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Biological mechanisms driving the seasonal changes in the internal loading of phosphorus in shallow lakes

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Abstract Because of the obvious importance of P as a nutrient that often accelerates growth of phytoplankton (including toxic cyanobacteria) and therefore worsens water quality, much interest has been devoted to P exchange across the sediment-water interface. Generally, the release mode of P from the sediment differed greatly between shallow and deep lakes, and much of the effort has been focused on iron and oxygen, and also on the relevant environmental factors, for example, turbulence and decomposition, but a large part of the P variation in shallow lakes remains unexplained. This paper reviews experimental and field studies on the mechanisms of P release from the sediment in the shallow temperate (in Europe) and subtropical (in the middle and lower reaches of the Yangtze River in China) lakes, and it is suggested that pH rather than DO might be more important in driving the seasonal dynamics of internal P loading in these shallow lakes, i.e., intense photosynthesis of phytoplankton increases pH of the lake water and thus may increase pH of the surface sediment, leading to enhanced release of P (especially iron-bound P) from the sediment. Based on the selective pump of P (but not N) from the sediment by algal blooms, it is concluded that photosynthesis which is closely related to eutrophication level is the driving force for the seasonal variation of internal P loading in shallow lakes. This is a new finding. Additionally, the selective pump of P from the sediment by algal blooms not only explains satisfactorily why both TP and PO_4-P in the hypereutrophic Lake Donghu declined significantly since the mid-1980s when heavy cyanobacterial blooms were eliminated by the nontraditional biomanipulation (massive stocking of the filter-feeding silver and bighead carps), but also explains why TP in European lakes decreased remarkably in the spring clear-water phase with less phytoplankton during the seasonal succession of aquatic communities or when phytoplankton biomass was decreased by traditional biomanipulation. Compared with deep lakes, wax and wane of phytoplankton due to alternations in the ecosystem structure is also able to exert significant influences on the P exchange at the sediment-water interface in shallow lakes. In other words, biological activities are also able to drive P release from sediments, and such a static P release process is especially more prominent in eutrophic shallow lakes with dense phytoplankton.

Keywords: shallow lakes, internal P loading, algal blooms.

In the 20th century, limnological research of the world has traditionally been focused mostly on deep lakes. There are remarkable differences in many aspects between deep and shallow lakes: e.g., in deep lakes, stratification in summer prevents greatly the interactions between epilimnion and the colder hypolimnion and bottom sediments, and macrophytes are less important to the ecosystem because their distributions are limited to the margin of the lake. However, in shallow lakes, there are strong interactions between sediment and water, and macrophytes are important to the ecosystem[1].

P has probably received more attention than any other nutrient in limnology. The exchange of P between sediments and the overlying water is a major component of the P cycle in natural waters, and is regulated by an array of physical, chemical, and biological factors. Because of the obvious importance of P as a nutrient that often accelerates algal growth or even causes outburst of toxic cyanobacterial blooms, much interest has been devoted to P content of sediments and its movement into the overlying water[2].

The seasonal dynamics of P in shallow lakes differ profoundly from the typical pattern observed in deep stratified lakes. In deep lakes there is a continuous loss of P from epilimion to hypolimnion during the summer, and the mineralized P in the hypolimnion can only return to the epilimnion after the autumn turnover. However, in the pelagic region of shallow lakes, the intense sediment-water contact ensures a rapid return of most sedimentated material into the water column, and additionally, the relatively high sediment temperatures in summer increase mineralization rates, consequently leading to an increased release of nutrients from the sediment[1, 3].

Generally, the release mode of P from sediment differs greatly between shallow and deep lakes. Originally, it was believed that the stratified lakes with an anoxic hypolimnion in summer would suffer from internal P loading due to the redox-dependent release of iron-bound P[4,5], but that the shallow lakes with well-oxidized conditions throughout the water column prevented P release[6]. Latter, numerous studies indicated that sediments also release P even if the overlying water is aerobic[7,8], and that sediment P release in shallow lakes can constitute a substantial part of total P loading, sometimes even exceeding the external P loading[6,9,10]. Much of the P that has been absorbed by the sediment during eutrophication can be released to the water column later, and such internal P loading can cause a delay of many years in the response of P concentrations in lake water to a reduction of the external P loading[1, 11−14]; however, for N the sediment-buffer effect is less relevant[15]. For instance, in 27 Danish lakes that had received a substantial reduction in nutrient loading, even 4—16 years after the reduction in loading, the decrease in P concentration in most lakes was still far less than expected from the reduction[16].

More than half a century ago, it had been recognized that iron is very important in immobilizing P in sediments, but that iron-bound P is released only under reduced conditions. Therefore, much of the effort has been devoted to iron and oxygen, and also to relevant environmental factors, for example, turbulence and decomposition, with only occasional attention to pH[17]. Although some empirical relationships between lake concentration, external loading and sediment characteristics have been found, a large part of the P variation remains unexplained[1]. In the late 20th century, TP studies in 265 shallow lakes indicate that seasonal P variations in the water column were highly related to nutrient levels, with significant difference in TP between summer and winter in eutrophic systems[3,6,10]. However, no satisfactory explanations were given for this, and it seems impossible to attribute such a difference to the relatively high temperature in the surface sediments (stimulation of organic matter mineralization) or to a change in DO.

On the other hand, TP concentration in the water column decreased significantly following a reduction in algal biomass in biomanipulated shallow lakes in Europe[10]. It is suggested that biomanipulation may improve light climate at the sediment surface, stimulating periphytic algal growth and thereby oxygen production, chemical sorption, and biological uptake of P at the sediment surface[18].

Apparently, European limnologists paid little attention to the possible role of phytoplankton in the P exchange at the sediment-water interface, whereas phytoplankton biomass is probably more directly influenced by trophic level than any other biotic factor. Compared with deep lakes, shallow lakes have higher sediment surface per volume and thus more importance of sediment-water P exchange in the P dynamics of the overlying water. The sediment of shallow lakes may be in direct contact with the photic zone and thus the P exchange at the sediment-water interface may be strongly regulated by phytoplankton photosynthesis.

Recently, limnologists in China found a close relationship between internal P loading and algal blooms, after examining the long-term data of P (in both water column and sediment) and phytoplankton biomass for the past half century in Lake Donghu in the middle reaches of the Yangtze River[19]. Later, they found massive release of P from sediment with occurrence of cyanobacterial blooms through enclosure experiments, and hypothesized that enhancement in algal photosynthesis through increasing pH selectively pumps up P (but not N) from sediment[20,21]. Recent surveys in 33 shallow lakes in the middle and lower reaches of the Yangtze River show that there was a negative relationship between the N/P ratio of the lake water and the trophic level, and that the N/P ratio was significantly lower in summer than in spring-autumn[22], which is in agreement with the results from 265 Danish shallow lakes[3,6,10].

This paper reviews the field and experimental studies on P release from sediments in shallow lakes of the temperate Europe and the subtropical Yangtze River, and based on the mechanism that algal blooms selectively pump up P from sediment, proposes a new explanation that sediment P release driven by algal photosynthesis is the key for the close relationship between seasonal dynamics of internal P loading and trophic levels in shallow lakes.

1 Seasonal dynamics of TP in shallow lakes of Europe

Lakes in some European countries, like Denmark and the Netherlands, are almost all shallow. In the last century, due to ever-increasing eutrophic problems, there have been numerous studies and relevant data relating to nutrient dynamics in shallow lakes[1]

Danish scientists[3,6,10] studied seasonal variation in TP concentrations as percentage of winter values in 265 temperate lakes (Fig. 1). The lakes included in their analysis were mainly eutrophic (half of the lakes with a mean summer TP between 0.15 and 0.58 mg P L^{-1}), shallow (half of the lakes with a mean depth between 1.2 and 3.2 m), and relatively small (half of the lakes with an area of 0.15 and 137 ha). The lakes were sampled at least 10 times annually for the past 10—15 years. Each lake is only represented once. Only epilimnic (surface) samples were included. They found that seasonal P variation were highly related to nutrient levels: in lakes with a TP below 0.05 mg L^{-1}, seasonal variation was low and summer concentration did not differ much from winter values, whereas in more eutrophic systems, and particularly when TP was above 0.1 mg L^{-1}, summer concentrations were significantly and typically two- to threefold higher than winter values. Therefore, in shallow, temperate lakes, TP concentrations show more pronounced summer peaks with increase in trophic level, which is often attributed to increased inlet concentrations because wastewater constitutes a larger proportion during summer at low-river discharge. However, in most cases the increase can only be the result of increased internal loading[6].

Sondergaard *et al.*[10] studied seasonal P retention within three categories of mean summer concentrations of TP in 16 Danish lakes measured for 8 years. All the lakes were relatively small, turbid, eutrophic and with a short hydraulic retention time. To establish monthly mass balances, the main inlet of each lake was sampled 18—26 times annually, depending on seasonal variations in discharge, while the minor inlets were sampled less frequently, depending on their relative contribution to total contribution. Outlet samples were collected twice monthly during summer and once monthly during winter, i.e., 19 times annually. The lakes represent various loading histories but in most of the lakes the loading has been reduced within the past 10—15 years. Seasonally, large differences were recorded between eutrophic and less eutrophic lakes: in lakes with a TP below 0.1 mg P L^{-1}, mean P retention was positive throughout the year excepting July and August, while retention was negative from April to September in lakes with a TP > 0.1 mg P L^{-1}; retention was most negative in May and July (as high as 50%—65% of external loading), while in June retention was often less negative, particularly in lakes with a TP be-

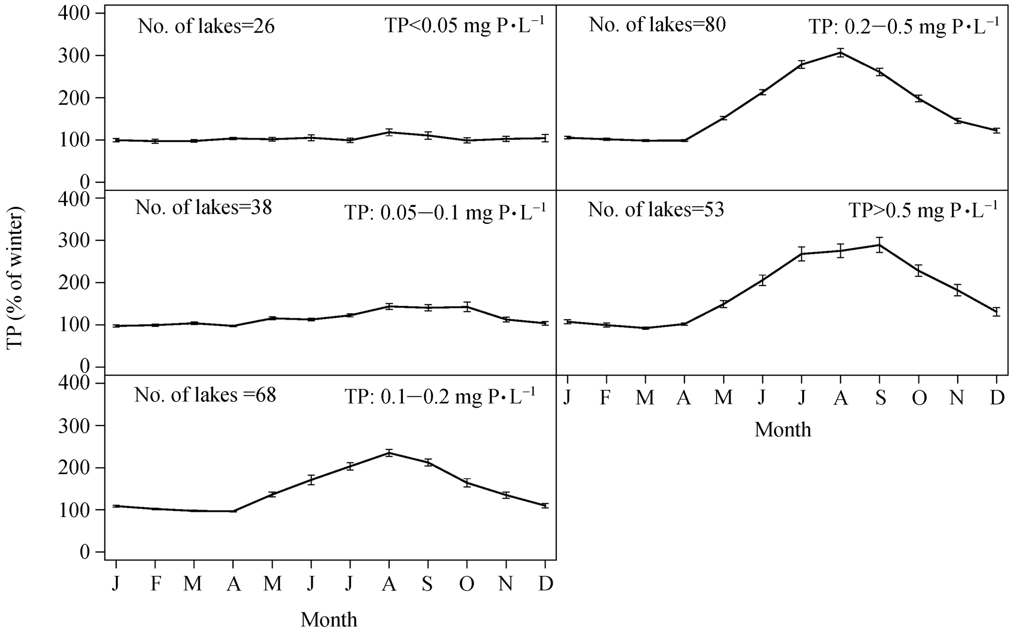

Fig. 1. Seasonal variation in TP concentrations as percentage of winter values (1 Jan to 31 March) in 265 Danish lakes with different categories of mean summer TP[6].

tween 0.1 and 0.2 mg P L^{-1}. A highly negative retention occurring in May in the most eutrophic lake suggests that the onset of the increasing biological activity in spring triggers the release of some of the P retained during winter.

Sondergaard *et al.*[6] reviewed literatures and offered several possible explanations for the seasonal variation in the sediment's capacity to retain P and its dependency on the trophic level: (1) stimulation of organic matter mineralization and the release of inorganic P as temperature increases; (2) photosynthetically elevated pH in eutrophic lakes increasing release rates from iron-bound P; (3) increased sedimentation of organic material related to the seasonal variation in phytoplankton productivity which, at higher temperatures, reduces the capacity of the uppermost sediment to retain P; and (4) declined penetration depth of oxygen and nitrate into the sediment as organic loading increases and mineralization processes are strengthened, and enhancement of redox-sensitive release in lakes with a large proportion of iron-bound P because of a decrease in the thickness of the oxidized surface layer with increasing temperatures.

It is suggested that the reduced negative retention in early summer (Fig. 2) is probably related to the so-called "clearwater phase" as a consequence of late-spring development of a high zooplankton biomass and its grazing on phytoplankton, and several possible mechanisms were given for this: reduced sedimentation of organic matter reduces oxygen consumption and enhances redox conditions, and improved light conditions increase benthic primary production and with it the uptake of P and oxidation of the sediment surface[6]. The decreased internal P loading in early summer was believed to be supported by the observation that in biomanipulation experiments a reduction of the zooplanktivorous fish biomass and, as a result, improved transparency, thus leading to decreased in-lake P has often been observed. However, it still remains unexplained why massive release of P from sediment occurred in summer after the clearwater phase and why internal P loading in summer was closely related to nutrient levels.

2 Effects of biomanipulation on internal P loading in shallow lakes

2.1 Effects of non-traditional biomanipulation on internal P loading

Xie and Xie[19] reported, for the first time, the

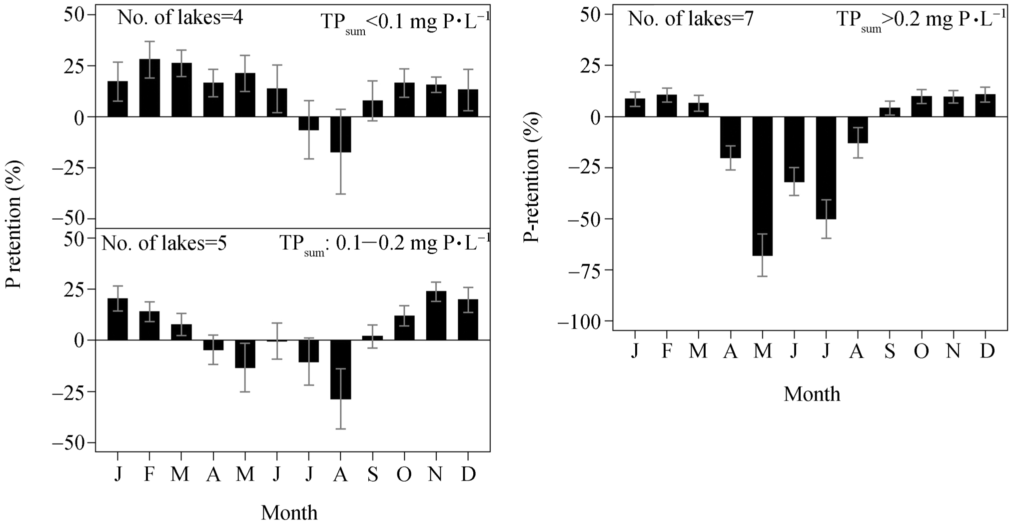

Fig. 2. Seasonal variation in P retention within three different categories of mean summer concentration of TP in 16 Danish lakes measured for 8 years[10].

phenomenon that there was a close relationship between internal P loading and algal blooms in the shallow eutrophic Lake Donghu after examining the long-term dynamics of P and phytoplankton during the 1950s and 1990s.

Lake Donghu is a medium-sized shallow lake in the middle reaches of the Yangtze River (surface area 27.9 m^2, mean depth 2.2 m). TP was relatively low in the 1950s, but increased rapidly in the 1970s because of heavy sewage P input and macrophyte destruction by overstocking of grass carp. TP reached the maximum in the mid-1980s, and declined sharply afterwards (Figs. 3 and 4). Heavy cyanobacterial blooms began to occur since the mid-1970s, but suddenly disappeared completely from the lake after 1985[23,24], which is mainly attributed to increasing stocking of filter-feeding (silver and bighead carps)[24,25]. During the outburst of cyanobacterial blooms, both phytoplankton and zooplankton biomass were high, and concentrations of TP and PO_4-P were also high. But after the disappearance of cyanobacterial blooms, both TP and PO_4-P declined significantly. The steady increases in TP and PO_4-P during the 1950s and 1980s could be attributed to massive discharge of sewage water from the surrounding area[26], but why did TP and PO_4-P show remarkable declines since the mid-1980s?

In 1979—1980, the annual P input of Lake Donghu was 88t, of which as much as 77% was retained in the lake[26]. In 1997—1998, the annual P input was 90t, of which as much as 80% was retained in the lake, and most of the P input was from sewage discharge (Fig. 5). Although the data of external loading of phosphorus to the lake are not sufficient, it seems unlikely to attribute the TP declines after the mid-1980s to a change of P input, as both P input and retention were slightly higher in 1997—1998 than in 1979—1980. In contrast, TP contents in the surface sediment showed a steady increase during the 1950s and 1990s, indicating an ever-increasing P in the sediments (Fig. 6).

Although external P loading did not change obviously between the 1980s and 1990s, P concentration in the water column declined significantly after the mid-1980s, which coincided with the disappearance of cyanobacterial blooms and thus with the drastic declines of phytoplankton biomass: in the mid-lake station (St. II), annual mean phytoplankton biomass was as high as 17.25 mg L^{-1} (cyanobacteria 78.3%) during 1979 and 1983, but declined to only 4.28 mg L^{-1} (cyanobacteria 12.6%) during 1989 and 1996[19]. This may indicate that increases in external P and N loading resulted in the outburst of cyanobacterial blooms which in turn enhanced internal P loading. The subsequent elimination of cyanobacterial blooms, neither by reduction of P input nor by removal of sediment, but through the non-traditional biomanipulation (stocking of silver and bighead carps), led to significant P de-

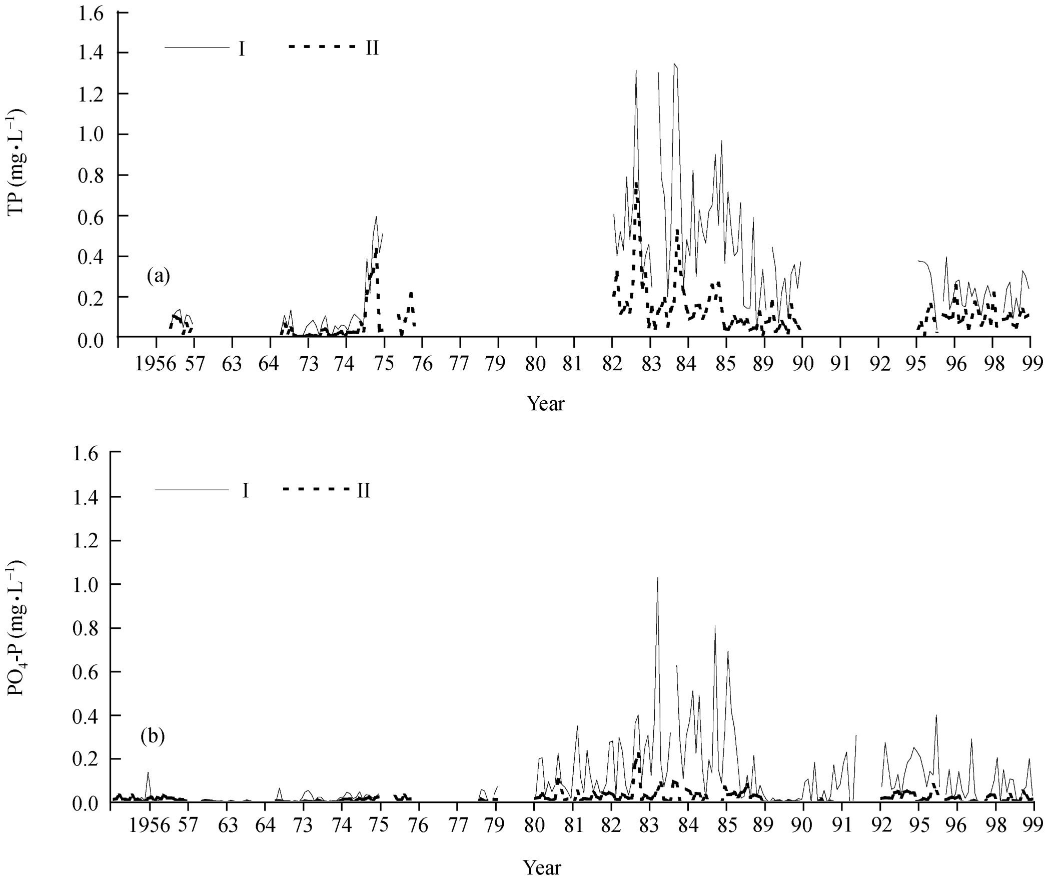

Fig. 3. Seasonal changes of TP and PO_4-P concentrations in the water column of Lake Donghu during 1957—1999[19].

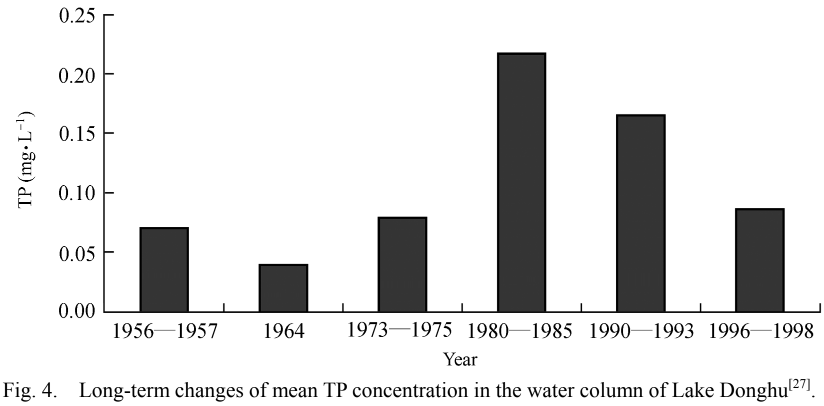

Fig. 4. Long-term changes of mean TP concentration in the water column of Lake Donghu[27].

clines in the water column, providing long-term ecological evidence for the significant enhancement of P release from sediments of shallow, eutrophic lakes by heavy cyanobacterial blooms.

2.2 Effects of traditional biomanipulation on internal P loading

It was recognized that in some shallow lakes of Europe, reduction of algal biomass by traditional biomanipulation led to significant declines of TP in the water column. For instance, Sondergaard *et al.* [10] reported that Lake Engelsholm, a eutrophic Danish lake, was biomanipulated from April 1992 to September 1994 by removing cyprinid fish, mainly bream (*Abramis brama*), which constituted 85% of the total catch, and roach (*Rutilus rutilus*). In total, 19.2 t, or 438 kg wet weight ha^{-1}, were removed, corresponding to 66% of the total fish stock estimated for 1990. Pre-

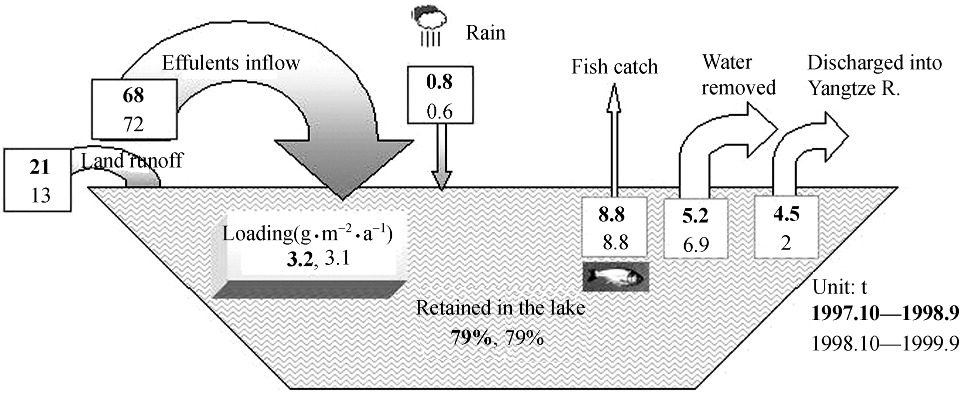

Fig. 5. Phosphorus budget for Lake Donghu[28].

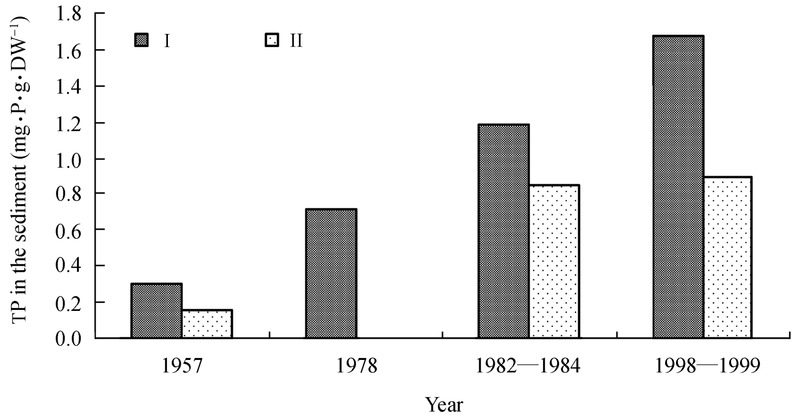

Fig. 6. TP variations in the surface sediments of Lake Donghu during 1957 and 1999[27].

conditions refer to the years 1989—1993 and post-conditions to 1994—1999. External TP loading remained unchanged during the investigation period. After the cyprinid reduction, there were marked changes in biological structure such as significant increase in number and size of *Daphnia* and remarkable reduction in chlorophyll *a*, and water quality was also improved greatly, i.e., Secchi depth increased from a summer level of 0.5—0.6 m to 1.2—2.0 m, and TP decreased from a summer mean concentration of 0.15 to 0.07 mg P L^{-1}, whereas winter TP were unaffected. Both the duration and levels of seasonal TP retention changed. Prior to biomanipulation, P retention was negative for six months (April to September), but after biomanipulation the period with negative retention declined to four months (May to August). Minimum mean retention, −6 mg P m^{-2} d^{-1} (July), was observed before biomanipulation, being only −2 mg P m^{-2} d^{-1} (June and August) after the intervention. Mean TP retention in winter was unchanged (Fig. 7). However, Sondergaard *et al.*[10] did not explain why declines in phytoplankton biomass led to TP declines in the lake water.

It is suggested that biomanipulation increases chemical sorption and biological uptake of P by surface sediment through improving light condition at the sediment surface and thus promoting periphytic algal growth and oxygen production[18], but relevant experimental evidences are still lacking.

Traditional biomanipulation mainly focuses on the feeding of the pelagic fishes on zooplankton. However, recent studies indicate that benthivorous fish (e.g. bream *Abramis brama*) has a significant impact on the resuspension of sediment as well as on the release of P from the sediment[29−32] and that reduced bioturbation, that is, feeding by benthic fish at the sediment surface, may also reduce the P release from sediment to water[18]. The effects on lake water quality of fish-medi-

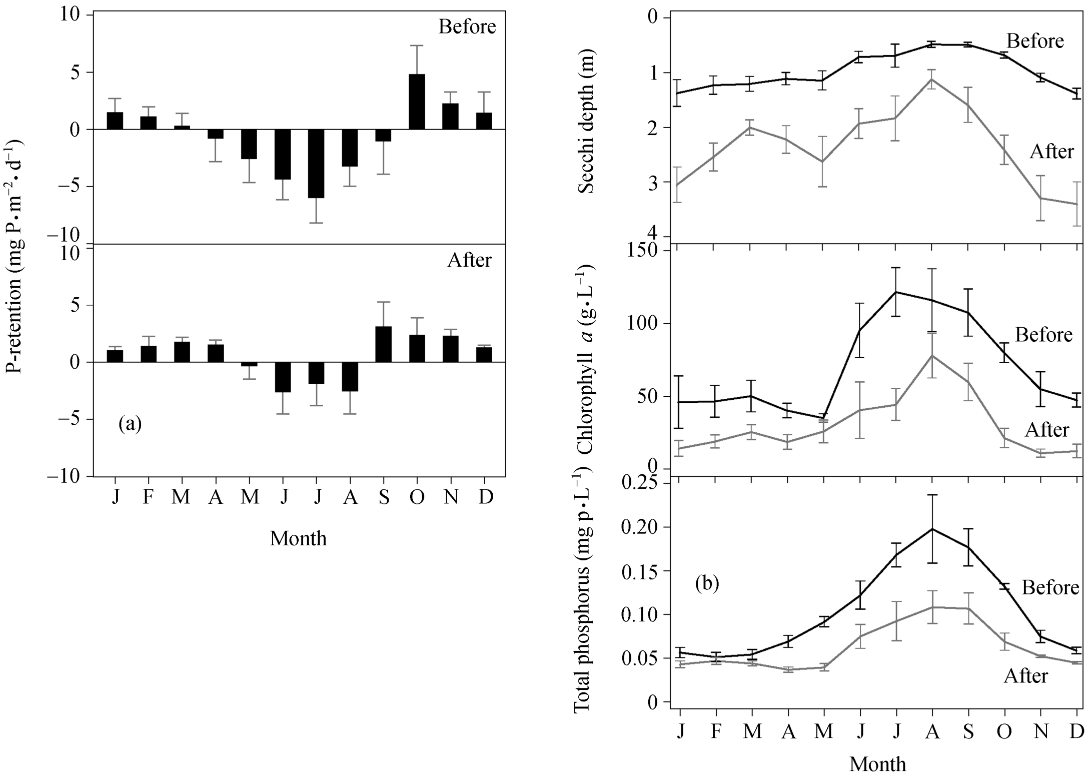

Fig. 7. Changes in water quality parameters in Lake Engelsholm, Denmark, before and after biomanipulation. (a) Monthly retention of TP (±SE), (b) mean Secchi depth, chlorophyll *a*, and total phosphorus (TP)[10].

ated P release from the sediment are sometimes believed to be stronger than those achieved through reduced planktivorous and top-down control on phytoplankton[33, 34].

3 Selective pump of P from the sediment by cyanobacterial blooms

Cyanobacterial blooms, an obvious and problematic symptom of eutrophication, have been the hot subject of freshwater ecology during the past half century[35]. However, in the last century there was no any experimental study to examine the effects of algal blooms on the nutrient exchange at the sediment-water interface. Xie *et al.*[35] conducted enclosure experiment in the summer of 2000 to examine the possible effects of adding N and P on the cyanobacterial blooms in Lake Donghu. They fortunately observed quite different responses of sediment N and P to cyanobacterial blooms, leading to the finding that cyanobacterial blooms selectively pump up P from the sediment.

Eight polyhexene enclosures were placed into Lake Donghu, and the enclosures (2.5 m×2.5 m×3 m) were sealed off from the sediments at the bottom and filled with lake water to a depth of 2.5 m. Nutrient-rich sediments from the lake were added into six enclosures to a depth of 5 cm (E1-E6) as internal P and N sources, while the other two enclosures (E7-E8) were sediment-free. Inorganic P and N were added into E1-E2 and E3 and E4, respectively, while no nutrients were added into E5-E8. Water samples for analysis were also taken from the lake water around the enclosures (L1, L2).

In mid-August, *Microcystis* biomass increased greatly (Fig. 8) with the development of surface blooms in all the enclosures. There was a persistent coincidence between the outburst of *Microcystis* blooms and the increase of both TP and PO_4-P concentrations in the water of the enclosures with sediments, while in the sediment-free enclosures, TP and PO_4-P concentrations remained rather stable throughout the experiment (Figs. 8 and 9) in spite of the appearance of *Microcystis* blooms. With the development of cyanobacterial blooms, pH increased re-

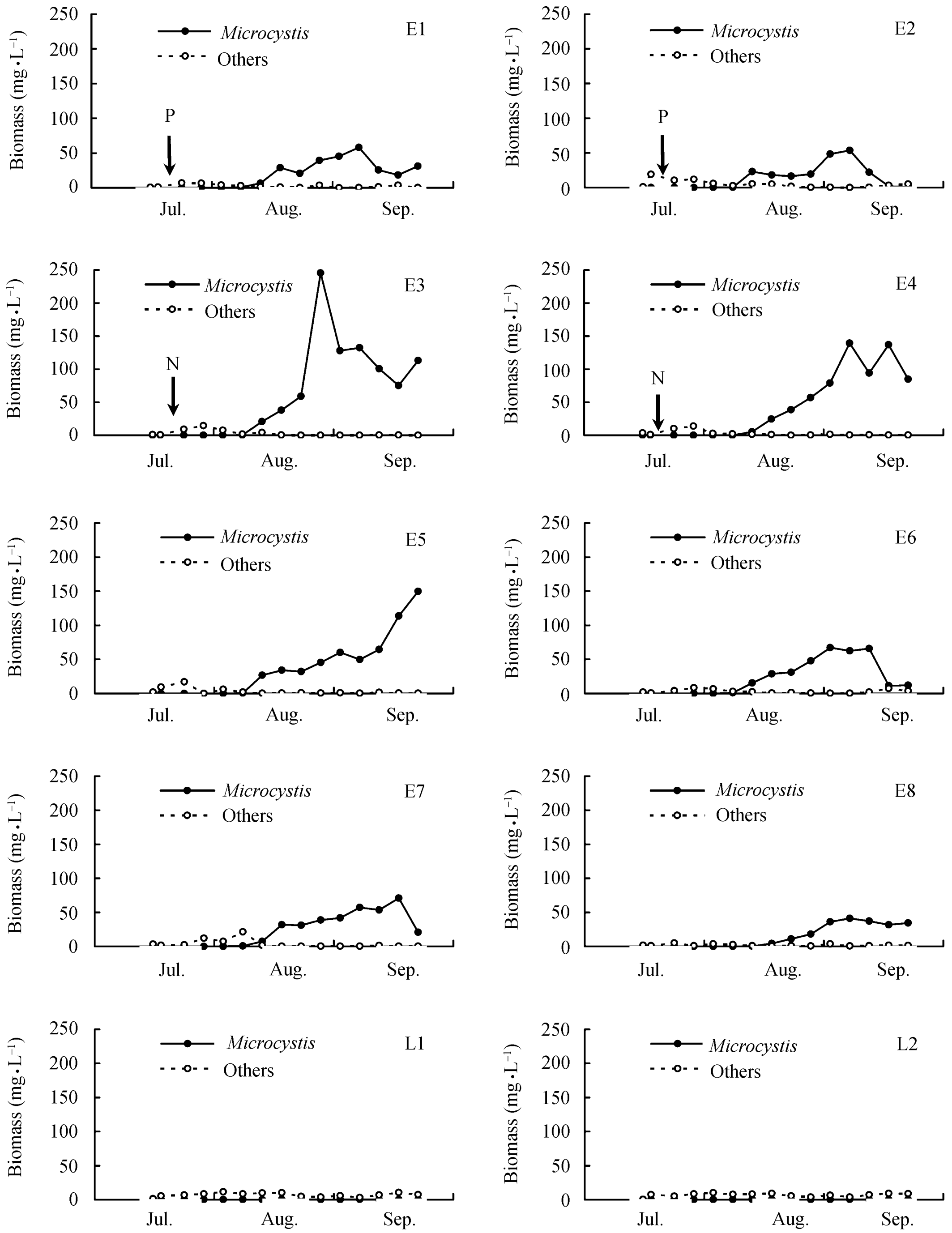

Fig. 8. Changes in phytoplankton biomass (wet weight) in the enclosures and the surrounding lake water of Lake Donghu[20].

markably in all enclosures, but DO concentration showed no obvious trends. These results indicate that *Microcystis* blooms induced a massive release of dissolved P from the sediment probably mainly through photosynthetically-caused high pH. While, in the lake water outside the enclosures, algal biomass remained low, and both TP and PO_4-P showed regular fluctuations (Fig. 10).

How did cyanobacterial blooms affect N dynamics in the above enclosure experiment? In spite of the massive cyanobacterial blooms, TN remained relatively stable except that there were gradual declines in

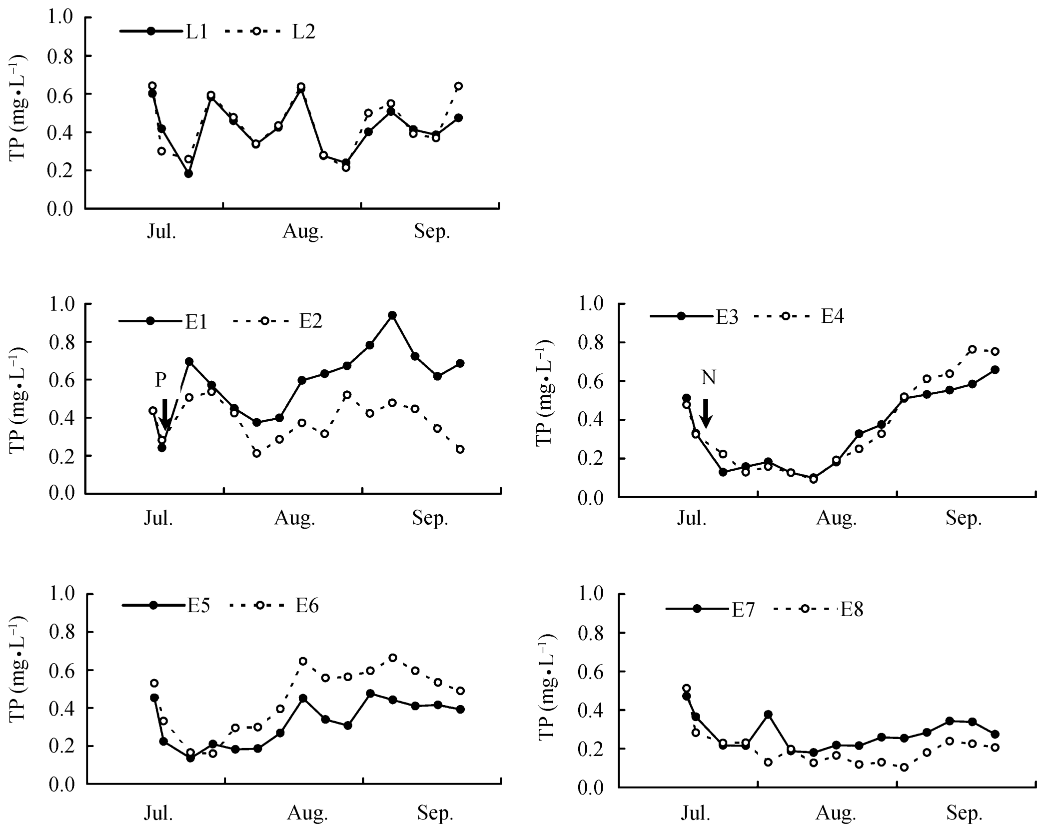

Fig. 9. Changes in TP concentration in the enclosures and the surrounding lake water of Lake Donghu[20].

the N-added E3-E4, while NO_3-N showed significant declines in all the enclosures. Therefore, cyanobacterial blooms selectively induced massive release of P (but not N) from the sediment, consequently leading to significant declines in the ratio of N/P. This finding poses a great challenge to the authority of the traditional N/P theory that is widely used to explain why cyanobacterial blooms occur.

Of the major hypotheses that explained the success of cyanobacteria, the most prevalent and disputed explanation may be the TN: TP ratio. In an analysis based on 17 lakes located worldwide, the Canadian scientist Smith V.H. found that bloom-forming cyanobacteria tended to dominate in lakes where the TN:TP mass ratio was less than 29. This conclusion has led to the so-called "TN: TP rule" that increasing the mass ratios above 29 will reduce the proportion of cyanobacteria as a fraction of the total algal biomass. He published this result in *Science* in 1983[36]. Since then, there have been many substantial discussions on this, some support the "TN: TP rule"[37−40], but others hold the reverse view, e.g., some researchers[41,42] have recognized that even when such a response is observed, it may be due to the increasing P concentrations rather than a decrease in the N: P ratio. Paerl *et al.*[35] suggested that the "N: P rule" is less applicable to highly eutrophic systems when both N and P loadings are very large and N and P inputs may exceed the assimilative capacity of the phytoplankton. Neither laboratory nor whole-lake studies provide conclusive evidence that N: P plays a major role in cyanobacterial dominance. Takamura *et al.*[37] reported that in Lake Kasumigaura, the TN: TP ratios of the water were mostly less than 10 during the *Microcystis* blooms, but exceeded 20 after the disappearance of the blooms, which was attributed to an increase in N loading. Both the long-term studies[19] and the enclosure experiments[20,21] in Lake Donghu indicate that in eutrophic lakes, cyanobacterial blooms enhance P release from the sediment probably due to photosynthetically-caused high pH, thus decreasing the N/P ratio in the overlying water.

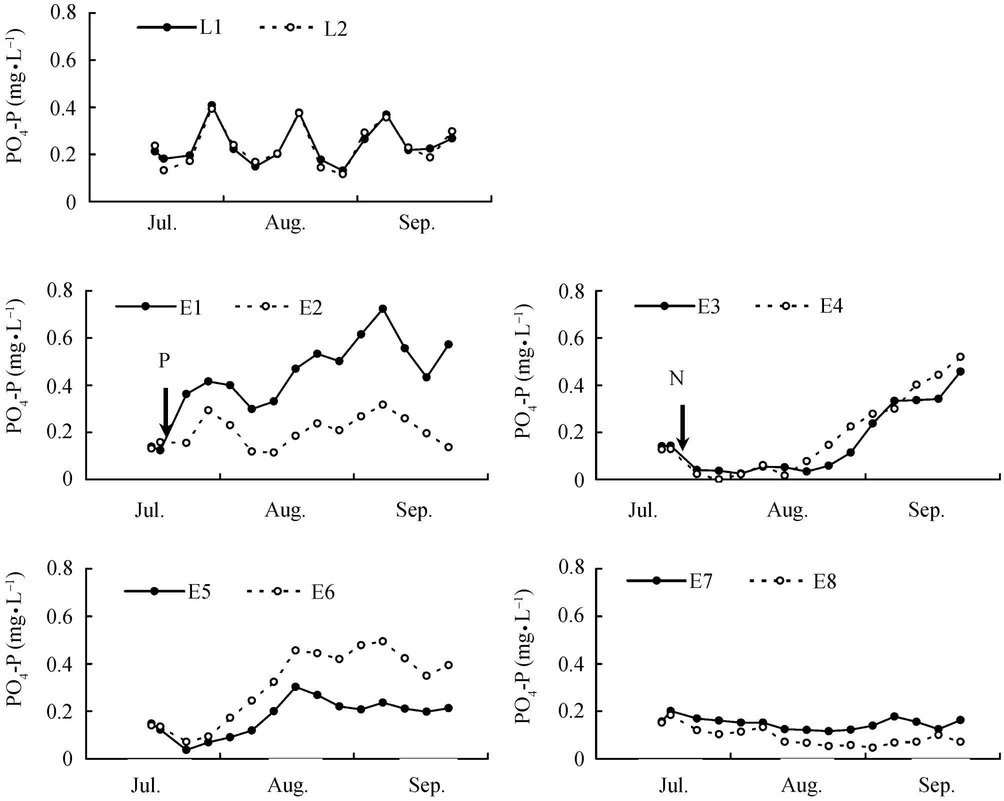

Fig. 10. Changes in PO_4-P concentration in the enclosures and the surrounding lake water of Lake Donghu[20].

Xie *et al.*[21] conducted an enclosure experiment in 2001. Eight polyhexene enclosures were placed into Lake Donghu, and the enclosures (2.5 m×2.5 m×3 m) were sealed off from the sediments at the bottom with a depth of 2.5 m. E1, E2, E5 and E6 were filled with eutrophic lake water, while E3, E4, E7 and E8 were filled with about 90% tap water and 10% lake water for inocula. The sediments gathered from the eutrophic Station I were dropped into E1-E4 and the sediments gathered from the less eutrophic Station III were dropped into E5-E8 to a depth of about 5cm, respectively. *Microcystis* blooms occurred in the enclosures (E1-E4, E5-E6) either with an initial TN: TP <29 or TN: TP >29 where the nutrients (N, P) were high enough. *Microcysitis* blooms never occurred in the enclosures (E7-E8) with low P concentration in spite of the presence of sufficient N. After two months, TP contents in the sediments declined from 4.01 mg g^{-1} to 2.30—2.61 mg g^{-1} in E1-E4, but changed little in E5-E8 (from 0.77 mg g^{-1} to 0.75—0.83 mg g^{-1}). The P-rich sediments served as an important source for the P supply in the water column, and such a process was activated greatly by the outburst of *Microcystis* blooms which pumped up selectively P from the sediments and thus decreased the TN: TP ratios. Therefore, the low TN: TP ratio is not a cause but rather a result of *Microcystis* blooms. It should be noted, however, that in E5-E6 that were filled with P-rich water but added with P-poor sediments, there was no obvious P release from the sediment and TP was relatively stable in the water column, in spite of the presence of cyanobacterial blooms.

4 Seasonal patterns of internal P loading and the relevant biological mechanisms

From the studies of Europe and China[3, 10, 19, 22], the seasonal patterns of internal P loading in shallow lakes can be summarized as follows: (1) P concentration in the lake water exhibits a seasonal variation with magnitude depending on eutrophication level, i.e., P variation is small in low nutrient level, and becomes large as nutrient level increases, reaching the greatest (mean

TP is several times higher in summer than in winter) in the hypereutrophic water; (2) P release from sediment (internal P loading) also shows an obvious seasonality with strong dependency on eutrophication level, i.e., in less eutrophic lake, P retention is positive during most of the year only with negative value in mid-summer, but the duration of negative retention increases with increasing TP concentration, with highly negative retention occurring in warmer seasons; and (3) changes in biological community can cause significant alternations of internal P loading, as evidenced by the observation that internal P loading declines significantly following reduction of phytoplankton biomass by traditional or nontraditional biomanipulation, or in the spring clear-water phase during the seasonal succession of biological communities.

Among the various factors in relation to the seasonal pattern of internal P loading in shallow lakes, pH is probably a more important factor than DO, i.e., intense photosynthesis of phytoplankton increases pH of the lake water and thus may increase pH of the surface sediment, leading to enhanced release of P (especially iron-bound P) from sediment. This is supported by the experimental studies[20] conducted in Lake Donghu using enclosures: outburst of cyanobacterial blooms increased pH through increased photosynthesis, and therefore selectively pumped up massive P (but not N) from the sediment. Such a P release process was more significant when the sediments had high nutrient contents, quite similar to the observation that in 265 Danish lakes, internal P loading in summer increased with increase in eutrophation level. The finding that cyanobacterial blooms selectively pump up P from the sediment not only negates the popular “N:P rule” for the outbreak of cyanobacterial blooms, but also provides a convincing mechanism for the seasonal pattern of internal P loading in shallow lakes, i.e., photosynthesis which is closely related to eutrophication level is the driving force for the seasonal variation of internal P loading in shallow lakes.

Actually, the finding that algal blooms selectively pump up P from the sediment not only explains satisfactorily why both TP and PO_4-P in the hypereutrophic Lake Donghu declined significantly since the mid-1980s when heavy cyanobacterial blooms were eliminated by the nontraditional biomanipulation (massive stocking of the filter-feeding silver and bighead carps) [19,24], but also explains why TP in European lakes decreased remarkably in the spring clear-water phase with less phytoplankton during the seasonal succession of aquatic communities or when phytoplankton biomass was decreased by traditional biomanipulation[10].

In conclusion, (1) the selective pump of P (but not N) from the sediment by algal blooms is an important factor affecting P exchange at the sediment-water interface in shallow lakes; (2) photosynthesis of phytoplankton is a diving force for the seasonal variation of internal P loading in relation to eutrophication level; and (3) compared with deep lakes, wax and wane of phytoplankton due to alternations in the ecosystem structure is also able to exert influences or even more significant influences on the P exchange at the sediment-water interface in shallow lakes.

It should be noted, however, that this paper dealt with relatively small-sized lakes, and therefore the associated P release process was mostly of static or quasi-static state, whereas the situations in the large shallow lakes like Lakes Taihu and Chaohu might be much more complex[43,44]. Even so, the biological mechanisms behind the internal P loading in shallow lakes still provide useful information for the understanding on the mechanisms of internal P loading in large shallow lakes. Further studies are needed to reveal the mechanisms for the selective pump of P from the sediment, i.e., phenomenally phytoplankton photosynthesis selectively promotes P (but not N) release from the sediment, but it still remains unclear why high pH favor P release from the sediment, and how the geochemical behavior of iron, enzyme and microorganisms are involved functionally in this process.

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