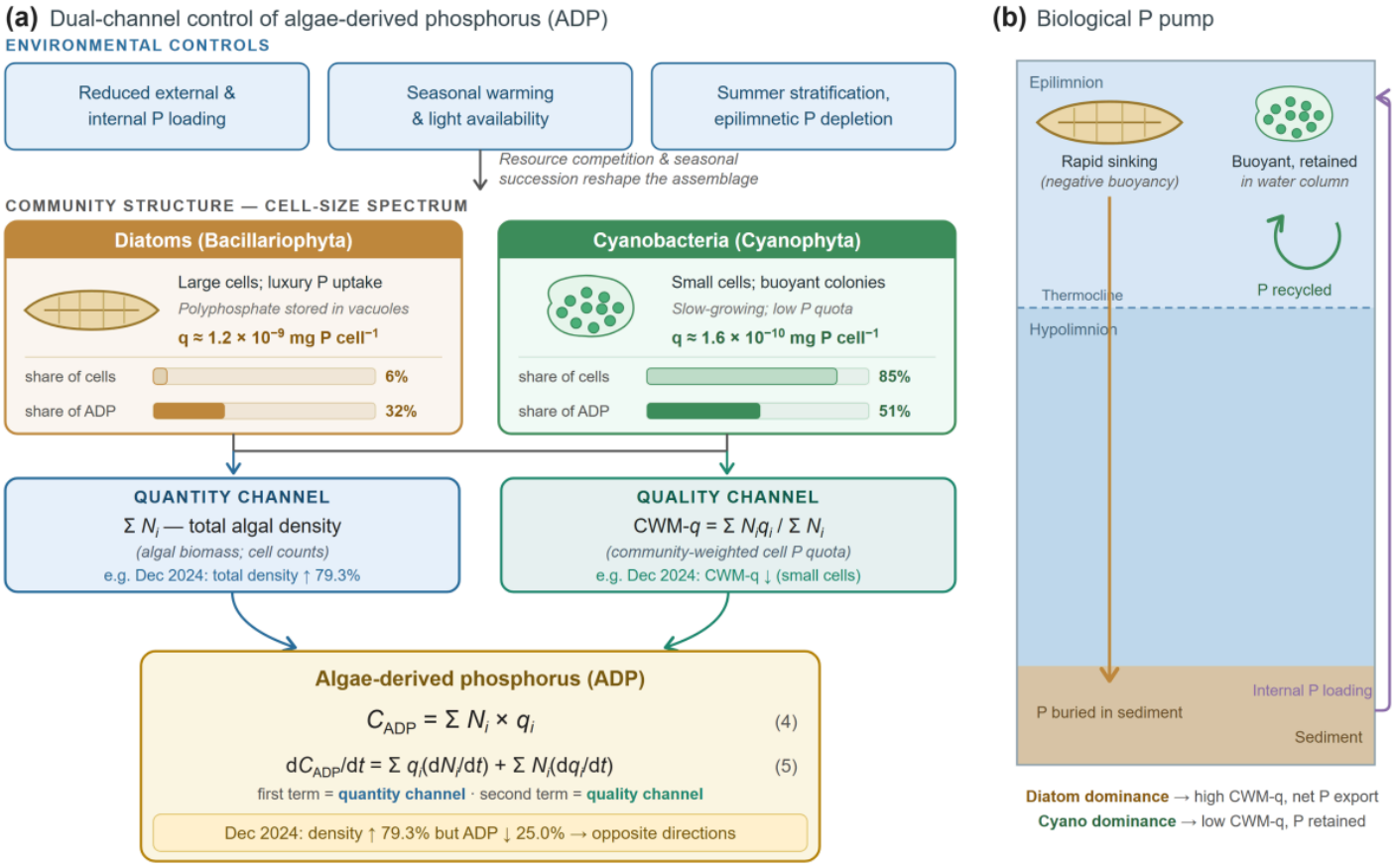


Figure 5

Monthly variations in ADP contribution by different algal phyla in Lake Taihu, 2021-2025



Shares of cell density and of ADP are pooled over all 60 months of 2021–2025 (whole-lake monthly means); n = 60.
q of diatoms and cyanobacteria back-calculated from the December 2024 density–ADP exchange (Sect. 3.5) and cross-checked against the 60-month record.
Cell-specific P of Microcystis spp. measured in this study (1.46 × 10−10 mg P cell−1).
q scales with cell biovolume (allometric exponent ≈ 0.7–1.0). N, cell density; q, cell-specific P quota; CWM-q, community-weighted mean q; ADP, algae-derived phosphorus.

Figure 6

Conceptual framework linking algal community structure to algae-derived phosphorus (ADP) in Lake Taihu: (**a**) Environmental drivers reshape the cell-size structure of the assemblage; ADP then responds through a quantity channel (total density) and a quality channel (community-weighted cell-specific P quota, CWM-*q*), which may reinforce or offset each other; (**b**) Fast-sinking diatoms export P to the sediment; buoyant cyanobacteria retain and recycle it in the water column.

Supplementary Files

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