Suspended phosphorus sustains algal blooms in a dissolved phosphorus-depleted lake

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ARTICLE INFO

ABSTRACT

The expansion of algal bloom in surface waters is a global problem in the freshwater ecosystem. Differential reactivity of organic phosphorus (P_o) compounds from organic debris, suspended particulate matter (SPM), and sediment towards hydrolysis can dictate the extent of supply often limited inorganic P (P_i) for algal growth, thereby controlling the extent of bloom. Here, we combined solution P-31 nuclear magnetic resonance (^{31}P NMR), sequential extraction, enzymatic hydrolysis, and 16S rRNA measurements to characterize speciation and biogeochemical cycling of P in Lake Erhai, China. Lower ratios of diester-P/monoester-P in SPM in January (mean 0.09) and July (0.14) than that in April (0.29) reflected the higher degree of diester-P remineralization in cold and warm months. Both H_2O-P_i and P_o were significantly higher in SPM (mean 1580 mg $\cdot$kg^{-1} and 1618 mg $\cdot$kg^{-1}) than those in sediment (mean 8 mg $\cdot$kg^{-1} and 387 mg $\cdot$kg^{-1}). In addition, results from enzymatic hydrolysis experiments demonstrated that 61% P_o in SPM and 58% in sediment in the H_2O, NaHCO$_3$, and NaOH extracts could be hydrolyzed. These results suggested that H_2O-P_i and P_o from SPM were the primarily bioavailable P sources for algae. Changes of P_i contents (particularly H_2O-P_i) in algae and alkaline phosphatase activity (APA) during the observation periods were likely to be controlled by the strategies of P uptake and utilization of algae. P remobilization/remineralization from SPM likely resulted from algae and bacteria (e.g., *Pseudomonas*). Collectively, these results provide important insights that SPM P could sustain the algal blooms even if the dissolved P was depleted in the water column.

1. Introduction

Algal blooms triggered by nutrient loading have been one of the lingering issues in the recovery of freshwater ecosystem health on the Earth (Li et al., 2015). Reduction of external nutrient loading is the most common remedial measure to mitigate algal blooms. However, the duration, frequency, and magnitude of algal blooms appear to be elevated in many freshwater lakes, such as Lake Erhai in China, Lake Kasumigaura in Japan, and Lake Erie in North America (Shinohara et al., 2012; Huang et al., 2020; Wang et al., 2021b; Hou et al., 2022; Ji et al., 2022). One of the potential reasons for these results is attributed to the internal loading of phosphorus (P) (Joshi et al., 2015; Li et al., 2017a, b).

Similar to sediment, P released from dead algae and suspended particulate matter (SPM) in the water column provide a significant feedback loop to replenish P for algal blooms (Shinohara et al., 2012; Li et al., 2017a, b; Feng et al., 2018). Despite their importance, currently little is known regarding the P speciation of algae, SPM, and sediment. Existing knowledge on inorganic P (P_i) pools of SPM depends heavily on sequential extraction (Tang et al., 2018; Zhang et al., 2021). Sequential extraction method developed by Hedley et al. (1982) is the most commonly used for P_i pools in sediment (Zhu et al., 2013; Wang et al., 2021b). In reality, particulate organic P (POP) in the water column accounted for 47~87% of their corresponding total P (TP) (Yang et al., 2021a). In addition, P_i released from POP remineralization in the water column under enzymes can provide P source for algae (Giles et al., 2015; Li et al., 2017b). Nevertheless, POP in the water column is often

classified as refractory species (Pan et al., 2013; Pu et al., 2021). Taken above-mentioned into consideration, P speciation and their remineralization (e.g., Li et al. 2015, Feng et al. 2018, Pan et al. 2020, Ni et al. 2022) and bio-availability of algae, SPM, and sediment is turnover need more attention because those of characteristics determine the mechanisms of P regeneration (Zhu et al., 2013; Li et al., 2015, 2017b).

Identifying the sources and cycling of dissolved P in the water column is complex due to (i) a low concentration of dissolved P in the water column compared to SPM and sediment P; (ii) active and variable transformations of P_i and P_o; (iii) co-occurring biotic and abiotic reactions of P; and (iv) variable strategies by (micro)organisms for P uptake and utilization as a function of the concentrations and compositions of P_o and P_i (Jaisi and Blake, 2014). Such characteristics not only hinder the identification of sources and cycling of P, but also hamper the formulation of effective nutrient management measurements in aquatic ecosystem. Therefore, complementary methods are required to identify the composition and bio-availability of P compounds and P pools of algae, SPM, and sediment for a better understanding of the biogeochemical and dynamic cycling of P.

Solution ^{31}P nuclear magnetic resonance spectroscopy (^{31}P NMR) is a state-of-the-art, nondestructive technique for identifying P compounds in environmental samples (Tate and Newman, 1982; Cade-Menun and Preston, 1996; Shinohara et al., 2012; Read et al., 2014). In addition, enzymatic hydrolysis provides a better method for accessing bioavailable P_o due to its similar reactions associated with P_o remineralization in lake ecosystem (Quiquampoix and Mousain, 2005; Monbet et al., 2007; Zhu et al., 2013; Ni et al., 2022). Major groups of compounds discriminated by NMR are orthophosphate monoesters (monoester-P), orthophosphate diesters (diester-P), pyrophosphate (pyro-P), and orthophosphate (ortho-P). Bioavailable P_o pools in the H_2O, $NaHCO_3$, and NaOH extracts identified by enzymatic hydrolysis include monoester-P, diester-P, and phytate-like P. These compounds can originate from algae, SPM, and sediment but their relative concentration vary, thus may provide useful information for probing into P transformation and recycling.

Lake Erhai, the second largest freshwater lake on Yunnan-Guizhou plateau, is one of the most concerned lakes in China and an important drinking water source for Dali city, Yunnan province. In recent years, external P inputs have been effectively controlled, whereas large-scale algal blooms still occur annually (Ji et al., 2017; Chen et al., 2021). Concentrations of TP (~ 0.05 mg·L^{-1}) in the water column are often five times greater than those of soluble reactive P (SRP, < 0.01 mg·L^{-1}) and dissolved P_o (DOP, < 0.01 mg·L^{-1}) (Ji et al., 2017; Yang et al., 2021b). Under this condition, we hypothesize that P released from SPM is a critical P source for algae. To test this hypothesis, we carried out a set of systematic research in P speciation in algae, SPM, and sediment. The objectives of our research were to: (1) characterize the P speciation of algae, SPM, and sediment; (2) compare the differences of bioavailable P_o among them; (3) explore the potential mechanisms of P released from SPM. Solution ^{31}P NMR, sequential extraction, enzymatic hydrolysis, and 16S rRNA were collectively employed to achieve the objectives and test the hypothesis. Results obtained from this study contributed to a better understanding of the reasoning behind the repeated algal blooms in dissolved P-depleted lakes.

2. Materials and methods

2.1. Sample collection and preparation and analysis of physicochemical properties of water

Water, algae, and sediment were collected at the same sites (Fig. S1) in January, April, and July in 2021. The detailed description of study sites is available in Supplementary Materials. 60 L lake water from surface water (below 0.5 m surface water) and bottom water (above 0.5 m sediment) was collected at each site using a Niskin sampler, respectively. SPM were collected for analyzing P speciation filtered by 60 L

lake water with precombusted (450 °C, 4 h) and preweighted GF/F glass-fiber filters (GF/F, 0.7 μm Whatman, UK). Additional samples of lake water (5 L) were collected at the same sites. 1.5 L was used for algal abundance analysis with the addition of 3–5 mL of formaldehyde, and another 0.5 L was used for physicochemical properties analysis, and the remainder of 3 L was filtered through 0.22 μm filters for 16S rRNA analysis. Algae (below 0.5 m surface water) was collected using a phytoplankton collector (200 mesh, diameter 0.064 mm) and stored in a clean polyethylene bottle. Samples of sediment were collected by using a gravity core sampler from all sites. All samples were stored at 4 °C and immediately transported to the laboratory for analysis. Each sediment core was sliced from the top of the core to obtain 0–2 cm section and was stored in two clean centrifuge tubes. Algae mass was carefully and repeatedly washed by using ultrapure water to remove associate contents except algae (Feng et al., 2016a, 2018). After preprocessing, algae, SPM, and sediment were frozen at -80 °C first before freeze drying. Subsequently, algae and sediment were ground and sieved through a 200 mesh. The lyophilized SPM and sieved samples were stored at -20 °C until analysis.

Dissolved oxygen (DO), temperature (T), and pH of water column were measured by a multi-parameter water quality monitor (YSI, 6600V2, Co, USA). Concentrations of TP of water samples were quantified by using a molybdenum blue method after digesting in potassium persulfate (note: the concentrations of SRP in water samples filtered by GF/F glass-fiber filters during observation periods were lower than 10 μg·L^{-1}) (Murphy and Riley, 1962). Alkaline phosphatase activity (APA) and algal abundance from water samples were measured by *p*-nitrophenyl phosphate colorimetric method and optical microscopy counting, respectively (Gage and Gorham., 1985; Boon, 1989). Concentrations of SPM in water samples were calculated by gravimetric method.

To further assess the hydrolyzability of P_o in different P pools of algae, SPM, and sediment, additional samples (including algae, SPM, and sediment) were collected in November in 2022. The methods of samples collection were same to above-mentioned.

2.2. Sample preparation and ^{31}P NMR analysis

Solution ^{31}P NMR was employed to analyze the composition of P compounds. A sufficient amount sample [algae (0.2 g), SPM (40 L lake water collected on four glass-fiber filters), and sediment (2 g)] was extracted using 40 mL of 0.25 M NaOH and 0.05 M EDTA solution for 16 h (Cade-Menun and Preston, 1996). These samples were centrifuged (14, 000 rpm) at 4 °C for 15 min after extraction. The supernatant was filtered through a filter (GF/F). Triplicate samples (approximately 2 mL each) were collected for the measurement of TP and P_i concentrations. The method for analyzing TP concentrations with NaOH-EDTA extracts was the same as that of water samples. P_i concentrations extracted by NaOH-EDTA were measured by a molybdenum-blue method (Murphy and Riley, 1962). Subsequently, the filtrate was freeze-dried (-80 °C) for several days and then the lyophilized samples were stored at -20 °C until ^{31}P NMR analysis (see details in Supplementary Materials).

2.3. Analysis of P pools and bioavailable P_o

Sequential extraction proposed by Hedley et al. (1982) has been gradually applied to analyze the sediment P pools (Zhu et al., 2013; Wang et al., 2021b; Pu et al., 2023), although the method was originally used to characterize soil P pools. Here, sequential extraction was employed to analyze P pools of algae, SPM, and sediment (solid:solution=1:60, Hedley et al., 1982). Briefly, a sufficient amount of sample (algae (0.2 g), SPM (10 L lake water collected on a glass-fiber filter), and sediment (0.2 g)) was sequentially extracted by using ultrapure water, 0.5 M NaHCO₃ (pH=8.50), 0.1 M NaOH, and 1 M HCl for 16 h. The samples were centrifuged at 4390 g for 15 min after extraction. The supernatant was filtered by using filters (GF/F). The filtrate was

collected for analyzing P_i contents (Murphy and Riley, 1962). Contents of TP in algae (0.2 g), SPM (10 L lake water collected on a glass-fiber filter), and sediment (0.2 g) were measured by using the combustion method (Aspila et al., 1976). P_o of algae, SPM, and sediment was calculated by the difference between TP and P_i (Tang et al., 2018; Yang et al., 2021a).

To further access the contents of bioavailable P_o in the different P pools of algae, SPM, and sediment extracted by sequential extraction, enzymatic hydrolysis experiments were performed following Zhu et al. (2013) report using three main enzymes (Table S1): alkaline phosphatase (APase), phosphodiesterase (PDEase), and phytase. Choice of these enzymes were intended to characterize bioavailable P_o pools, monoester-P, diester-P, and phytate-like P, respectively (see details in Supplementary Materials).

2.4. Illumina MiSeq sequencing of 16S rRNA genes

The microbial community in the water column and sediment were investigated from phylum to genus level. All samples were performed by high-throughput sequencing analysis at Sangon Botech Co., Ltd (Shanghai, China) that referred to a previous study (Yang et al., 2021c). Briefly, total genomic DNA was extracted from 0.5 g sediment and SPM filtered by filters (see Section 2.1) using the E.Z.N.A™ Mag-Bind Soil DNA Kit (M5635–02, OMEGA). 16S rRNA genes were amplified using primers 341F (CCTACGGGNGGCWGCAG) and the reverse primers 805R (GACTACHVGGGTATCTAATCC), targeting the V3-V4 variable regions. 16S rRNA gene amplicon sequencing was performed on the Illumina MiSeq platform (Illumina, Inc., San Diego, CA, USA) at Sangon Biotech Co., Ltd. The sequences (97% similarity) were clustered into the same operational taxonomic units. Classification information of species from phylum to genus level was assigned according to the ribosomal database project classifier.

3. Results and discussion

3.1. Composition difference of P compounds in different substances

Contents of NaOH-EDTA TP, TP and extraction efficiency (calculated as (NaOH-EDTA TP) / TP) of algae, SPM, and sediment were shown in Fig. S2. In descending order of contents of NaOH-EDTA TP and TP, the average P contents of three substances were SPM > algae > sediment (Fig. S2). The extraction efficiency of these substances ranged from 26% to 114% (Fig. S2). Such dramatic changes of the extraction efficiency likely resulted from the substantial differences of these substances. Moreover, similar ranges of the extraction efficiency have been reported, for example, 20% to 102% in other freshwater ecosystems (Shinohara et al., 2012; Feng et al., 2016b; Xie et al., 2019; Yang et al., 2020).

Composition of P compounds in algae, SPM, and sediment identified by applying solution ^{31}P NMR, included ortho-P, monoester-P, diester-P, and pyro-P (Figs. 1 and S3, 4). Multiple peaks of monoester-P and diester-P were observed in all samples (Fig. 1), which was similar to previous findings from other freshwater ecosystems, suggesting that multiple peaks of monoester-P and diester-P from algae, SPM, and sediment were also observed (Shinohara et al., 2012; Li et al., 2017b; Feng et al., 2020; Yang et al., 2020). Monoester-P in all samples included α-glycerophosphate, β-glycerophosphate, and unknow monoester-P (Figs. 1 and S3). DNA, RNA, and phospholipids were dominant diester-P compounds in whole samples (Figs. 1 and S3). However, polyphosphate (poly-P) was not observed in overall samples (not shown). Similar results for poly-P peaks from algae, SPM, and sediment were not observed by solution ^{31}P NMR in other freshwater ecosystems (Li et al., 2015; Feng et al., 2020; Yang et al., 2020), likely due to the low concentrations/contents of poly-P in all samples and the presence of degradation of poly-P during the alkaline extraction, lyophilization procedure, and ^{31}P NMR analysis (Cade-Menun et al., 2006; Wang et al.,
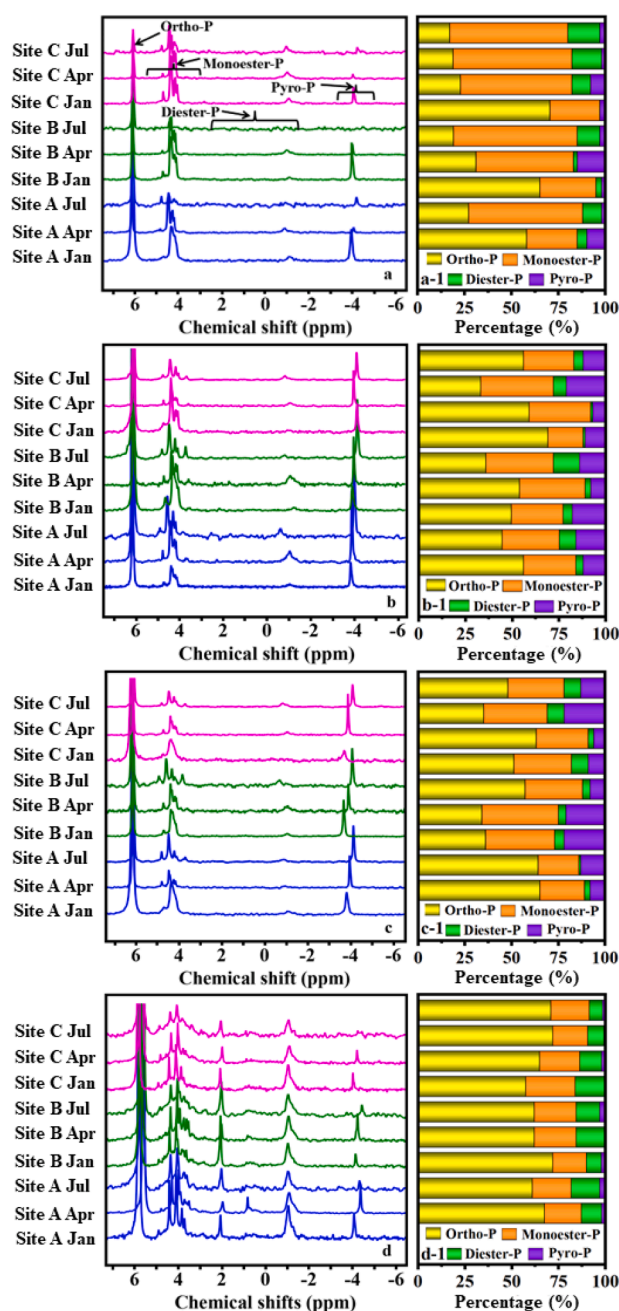

Fig. 1. ^{31}P NMR spectra of algae, suspended particulate matter (SPM), and sediment in January, April, and July at all sample sites extracted by NaOH-EDTA solution. Note: panels a, b, c, and d represent the spectra of algae, SPM in surface water, SPM in bottom water, and sediment, respectively, panels a-1, b-1, c-1, and d-1 represent the percentage of their corresponding P compounds to NaOH-EDTA TP. Ortho-P, orthophosphate; Pyro-P, pyrophosphate; Monoester-P, orthophosphate monoesters; Diester-P, orthophosphate diesters. Ortho-P (5.5~7.0 ppm), Pyro-P (−3.3~−5.0 ppm), Monoester-P (3.0~5.5 ppm), and Diester-P (−1.5~2.5 ppm) (see Supplementary Materials).

2021a). Moreover, contents of P compounds and their corresponding percentages were further analysis. Results showed that contents and percentages of biogenic P of algae (average 937 mg·kg^{-1} and 64%) and SPM (average 1351 mg·kg^{-1} and 50%) were significantly higher than those of sediment (average 138 mg·kg^{-1} and 35%) (Figs. 1, S4, and Table S2). These results suggest that biogenic P of algae and SPM could be released during or after sedimentation.

Relative remineralization efficiency for diester-P and monoester-P can be expressed by diester-P/monoester-P ratios. A lower diester-P/

monoester-P ratio reflects the higher degree of diester-P remineralization, because monoester-P is more chemically stable than diester-P (Paytan et al., 2003; Ahlgren et al., 2006) and diester-P degradation generates monoester-P. Accordingly, lower ratios of diester-P/monoester-P from SPM in January (mean 0.09) and July (0.14) than those in April (0.29) were observed, showing the higher degree of diester-P remineralization during these periods. Moreover, the diester-P/monoester-P ratios in algae (mean 0.15) and SPM (mean 0.17) were markedly lower than those of sediment (mean 0.55) (Table S2), which might reflect the substantial degradation and/or reproduction during or after sedimentation. The possible explanation for the low diester-P/monoester-P ratios in algae and SPM is that the presence of α-glycerophosphate and β-glycerophosphate likely resulted from degradation of phospholipids due to alkaline extraction and relative long ^{31}P NMR analysis time (generally > 10 h) (Turner et al., 2003; Doolette et al., 2009). Alternatively, phospholipids could also be naturally hydrolyzed as α-glycerophosphate and β-glycerophosphate induced by sunlight and/or phosphodiesterase (Turner et al., 2003; Li et al., 2019; Guo et al., 2020). Further work is urgently needed to differentiate natural degradation from artificial hydrolysis in future. The reasonable interpretation for the higher diester-P/monoester-P ratios in sediment is primarily attributed to increased DNA of sediment (Fig. 1). The presence of DNA in SPM and sediment might be the result of sedimentation because DNA is relatively recalcitrant to hydrolyze relative to other P_o molecules (e.g., RNA) (Westmeimer, 1987). Alternatively, DNA can be constantly produced in sediments (Li et al., 2015). Similar results have been reported in other lakes for sediment DNA reproduction (Shinohara et al., 2012; Jin et al., 2022).

3.2. Variation of P pools and bio-availability of P_o pools

3.2.1. Variation of P pools in algae, suspended particulate matter, and sediment

Contents of P pools and their corresponding percentages to TP in all samples were shown in Figs. 2 and S5. Contents of P_i pools (especially H_2O-P_i) in algae were gradually decreased from January to July, which might be attributed to P uptake and utilization strategies of algae (see 3.3). However, compared with the variation of contents of P pools in algae during the observation periods, the contents of P pools in SPM were irregular but relatively higher (beside sites A and C in January) (Fig. 2a, b, and c). Here, it is worth considering that the SPM P contents are dominantly controlled by two linked but not overlapping variables: SRP concentration and the adsorption capacity of SPM (River and Richardson, 2018; Ji et al., 2022; Walch et al., 2022). Variable SPM P contents reflected their complex processes and/or mechanisms of these two factors during the observation periods. Thus, more direct evidences for the characterizing P adsorption mechanisms on SPM and its composition are warranted. Sediment might be the result of SPM sedimentation, thus, P_o remineralization and P_i remobilization from SPM could have occurred during or after sedimentation. The collective contents and percentages of H_2O-P_i, $NaHCO_3$-P_i, $NaOH$-P_i, and P_o in algae (mean 1870 mg·kg^{-1} and 98%) and SPM (mean 4038 mg·kg^{-1} and 86%) were significantly higher than those of sediment (mean 696 mg·kg^{-1} and 65%) (Figs. 2 and S5).

H_2O-P_i and P_o from algae and SPM were the mainly bioavailable P sources for algal blooms. P_i extracted by H_2O is loosely adsorbed to SPM or sediment particles, which represents immediately available P. Contents of P_i in algae, SPM, and sediment extracted by H_2O ranged from 38 to 1231 mg·kg^{-1} (average 610 mg·kg^{-1}), from 397 to 3312 mg·kg^{-1} (average 1580 mg·kg^{-1}), and from 1 to 16 mg·kg^{-1} (average 8 mg·kg^{-1}), accounting for 3%–52% (average 29%), 25%–46% (average 35%), and 0%–2% (average 1%), respectively (Figs. 2 and S5). Similar results also
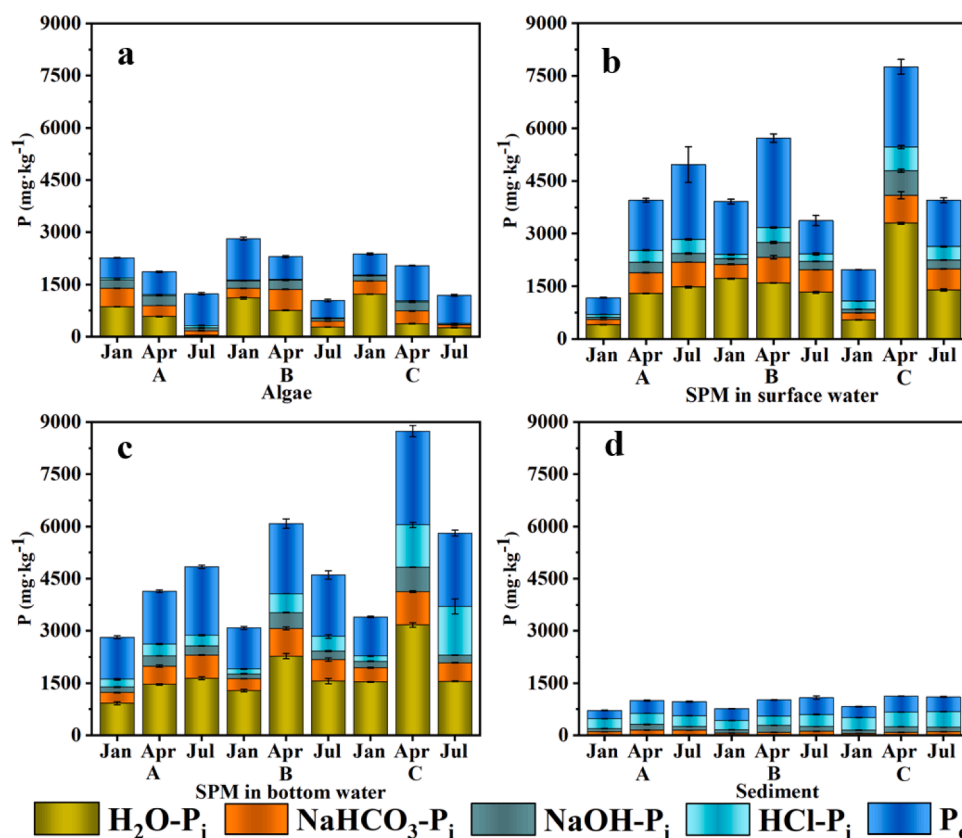

Fig. 2. Contents of P pools from algae, SPM, and sediment. Error bars represent the standard deviations of triplicate measurements.

demonstrated that contents of immediately available P (average 633 mg·kg^{-1}, 19% of the TP) of SPM extracted by NH_4Cl were fundamentally higher than those of sediment (average < 10 mg·kg^{-1}, <1% of the TP) in Lake Chaohu, China (Yang et al., 2020, 2022). These results suggested that immediately available P of SPM was a dominant P source for algal blooms. Contents of P_o in algae (468–1241 mg·kg^{-1}, average 767 mg·kg^{-1} and 44% of TP) and SPM (472–2879 mg·kg^{-1}, average 1618 mg·kg^{-1} and 37% of TP) were markedly higher than those of sediment (231–534 mg·kg^{-1}, average 387 mg·kg^{-1} and 40% of TP). These observations demonstrated that the most of P_o from algae and SPM could be released during or after sedimentation and thus provided primarily bioavailable P_o for algae.

Results from ^{31}P NMR and sequential extraction provided relative comparison. Differences between ^{31}P NMR and sequential extraction were often described in lake sediments by previous studies (Dong et al., 2012; Yuan et al., 2017; Ni et al., 2019; Campos et al., 2022). The range of P_o/TP percentages from algae, SPM, and sediment measured by ^{31}P NMR ranged from 32% to 80% (mean 58%), from 20% to 50% (mean 36%), and from 26% to 42% (mean 33%), respectively (Fig. 1). In contrast, the range of P_o/TP percentages from algae, SPM, and sediment extracted by sequential extraction varied from 24% to 74% (mean 44%), from 25% to 49% (mean 37%), and from 33% to 47% (mean 40%), respectively (Fig. S5). Understanding the differences of P_o overestimation or underestimation is not straightforward, particularly because of (i) fundamental difference of extracts in the two methods; (ii) presence degradation of poly-P and diester-P during the pretreatment of sample and ^{31}P NMR analysis (Cade-Menun et al., 2006; Wang et al., 2021a); (iii) re-adsorption of extracted P onto colloidal particles and/or $CaCO_3$ of the residue (Wang et al., 2013); (iv) the occurrence of molybdate reaction between molybdate and ortho-P only rather than other P_i forms (e.g., pyro-P and poly-P) and thus underestimating the P_i concentrations of the extracts (Murphy and Riley, 1962; Cade-Menun et al., 2006). In addition, it is important to highlight that these two methods are not accurately quantified bioavailable P_o. Therefore, enzymatic hydrolysis was employed to further character the compositions and contents of bioavailable P_o in different P pools of algae, SPM, and sediment.

3.2.2. Bio-availability of P_o pools

Before performed by enzymatic hydrolysis, we analyzed the contents (e.g., P_i and P_o, see Supplementary Materials) of different P pools from algae, SPM, and sediment extracted by H_2O, $NaHCO_3$, NaOH, and HCl, which was shown in Figs. S6 and S7. After enzymatic hydrolysis, results demonstrated that monoester-P and diester-P were the main P_o species in different P_o pools of algae, SPM, and sediment (Fig. 3), which was consistent with the distribution of monoester-P and diester-P in these substances measured by solution ^{31}P NMR (Fig. 1).

Monoester-P and diester-P from algae and SPM were important P_o sources for algal blooms. Enzymatically hydrolyzable contents of monoester-P, diester-P, and phytate-like P from algae (average 695 mg·kg^{-1}) and SPM (average 824 mg·kg^{-1}) were substantially higher than those of sediment (average 56 mg·kg^{-1}) in the H_2O, $NaHCO_3$, and NaOH extracts, accounting for 126%, 61%, and 58% of their correspondingly total P_o of these extracts, respectively (Figs. 3 and S8). Similar results for contents of enzymatically hydrolyzable monoester-P and diester-P from sediment were observed in the same research area, which ranged from 20 to 58 mg·kg^{-1} (Pu et al., 2023). No hydrolyzable P_o in the HCl extract of algae, SPM, and sediment was observed during the enzymatic hydrolysis experiment (not shown), which is similar to a previous report showing no hydrolysable P_o in the same P pool of sediment (Zhu et al., 2013). Furthermore, based on the enzymatic hydrolysis, P_i released from SPM P_o remineralization in the lake could be reached to 7.2 t, which can increase the concentrations of SRP by 3 µg·L^{-1}. Altogether, the above results indicated that the majority of P_o from algae and SPM could be hydrolysable during or after sedimentation, causing P released from algae and SPM to water column and further
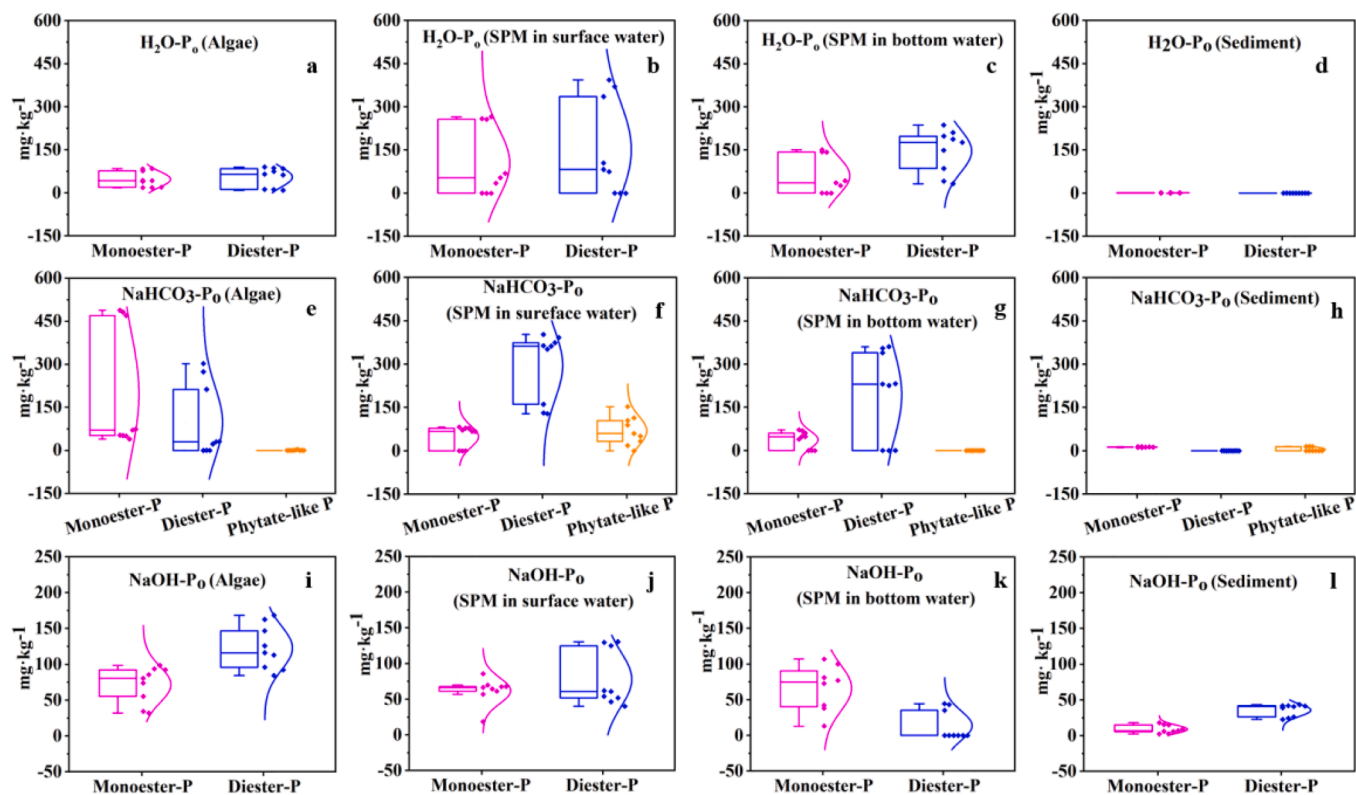

Fig. 3. Contents of enzymatically hydrolyzable monoester-P, diester-P, and phytate-like P in different P pools, including H_2O-P_o (a-d), $NaHCO_3$-P_o (e-h), NaOH-P_o (i-l). The box and whisker plots show the average (square), median (horizontal line), 25th and 75th percentile (lower and upper edge of box), and the 5th and 95th percentile (lower and upper whisker).

providing P source for algae.

3.3. Shift in strategies for P uptake by algae

Previous studies have demonstrated that dissolved P_i and P_o could be rapidly accumulated in algae and slowly utilized during the subsequent growth and reproduction (Jauzein et al., 2010; Laws et al., 2011; Ren et al., 2017). Furthermore, APA was regulated by P_i stress (Ren et al., 2017). However, these results were obtained in simulated system that performed in the laboratory. Our results from field investigations not only identify previous lab findings, but also gain some new insights. As was shown that (i) the higher degree of SPM diester-P remineralization in January and July than those in April was observed (see 3.1); (ii) APA in water column in January and July was approximately 16 and 45 times than those in April, respectively, which reflected the higher degree of monoester-P remineralization in January and July than those in April (Fig. S9); (iii) contents of H_2O-P_i and pyro-P of algae in January were ~22 times greater than that of algae in April and July (Figs. 1 and 2 and Fig. S4), in addition, algal abundance were gradually increased during the observation periods (Fig. S10), these results reflected the shift strategies for P uptake and utilization by algae in different P quota of algal cell. Taken together, dissolved P_i from P_o remineralization in the water column could be directly stored in algae in the form of ortho-P and pyro-P in January; algae heavily depended on its stored P_i for growth and reproduction in April; P supply for algal blooms in July can be heavily dependent on SPM P_o remineralization. However, these samples were collected at long time intervals, as a result, which might be lost some important information associated with the strategies of P uptake and utilization of algae. Therefore, increasing sample times are required to further clarify the strategies for P uptake and utilization by algae during the its growth and reproduction in ongoing work.

The hydrodynamics-driven changes in SPM mineralogy led to increasing P sorption, as was shown by the higher contents of P_i (particularly H_2O-P_i) in SPM than those in algae, especially in July (Fig. 2a, b). The underlying reason for the higher P contents of SPM is that SRP can bind preferentially with particulate surface beside biological uptake and assimilation (Yang et al., 2021a). Therefore, increasing the competition between algae and sorption sites of inorganic SPM for dissolved P_i in the water column during the algal blooms (e.g., July) might also lead algae to increasingly depend on POP

remineralization to meet its P needs (Olander and Vitousek, 2005; Helfenstein et al., 2018). This was also expressed by the enhancing APA in the water column with the increasing algal abundance (Figs. S9 and S10). To further reveal the P uptake and utilization strategies of algae, future work is required to quantify the adsorption of dissolved P_i on SPM in the water column and its effect on algal growth and reproduction.

3.4. Microbially driven P release from suspended particulate matter

Bacteria also play an essential role in P release except for algae. Strong correlations among P pools and P compounds from SPM to sediment and different bacterial communities at genus level in their corresponding mediums were observed, suggesting that SPM and sediment might enrich some specific taxa (Fig. 4a, b). We selected 10 genera in the water column and 10 genera in sediment as "core" genera due to their high relative abundances and significant positive or negative correlations with their corresponding P pools and P compounds (Fig. 5a, b). Fortunately, those of the selected core genera have members with reported capabilities in P solubilization/mineralization (e.g., *Pseudomonas* in the water column, *Thiobacillus* in sediment), which can transform P_o or insoluble P_i into dissolved P_i (Menkina, 1950; Paul and Sundara Rao, 1971; Illmer and Schhinner, 1992; Jorquera et al., 2008). In order to provide more information for P cycling, we further analyzed the relative abundance of phosphorus solubilization/mineralization bacteria (including inorganic phosphorus-solubilization bacteria, IPB; organic phosphorus mineralization bacteria, OPB) at genus level in the water column and sediment. These results indicate that relative abundance of both IPB (mean 16.60%) and OPB (mean 27.85%) in the water column were greater than those of in sediment (mean 0.84% for IPB and 2.29% for OPB) (Fig. S11), which highlighted that these key bacteria genera were responsible for P released from SPM during the sedimentation.

Moreover, iron cycling driven by redox transformations or microorganisms can also influence P release from P associated with iron (hydr)oxides (Fig. S12). Increasing studies have shown that the competition between some bacteria (e.g., Fe (III)-reducing bacteria, FeRB; Fe (II)-oxidizing bacteria, FeOB) and redox transformations for Fe (II) oxidation or Fe (III) reduction may increase (Crowe et al., 2007; Melton et al., 2014; Upreti et al., 2019; Fan et al., 2021; Chen et al., 2022). In addition, latest studies demonstrated that some bacteria (e.g., sulfate-reducing bacteria, SRB; sulfide-oxidizing bacteria, SOB) with the
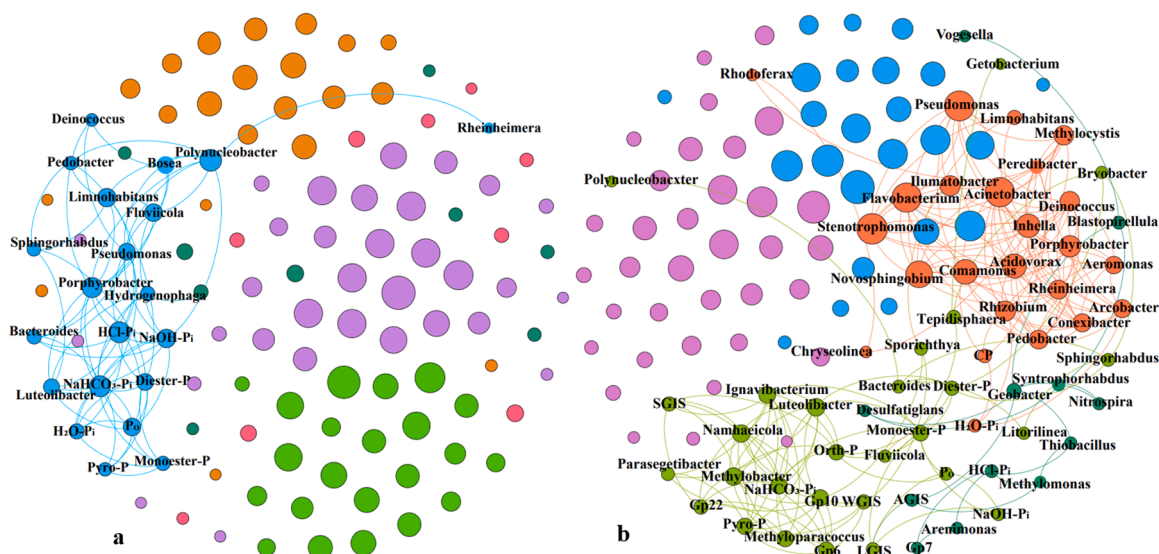

Fig. 4. Co-occurrence network drew by R software showing the correlation among bacterial genus level and P pools and P compounds from SPM and sediment as nodes colored by modularity class. Note: panel a represents water column, panel b represents sediment. Blank nodes or modules suggest that these microorganisms were irrelevant with P pools/compounds of SPM and sediment in co-occurrence network, so these bacterial communities were deleted. Note: Ortho-P, orthophosphate; Pyro-P, pyrophosphate; Monoester-P, orthophosphate monoesters; Diester-P, orthophosphate diesters.
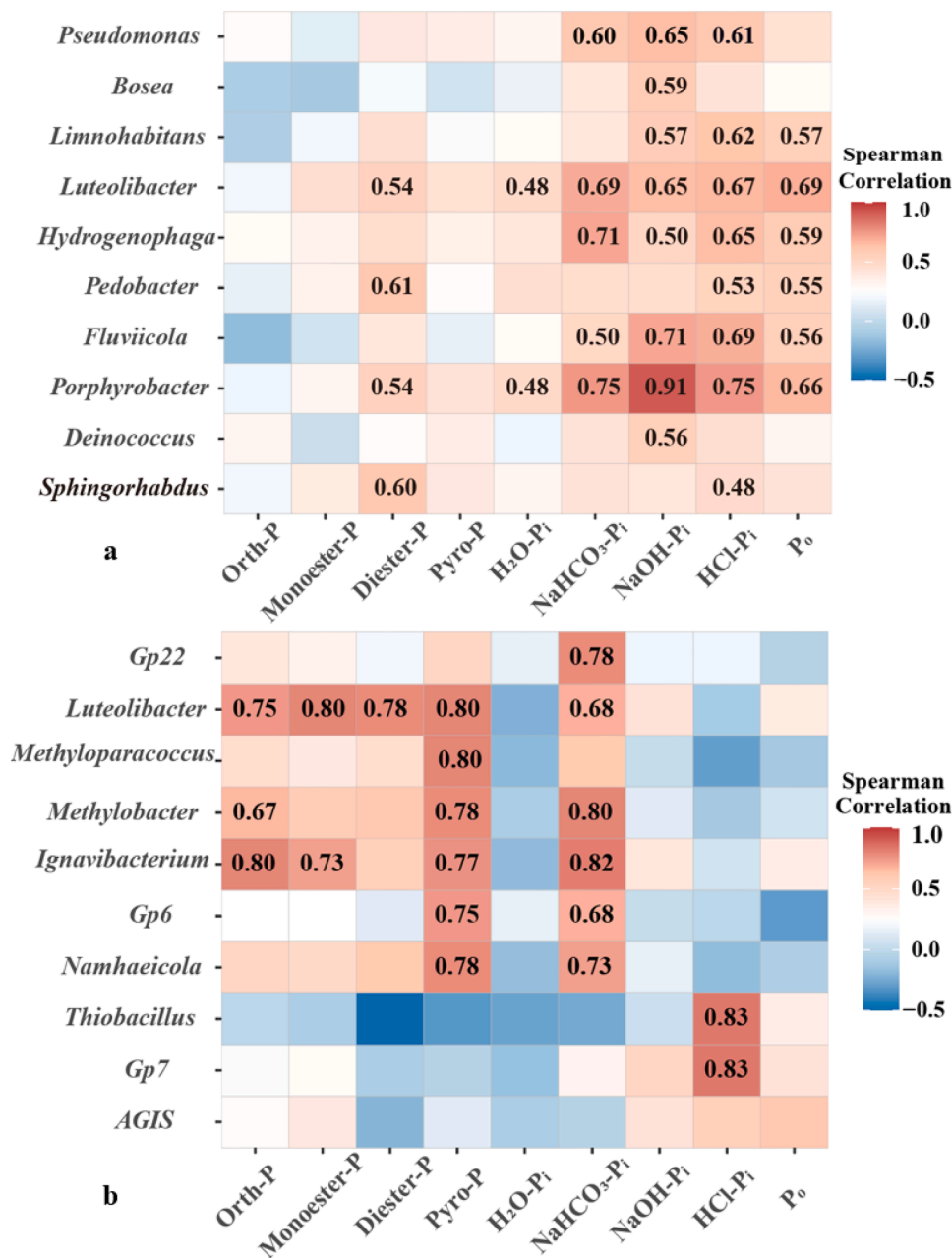
Fig. 5. Heatmap of Spearman's rank correlations coefficients among the P pools and P compounds of SPM and sediment drew by R software. Note: panels a and b represent the relative abundance of microbial communities at the genus level associated with the P cycle in water column and sediment, respectively. The correlation coefficients are indicated by hue ($P < 0.05$). Ortho-P, orthophosphate; Pyro-P, pyrophosphate; Monoester-P, orthophosphate monoesters; Diester-P, orthophosphate diesters. AGIS, Aminicenantes_genera_incertae_sedis.

capability of sulfate reduction or sulfide oxidization could affect the Fe speciation by mediating the S speciation (Baldwin et al., 2000; Arning et al., 2009; Yu et al., 2015; Chen et al., 2016; Fan et al., 2018; Berg et al., 2019; Li et al., 2022). Therefore, the relative abundance of FeRB, FeOB, SRB, and SOB was further analysis. Results demonstrated that the relative abundance of FeRB (mean 16.27%) and SRB (mean 5.88%) in the water column and FeRB (mean 2.04%) and SRB (1.59%) in sediment were obviously higher than their corresponding relative abundance of FeOB (mean 1.1%) and SOB (mean 0.4%) in the water column and FeOB (0.8%) and SOB (0.9%) in sediment (Fig. S13), respectively, suggesting that FeRB and SRB contributed greatly to P remobilization from SPM during sedimentation. Alternatively, the pathway of P released from SPM driven by abiotic reaction (such as T, pH, DO; Fig. S14) might be nonnegligible (Pan et al., 2013). Further work is required to quantify the relative contribution of above-listed factors for P release from SPM.

4. Conclusions

The integrated information from complementary technologies enabled us to summarize that P released from SPM during or after sedimentation provided a major P source for algal blooms under dissolved P-depleted water column. P compounds from algae, SPM, and sediment were identified, including ortho-P, monoester-P, diester-P, and pyro-P. Relative lower diester-P/monoester-P ratios of SPM in surface water in January and July than those of in April reflected the higher degree of diester-P remineralization in the water column during these periods. The H_2O-P_i and P_o (monoester-P and diester-P) from SPM were the primarily bioavailable P pools for algae. The strategies of P uptake and utilization of algae were further identified in the field investigation. Dissolved P_i in the water column could be stored in algae in the form of ortho-P and pyro-P in January. Algae heavily relied on its stored P_i for growth and reproduction in April. SPM P_o remineralization provided the primary P source for algal blooms in July. Algae and bacteria (e.g.,

Pseudomonas) were responsible for SPM P remineralization and/or remobilization. Overall, our findings provide new insights into the understanding of algal blooms with dissolved P-depleted water bodies, which are valuable for understanding P cycling processes and formulating effective nutrient management guidelines.

CRediT authorship contribution statement

Zuxue Jin: Methodology, Investigation, Formal analysis, Data curation, Writing – original draft, Visualization. **Peng Liao:** Conceptualization, Writing – review & editing. **Deb P Jaisi:** Methodology, Writing – review & editing. **Dengjun Wang:** Writing – review & editing. **Jingfu Wang:** Methodology, Conceptualization, Writing – review & editing, Project administration. **Heng Wang:** Formal analysis, Writing – review & editing. **Shihao Jiang:** Investigation, Formal analysis. **Jiaojiao Yang:** Investigation, Formal analysis. **Shuoru Qiu:** Formal analysis. **Jingan Chen:** Methodology, Writing – review & editing, Validation, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgments

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.watres.2023.120134.

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