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Different characteristics of sediment nitrogen and phosphorus recycling during cyanobacterial growth and their succession

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Abstract

Purpose Sediment internal nutrient loading plays an important role in algal blooms. Thus, understanding the specific characteristics of nutrient (nitrogen (N) and phosphorus (P)) recycling from sediment is important for clarifying the processes and mechanisms of cyanobacterial growth and succession.

Materials and methods Sediments and water samples were collected monthly from five sampling sites in Lake Chaohu for 1 year. N and P concentrations in surface and interstitial water were determined, and fractions of sediment organic matter, P, and iron were quantified. P adsorption characteristics were modeled with adsorption isotherms.

Results and discussion *Dolichospermum* was the dominant bloom species in the western lake in April, followed by *Microcystis* from May to September in the whole lake. The impulsive regeneration and release mode from iron-bound P and ammonium (NH_4^+-N) regeneration from sediment in spring triggered the *Dolichospermum* bloom. In early summer, continuous P release potential as well as nitrate accumulation and NH_4^+-N deficiency due to NH_4^+-N prior assimilation by *Dolichospermum* jointly drove the transition from *Dolichospermum* to *Microcystis* due to the energy saving and competitive advantage of rapid uptake and storage of inorganic P as well as a wide range of N utilization forms for *Microcystis*. All these facts put the *Dolichospermum* towards common N and P stress. Furthermore, in summer, NH_4^+-N rapid regeneration from organic algal detritus remineralization due to the decline of *Dolichospermum* developed *Microcystis* blooms.

Conclusions The specific mode and pathway of N and P recycling from sediment determined the dominant algal species based on the particular N and P utilization strategies of the algae. Pulsed and a vast amount of P release facilitated the *Dolichospermum* growth, while continuous and a small quantity of P release was in favor of *Microcystis* growth. Organic N hydrolysis from *Dolichospermum* detritus further supported the development of a *Microcystis* bloom.

Keywords Sediment · Nutrient recycling · Phosphorus · Nitrogen · Cyanobacterial bloom

1 Introduction

Cyanobacterial blooms in eutrophic lakes are severe environmental problems worldwide and of global concern due to the multiple harmful risks they pose towards aquatic ecosystem and human health (Jiang et al. 2017; Jia et al. 2019). Sediment internal loading plays an important role in the eutrophication of Lake Chaohu (Yang et al. 2020) and represents a significant supply for the growth of cyanobacteria (Cao et al. 2016). Phosphorus (P) migration and transformation caused by the microbes in sediments during cyanobacterial resuscitation phase may lead to the release of phosphorus from sediments and accelerate algae growth (Tu et al. 2022). In eutrophic Lake Dianchi, up to 70.2% of the released P could be absorbed by cyanobacteria (Cao et al. 2016). In Lake Taihu, cyanobacteria relied extensively

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on regenerated ammonium (NH_4^+-N) to sustain the bloom (Hampel et al. 2018). NH_4^+-N recycling supported toxic *Planktothrix* blooms in Sandusky Bay, Lake Erie (Hampel et al. 2019). Hence, algal bloom was mainly controlled by nitrogen (N) and P fluxes from sediment.

Nitrogen and P diffusive fluxes at the sediment–water interface in Erhai Lake showed different temporal and spatial variations (Zhao et al. 2018). The content of total P and N and their forms in water and sediment were rather dynamic during the year-long field investigation in the most polluted area of a shallow eutrophic lake (Lake Chaohu, China), the phosphate and NH_4^+-N fluxes showed evident seasonal variation, and higher fluxes were observed in warmer seasons especially during the period of algal bloom with high sedimentation (Yang et al. 2020). Meanwhile, the forms and content of P and N in water influenced the dominance of cyanobacteria (Ma et al. 2015). Green algal dominance quickly switched to cyanobacterial dominance after N and P enrichment in a greenhouse with elevated temperature (Wang et al. 2015). The response to nutrient enrichment differs among cyanobacterial species, which showed differential growth in relation to N and P concentrations (Loza et al. 2014).

Cyanobacterial dominance and composition of cyanobacterial blooms depended on the total N and total P levels as well as N to P ratios (Gonzlez-Madina et al. 2019). In Missisquoi Bay, Lake Champlain, *Dolichospermum* was the major bloom-forming cyanobacterium during summer, followed by a second intense bloom event of *Microcystis* in the fall; and the variation in the cyanobacterial population was strongly associated with inorganic and readily available fractions of N and P such as nitrites (NO_2^--N) and nitrates (NO_3^--N), NH_4^+-N, and dissolved organic P (Celikkol et al. 2021). The growth of *Microcystis* was influenced by the synergistic uptake and assimilation of nitrogen and phosphorus (Cai and Tang 2021). Furthermore, high concentrations of dissolved inorganic N and dissolved reactive P in Lake Taihu sediments potentially stimulated the initiation and maintenance of cyanobacterial blooms (Fan et al. 2022). The shallow, polymictic Ornamental Lake in Australia had suffered significant blooms of toxic *Anabaena* then *Microcystis* species every summer over the last decade; the prolific algal growth was controlled by the springtime P fluxes from the sediment, which was caused by diel stratification, combined with high oxygen consumption associated with organic carbon loading (Grace et al. 2010). Therefore, the temporal and spatial variation of P and N fluxes from sediment stimulated the initiation and transition of cyanobacterial blooms, which may be attributed to the different characteristics of sediment N and P recycling.

To explore the different characteristics of sediment N and P recycling during different dominated blooms and to test our hypothesis that the specific mode and pathway of sediment N and P recycling determines the pattern of algal succession, samples (including surface water and sediment) from five sampling sites in Lake Chaohu were collected monthly from January to December 2011 and were analyzed for chlorophyll *a* (Chl. *a*) in surface water, N and P species in surface water and interstitial water, labile organic matter, fractionation and sorption behaviors of phosphorus, extracellular enzymatic activities (EEA), and iron (Fe) in sediment. Through this study, we hope to (1) clarify the different modes and pathways of sediment N and P recycling and (2) illuminate the process that the different characteristics of sediment N and P recycling stimulated the initiation and transition of cyanobacterial blooms.

2 Materials and methods

2.1 Study sites and sample collection

Lake Chaohu, which is located in the middle of Anhui Province, China, is the fifth-largest shallow freshwater lake in China. The lake is commonly divided into three parts: western lake, central lake, and eastern lake. The western lake is evaluated as hypereutrophic status while the central and eastern lake stays in mesotrophic status (Shang and Shang 2007; Yu et al. 2011, 2014). In Lake Chaohu, cyanobacterial biomass showed high spatial–temporal changes, tending to increase in February and reaching a peak in April at some sites due to the growth of *Dolichospermum*; the second peak arrived in July and September and was caused by the rapid growth of *Microcystis* (Ren et al. 2021). Five sampling sites were established, and they were named with the initial letters of the rivers entering Lake Chaohu (to avoid confusion, sampling site X was named with the initial letter of another inflowing river, River Xiage). Sites X and T belong to eastern lake, site Z belongs to central lake, and sites S and N belong to western lake.

Surface water samples were taken by an organic glass hydrophore to analyze the N, P, and Chl. *a* concentration. Surface sediments samples were taken using a Peterson grab sampler to analyze P fractionation and sorption behavior, EEA, labile organic matter, and Fe. The interstitial water was separated from the sediment particles by centrifugation at 3000 r/min for 20 min. The supernatants were then filtered through a 0.45-μm membrane filter for analysis of N and P concentration. All samples were analyzed immediately after being back to the laboratory.

2.2 Nutrient forms in water samples

Chl. *a* was measured using the ethanol extraction method (Golterman et al. 1978). Soluble reactive phosphorus (SRP) concentration was detected by the molybdate blue method (Murphy and Riley 1962). Total P (TP) and dissolved total

P (DTP) were determined following digestion by $K_2S_2O_8$ according to GB11893-89 issued by State Environmental Protection Administration of China. Dissolved organic P (DOP) was calculated as DTP-SRP, and particulate P (PP) was calculated as TP-DTP. NH_4^+-N was determined by the indophenol-blue method described by Solórzano (1969) and Aminot et al. (1997), NO_3^--N was determined by a UV-spectrophotometry determination method, and NO_2^--N was determined by the α-naphthylamine method (Xu et al. 2005).

2.3 Nutrient forms in sediments

Sediment P fractionation was carried out according to Golterman (1996). This method groups sediment P into iron-bound P (Fe(OOH) ~ P), calcium-bound P ($CaCO_3$ ~ P), acid-soluble organic P (ASOP), and hot NaOH-extractable organic P (P_{alk}).

Ferrous iron (Fe^{2+}) and total iron (TFe) were extracted from sediment by HCl and were determined according to the 1, 10 phenanthroline spectrometric method (Hauck et al. 2001). Before TFe was measured, all iron was reduced to the ferrous state with hydroxylamine hydrochloride (Stookey 1970). Ferric iron (Fe^{3+}) was calculated as TFe-Fe^{2+}.

Protein (PRT) analysis was conducted following extraction with NaOH (0.5 mol/L, 4 h) and was determined according to Hartree (1972) and modified by Rice (1982) to compensate for phenol interference and expressed as bovine serum albumin equivalents. Carbohydrates (CHO) were analyzed according to Gerchakov and Hatcher (1972) and expressed as glucose equivalents. Lipids were extracted by direct elution with chloroform–methanol according to Bligh and Dyer (1959) and Marsh and Weinstein (1966).

2.4 Phosphorus sorption in sediments

Phosphorus sorption characteristics of sediments were studied by batch incubation experiments (Li et al. 2014). Batch P sorption isotherm experiments were conducted in triplicate for sediment homogenates under reducing condition, using 0.01 mol L^{-1} KCl solution containing 0, 0.1, 0.2, 1, 2, 5, 8, 10, 15, 20, 25, 30, 40, and 50 mg P L^{-1} KH_2PO_4 as sorption solution matrices. The sealed centrifuge tubes with the mixed solution were shaken on a reciprocal shaker at a speed of 200 cycles min^{-1} for 24 h at 25 ± 3 °C. The suspension was centrifuged at 3500 rpm for 20 min. The supernatants were filtered through a 0.22-μm mixed cellulose ester membrane and determined for SRP. Phosphorus sorption parameters of sediments were simulated by the Langmuir and Freundlich isothermal model:

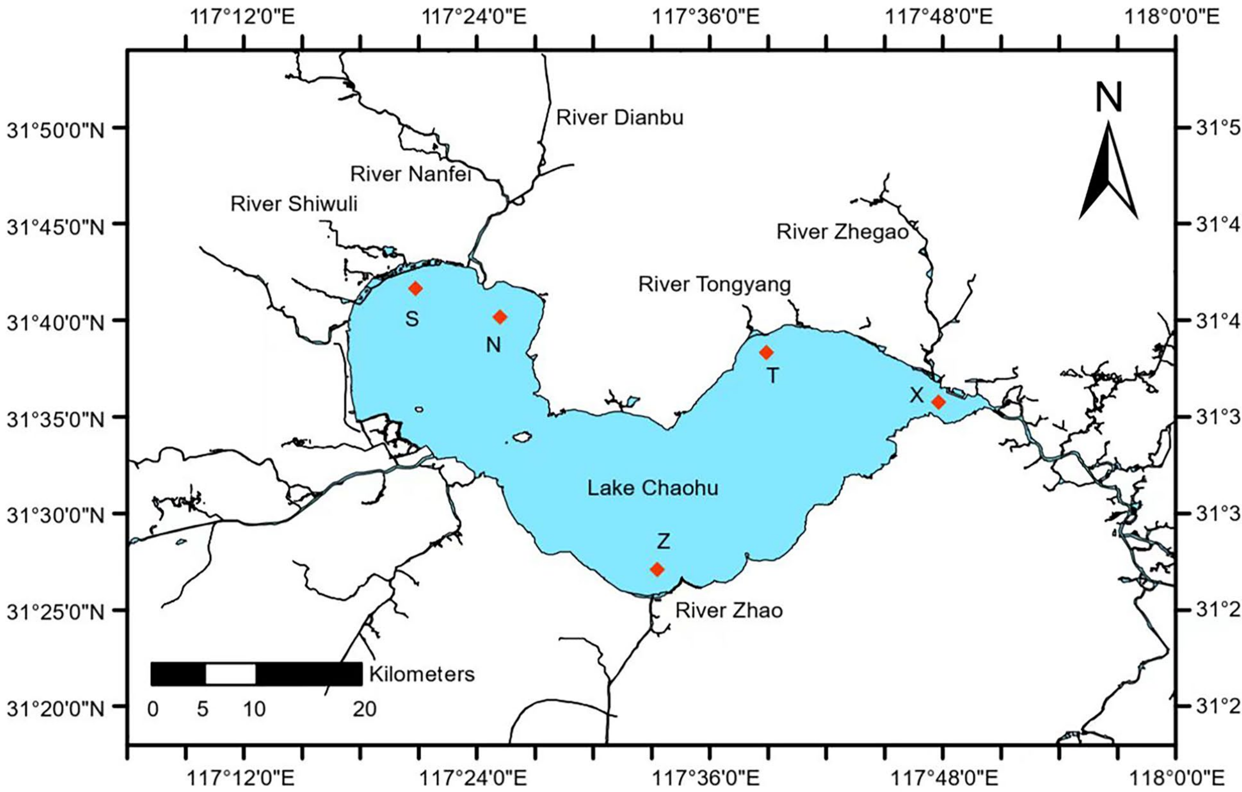

Fig. 1 Map of the study lakes showing the sampling sites

Langmuir equation: $Q = Q_{max}K_LC/(1 + K_LC) - Q_{0L}$
Freundlich equation: $Q = K_FC^n - Q_{0F}$
Q: amount of P sorbed by the solid phase after 24-h equilibrium ($mg\ kg^{-1}$)
C: P concentration in solution after 24 h equilibrium ($mg\ L^{-1}$)
Q_{max}: the maximum P sorption ($mg\ kg^{-1}$)
K_L: Langmuir adsorption energy parameter ($L\ mg^{-1}$)
K_F: Freundlich adsorption energy parameter ($mg\ kg^{-1}$)
Q_{0F} and Q_{0L}: amount of P sorbed by the solid phase before the P sorption experiments ($mg\ kg^{-1}$)
n: content ($L\ kg^{-1}$)

Equilibrium P concentration (EPC_0) was measured by the Freundlich equation, where no P sorption or desorption occurs. The P sorption maximum (Q_{max}) was measured by the Langmuir equation.

2.5 Extracellular enzymatic activity in sediments

Heterotrophic microorganisms in sediments produce extracellular enzymes to hydrolyze organic macromolecules, so their products can be transported inside the cell and used for energy and growth (Schmidt et al. 2021). Extracellular enzymatic activity is typically measured by addition of a fluorescently labeled substrate to an environmental sample, and hydrolysis is detected either as an increase in fluorescence as a fluorophore is cleaved (Hoppe 1983) or as a change in molecular weight distribution as a fluorescent substrate is hydrolyzed into lower molecular weight products (Arnosti 1996, 2003). Leucine aminopeptidase activity (LAP) and β-D-glucosidase activity (GLU) were measured fluorometrically according to Boetius and Lochte (1994), using the methylumbelliferone (MUF)–labeled substrates MCA-leu

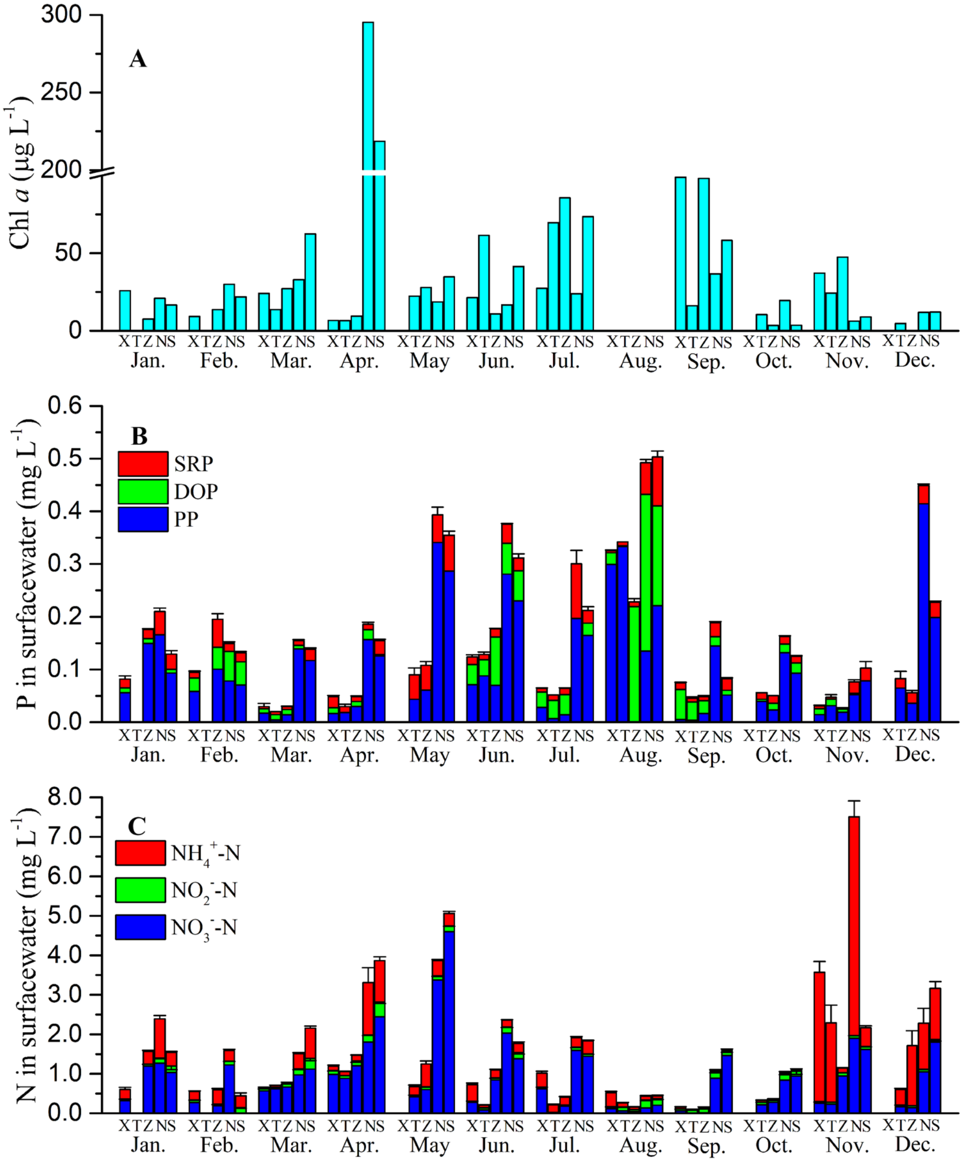

Fig. 2 The comparison of chlorophyll a (Chl. a), nitrogen (N), and phosphorus (P) species in surface water at different sampling sites from January to December. SRP soluble reactive phosphorus, DOP dissolved organic phosphorus, PP particulate phosphorus, NH_4^+-N ammonium, NO_2^--N nitrite, NO_3^--N nitrate

(L-leucine-4-methylcoumarinyl-7-amid HCl) and MUF-glu (MUG-Beta-D-glucopyranoside), respectively. Alkaline phosphatase (AP) was analyzed spectrophotometrically as p-nitrophenol (p-NP) resulting from the cleavage of phosphate from p-nitrophenylphosphate (p-NPP) (Sayler et al. 1979). Dehydrogenase activity (DHA) was determined by UV spectrophotometry according to Neto et al. (2007), with triphenyltetrazolium chloride as substrates.

2.6 Statistical analysis

All samples were analyzed in triplicate and the data are expressed as the average. Independent-sample *T* test was performed using the SPSS 18.0 package (SPSS, Chicago, IL), with a value of 0.05 or 0.01 selected for significance Fig. 1.

3 Results and discussion

3.1 Phosphorus recycling patterns

The significantly higher Chl. *a* concentration in western lake (sites N and S) in April ($P < 0.01$, Fig. 2a) and in the whole lake from May to September (Fig. 2a) indicated that severe algal bloom occurred in western lake in April and in whole lake from May to September. *Dolichospermum* was the dominant bloom species in western lake in April, followed by *Microcystis* from May to September in the whole lake. However, in April, the SRP concentration of surface water in western lake did not obviously decrease as algal blooms occurred and P was absorbed by *Dolichospermum* (Fig. 2b), indicating continuous P replenishment from sediment evidenced by significantly higher Fe(OOH) ~ P in sediments of western lake (sites N and S) ($P < 0.01$, Fig. 4a). Moreover, in April, the decrease of Fe^{3+} and the increase of Fe^{2+} as well as the increase of SRP in interstitial water in western lake (sites N and S) supported the above conclusion of the desorption of Fe(OOH) ~ P and P release from sediment to the interstitial water (Figs. 3a and 4c); that is to say, ferric iron was reduced to ferrous iron, finally leading to the release into interstitial water of inorganic P as SRP from Fe(OOH) ~ P. The re-dissolution of solid Fe(OOH) ~ P pools is the most important source of labile P and aggravates the P budget in lake water via anaerobic intervals (Yuan et al. 2019). Hence, desorption of Fe(OOH) ~ P was mainly responsible for P recycling in western lake. In April, the AP

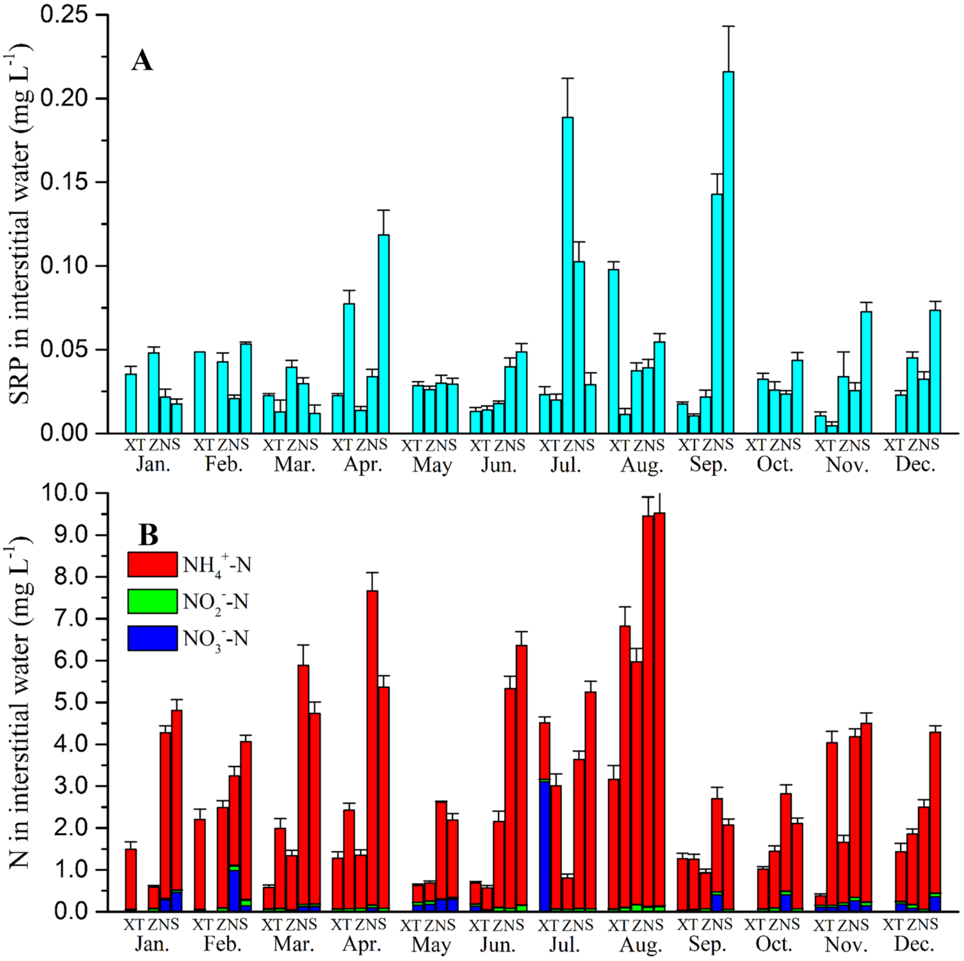

Fig. 3 The comparison of nitrogen (N) and phosphorus (P) species in interstitial water at different sampling sites from January to December. SRP soluble reactive phosphorus, NH_4^+-N ammonium, NO_2^--N nitrite, NO_3^--N nitrate

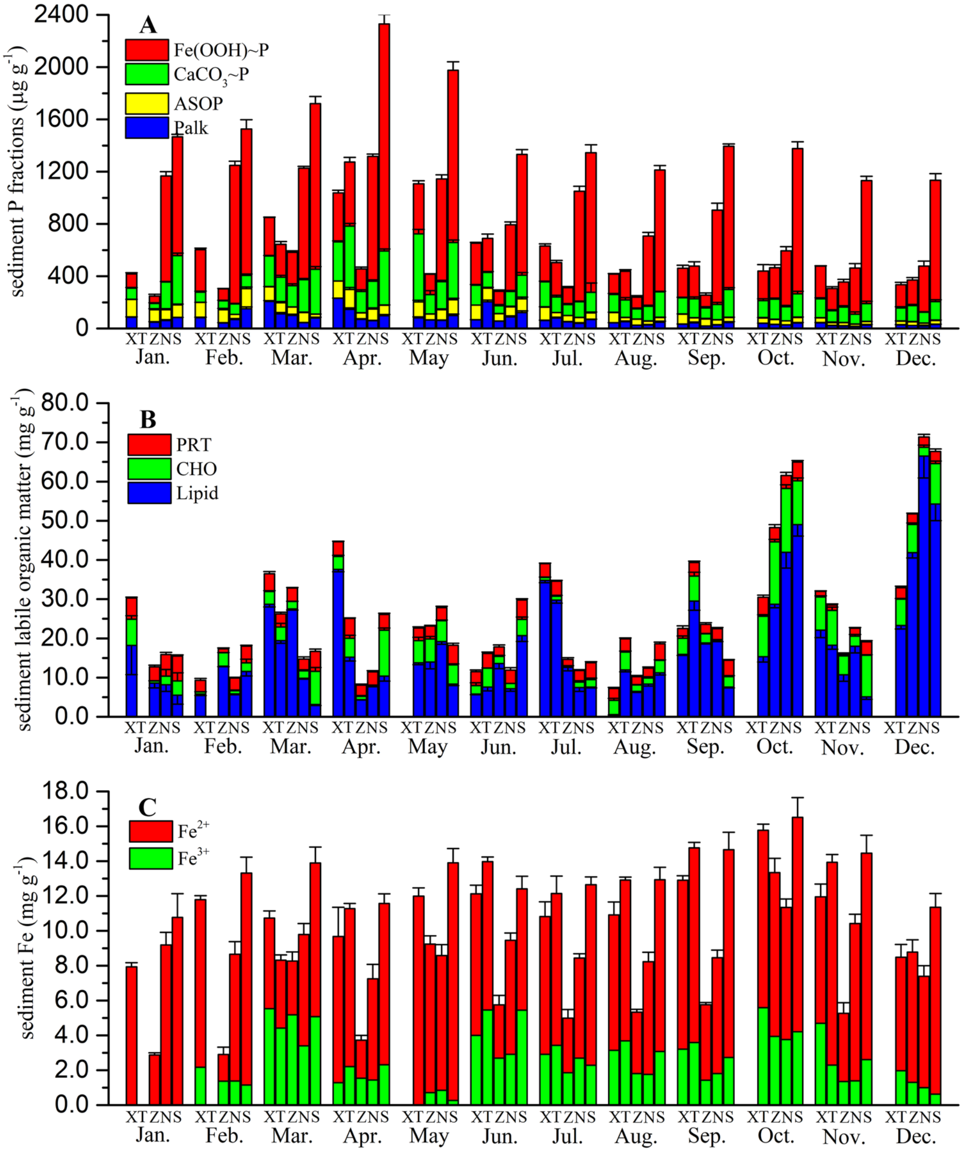

Fig. 4 The comparison of different P forms, iron (Fe), and labile organic matter in sediment at different sampling sites from January to December. Fe(OOH) ~ P iron-bound P, CaCO$_3$ ~ P calcium-bound P, ASOP acid-soluble organic P, P$_{alk}$ hot NaOH-extractable organic P, PRT protein, CHO carbohydrates

activity showed the higher levels than the other months in western lake (sites N and S) (Fig. 5a), suggesting that the hydrolysis of organic P may be another P source for the growth of *Dolichospermum*. The *Dolichospermum* culture experiments in different eutrophication scenarios showed that the expression of genes involved in P uptake, e.g., those involved in P-transport and the hydrolysis of phosphomonoesters, was upregulated in P-deficient cultures (Wang et al. 2018). AP was regulated by P availability in monocultures of *Dolichospermum*, but no cell bound extracellular phosphatase was found on *Microcystis* even in the culture without P supply (Wan et al. 2019). Therefore, the P sources required by *Dolichospermum* in western lake mainly derived from the impulsive release of Fe(OOH) ~ P and the hydrolysis of organic P, of which the former is more important.

Hydrolysis of polymers through extracellular enzymes is the first and acknowledged rate-limiting step in the decomposition of organic matter in aquatic environments (Cunningham and Wetzel 1989; Chróst 1992). GLU, LAP, and AP are extracellular enzymes hydrolyzing carbohydrates, organic N, and organic P and mediating C, N, and P cycling, respectively. In western lake, after the decline of *Dolichospermum*, with the increase of algae detritus, the sediment labile organic matter (PRT, CHO, and lipid) did not obviously increase from May to September (Fig. 4b), and extracellular enzymatic activities maintained a constantly high level during this period (Fig. 5a–c), indicating that the quick organic matter decomposition led to the rapid consumption of labile organic matter. The decomposition of organic carbon is always accompanied by a shift of redox status expressed by DHA (potential of oxidation and dehydrogenation of organic compounds) (Simčič 2005), which measures microbial metabolic activity as respiratory electron transport and has proved to be a good tool for estimating the respiratory potential of

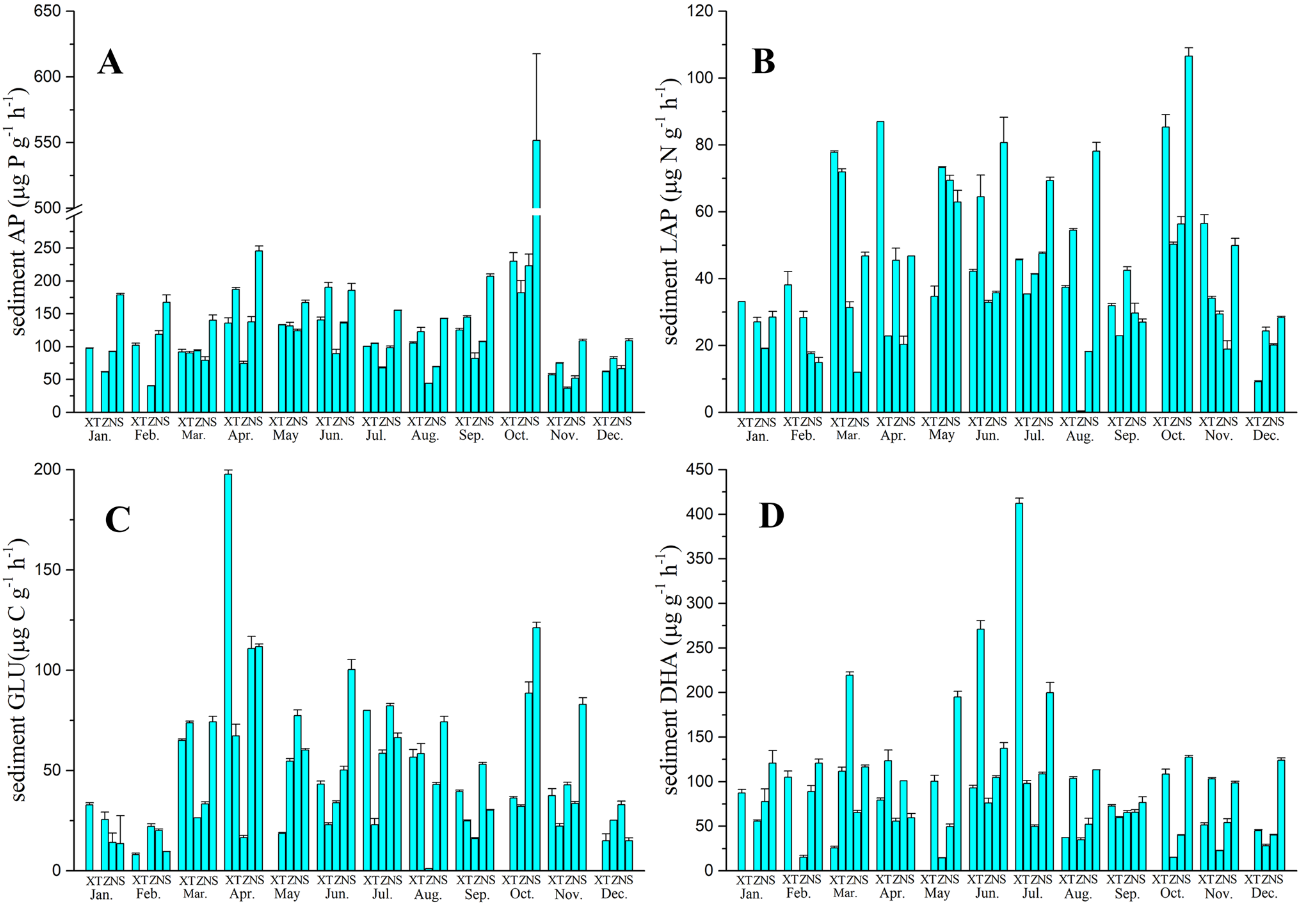

Fig. 5 The comparison of enzymatic activities in sediment at different sampling sites from January to December. AP alkaline phosphatase, LAP leucine aminopeptidase, GLU β-D-glucoside, DHA dehydrogenase activity

sediment (Broberg 1984; Blenkinsopp and Lock 1990). High respiratory potential (DHA) can trigger the change of redox potential and the formation of anaerobic status (Li et al. 2016). In this process, the bottom anaerobic status was formed expressed as high DHA (Fig. 5d); SRP was continually regenerated through the desorption of Fe(OOH) ~ P and released into the surface water based on the data of the continuous decrease of Fe(OOH) ~ P and Fe^{3+}, the increase of Fe^{2+}, and a constantly higher SRP concentration in surface water from May to August (Figs. 2b and 4a, c). The AP activity did not obviously increase from May to September (Fig. 5a), suggesting that extracellular alkaline phosphatase did not play a key role in P release during *Microcystis* bloom. At the same time, EPC_0 could be used to estimate the function for sediment to act as sink or source of P and has been proved as a key index to indicate the P release potential and flux rate from sediments to water (Dong et al. 2011; Fu et al. 2022). In this study, compared to central and eastern lake (sites X, T, and Z), EPC_0 in sediments of western lake maintained a higher level from April to August ($P < 0.01$, Fig. 6a), and the Q_{max} was similar (Fig. 6b), indicating that the decline of *Dolichospermum* and decomposition of labile organic matter lead to significantly higher P release potential to water column in western lake. The released P was quickly utilized by *Microcystis*, in terms of continuous higher SRP and PP in surface water in western lake from May to August (Fig. 2b). Therefore, impulsive regeneration and release from Fe(OOH) ~ P triggered the *Dolichospermum* bloom, and then, continuous and rapid P release potential drove the transition from *Dolichospermum* to *Microcystis* due to the energy saving and competitive advantage for *Microcystis* to rapidly uptake and store inorganic P, which put the coexisting *Dolichospermum* into P stress.

3.2 Nitrogen recycling patterns

As mentioned above, in April, the Chl. *a* concentration in western lake (sites N and S) was significantly higher than that of central and eastern lake (sites X, T, and Z) ($P < 0.01$, Fig. 2a). Nevertheless, the NH_4^+-N and NO_3^--N in surface water, as well as NH_4^+-N in interstitial water, did not decrease but increase in this period (Figs. 2c and 3b). On the one hand, in March and April, higher LAP activity in western lake (sites N and S) (Fig. 5b) fueled the NH_4^+-N production in interstitial water by ammonification. Subsequently, NH_4^+-N was released into water column and simultaneously transformed partially into NO_3^--N in surface water due to nitrification. On the other hand, *Dolichospermum* was the dominant bloom species in western lake in April. Previous research showed that growth rates of *Dolichospermum* was significantly higher when grown on NH_4^+-N relative to NO_3^--N, and the existence of NH_4^+-N and urea significantly lowered N_2 fixation of *Dolichospermum* (Kramer et al. 2022). Thus, *Dolichospermum* growth gave priority to NH_4^+-N, which inevitably led to the decrease of NH_4^+-N and the accumulation of NO_3^--N, in terms of the lower NH_4^+-N and higher NO_3^--N in surface water in May (Fig. 2c). Besides, the decline of *Dolichospermum* produced abundance of organic N, which might provide enough N source for the breakout of *Microcystis* bloom.

Organic N produced by *Dolichospermum* bloom was rapidly mineralized into NH_4^+-N with *Dolichospermum* collapse from spring to summer based on the data of continuous lower PRT content and higher LAP activity from May to September (Figs. 4b and 5b). As mentioned above, organic carbon, N, and P decomposition increased from May to September in terms of low sediment labile organic matter (PRT, CHO, and lipid) content (Fig. 4b) and a constantly high AP, LAP, and GLU in this time (Fig. 5a–c). And NH_4^+-N was partially released into water column and simultaneously transformed into NO_3^--N by nitrification in surface water (Li et al. 2021), in terms of the higher NH_4^+-N in interstitial water and higher NO_3^--N in surface water before May (Figs. 2c and 3b). But from June to October, both NH_4^+-N and NO_3^--N in surface water were very low (Fig. 2c), which may be due to rapid assimilation by *Microcystis*. *Microcystis* can utilize different forms of inorganic and organic N, with the greatest capacity for NH_4^+-N uptake and the least for glutamic acid uptake (Lee et al. 2015). High concentration of NO_3^--N facilitated the dominance of *Microcystis*, and *Microcystis* displayed faster growth rates in NH_4^+-N than in NO_3^--N (Tan et al. 2019). Moreover, in the presence of SRP enrichment, the maximal uptake velocity of NH_4^+-N by *Microcystis* substantially increased without evidence of saturation (Yang et al. 2017). Additionally, in this study, anaerobic condition limited the nitrification, resulting in the NH_4^+-N accumulation in interstitial water in summer (Fig. 3b), which could provide a continuous N source for *Microcystis* blooms. Thus, we may conclude that in spring, NO_3^--N accumulation due to NH_4^+-N prior assimilation of *Dolichospermum* initiated the transition from *Dolichospermum* to *Microcystis*, and in summer, NH_4^+-N rapid regeneration from organic algal detritus remineralization due to the decline of *Dolichospermum* developed *Microcystis* blooms.

Finally, the decline of *Microcystis* blooms led to accumulation of sediment labile organic matter (PRT, CHO, and

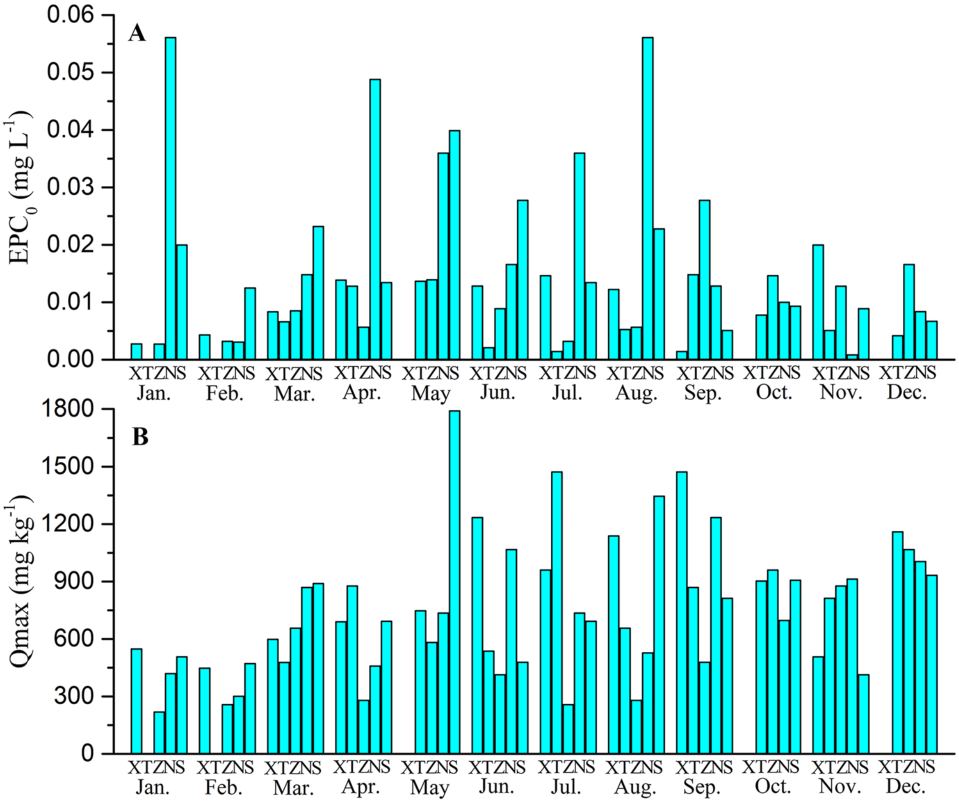

Fig. 6 The comparison of phosphorus sorption parameter of sediment at different sampling sites from January to December. EPC_0 equilibrium phosphorus concentration, Q_{max} phosphorus sorption maximum

lipid), and extracellular enzyme activity decreased due to low temperature based on the data of remarkable increasing PRT, CHO, and lipid content from October to December and decreasing AP, LAP, and GLU in November and December (Figs. 4b and 5a–c), which suggested that labile organic matter was stored in sediment at the end of algal bloom and can provide abundant N and P for algal bloom the next year.

4 Conclusions

Dolichospermum was the dominant bloom species in western lake in April, followed by *Microcystis* from May to September in the whole lake. The impulsive regeneration and release mode from Fe(OOH) ~ P and NH_4^+-N regeneration from the sediment in spring triggered the *Dolichospermum* bloom. In early summer, the continuous and rapid P release potential as well as NO_3^--N accumulation and NH_4^+-N deficiency due to NH_4^+-N prior assimilation by *Dolichospermum* jointly drove the switch from *Dolichospermum* to *Microcystis* due to the energy saving and competitive advantage of rapidly uptake and store inorganic P as well as a wide range of N utilization forms for *Microcystis*. All these facts put the *Dolichospermum* towards N and P common stress. Furthermore, in summer, NH_4^+-N rapid regeneration from organic algal detritus remineralization due to the decline of *Dolichospermum* developed *Microcystis* blooms. Hence, the mode and pathway of P regeneration and release from sediment determined algal bloom species based on algal own special P utilization strategies. In detail, pulsed and a vast amount of P release facilitated the *Dolichospermum* growth, while continuous and a small quantity of P release was in favor of *Microcystis* growth. Organic N hydrolysis from *Dolichospermum* detritus further supported the development of *Microcystis* bloom.

Author contribution The study conception and design were performed by Hui Li, Chunlei Song, Yiyong Zhou, and Xiuyun Cao. Material preparation and data collection were performed by Hui Li and Daizhong Huang, and data analysis was performed by Hui Li, Wenjuan Shen, Yun He, and Jianfen Li. The first draft of the manuscript was written by Hui Li and revised by Chunlei Song. All authors read and approved the final manuscript.

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Data availability The data that support the findings of this study are openly available in https://pan.baidu.com/s/16IluhwQgalYtn4p--kqF8g.

Declarations

Competing interests The authors declare no competing interests.

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