Preferential regeneration of P relative to C in a freshwater lake

Jingan Chen [a, *], Yan Zeng [a], Jia Yu [a, b], Jingfu Wang [a], Haiquan Yang [a], Yaoting Lu [a, b]

[a] State Key Laboratory of Environmental Geochemistry, Institute of Geochemistry, Chinese Academy of Sciences, Guiyang, 550081, PR China
[b] University of Chinese Academy of Sciences, Beijing, 100049, PR China

HIGHLIGHTS

- TOC/P ratios are lower in SPM than surface sediments.
- The preferential regeneration of P relative to C occurs in lake system.
- A significant percentage of P may be regenerated during seston transportation.
- A positive feedback loop exists among water anoxia, P regeneration and algal bloom.

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ABSTRACT

Particulate organic matter (POM) is the main carrier of carbon (C), nitrogen (N), and phosphorus (P) in the biogeochemical cycle. Previous investigations have found that the regeneration of C, N, and P is obviously different during the degradation of POM in marine environments. However, little attention has been paid to lake system thus far. In an initial attempt to characterize the regeneration behaviors of C and P in lake system, contents of C, N, and P in suspended particulate matter (SPM) and surface sediments of Hongfeng Lake were systematically investigated in this study. The results showed that the total organic carbon (TOC) to total phosphorus (TP) ratios (TOC/P) were obviously lower in SPM than in surface sediments, which demonstrated the preferential regeneration of P relative to C in lake system for the first time. Possible mechanisms for such include reductive dissolution of Fe oxyhydroxide and poly-P remineralization under hypoxic/anoxic conditions.

Based on the difference in the TOC/P ratios between SPM and surface sediments, about 25.1 t P was estimated to be released annually from settling seston and sediments in Hongfeng Lake, which is much higher than the previous results on the P release flux from sediment. This indicates that a significant percentage of P may be regenerated during particulate matter transport in the water column, providing new insight into the P regeneration in lake system. The preferential regeneration of P may result in a positive feedback loop among bottom water anoxia, enhanced P regeneration, and algal bloom in sub-deep lakes.

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1. Introduction

It is well known that N and P are the primary nutrients governing the trophic status of lakes. The biogeochemical cycles of C, N, and P are tightly coupled by lake primary production and organic matter (OM) degradation. The growth process of phytoplankton is certainly accompanied by photosynthetic uptake of C, N and P, while the degradation of OM releases synchronously C, N and P back to the water body (Bratkic et al., 2012; Chen et al., 2018a).

Previous investigations showed that the regeneration of C, N, and P was obviously different during the degradation of POM (Bishop et al., 1977; Knauer et al., 1979; Krom and Berner, 1981; Ruttenberg, 1990). Based on a comparative study, Ingall et al. (1993) revealed that P was preferentially regenerated relative to C during the degradation of OM, resulting in higher organic C/P ratios under anaerobic conditions than under aerobic conditions. Recently, Viktorsson et al. (2013a, 2013b) found that the benthic fluxes of dissolved inorganic P were much higher when the overlying water was anoxic than when the overlying water was oxic. The burial efficiency of sediment organic P under anoxic conditions was less than 12%, which suggests that anoxic sediments are very efficient in recycling deposited organic P and make an important

* Corresponding author.
E-mail address: chenjingan@vip.skleg.cn (J. Chen).

contribution to the P load of the overlying water and eutrophication (Viktorsson et al., 2013a, 2013b). Investigations of SPM also indicated that the ratios of C/N and C/P of particulate matter increased with depth, which suggests that the mineralization of particulate N and particulate P is quicker than that of particulate C in oceans (Knauer et al., 1979; Martin et al., 1987; Karl et al., 1996; Christian et al., 1997; Boyd et al., 1999; Boyd and Trull, 2007).

Although the activation of C, N, and P of the particulate matter in marine environment has been extensively investigated, little attention has been paid to freshwater lakes thus far. Only a few studies have reported that the ratio of C:N:P in particulate matter differed between oceans and lakes (Sterner et al., 2008; Chen et al., 2015). Excessive inputs of N and P are the main causes for eutrophication in freshwater lakes (Schindler, 1977; Jickells, 1998). Many investigations have revealed that despite the decrease in external nutrient input, phosphate levels have not declined noticeably as expected. P released from sediment is thought to be the primary cause (Marsden, 1989; Vandermolen and Boers, 1994; Sondergaard et al., 1999, 2003; Rockwell et al., 2005; Burger et al., 2007; Elsbury et al., 2009). However, it remains to be answered whether P is regenerated preferentially relative to C in lakes. Therefore, in this initial attempt to characterize the regeneration behaviors of C and P in lake system, C, N, and P contents in SPM and surface sediments of Hongfeng Lake were systematically investigated.

Hongfeng Lake is a freshwater lake located in Guizhou Province, Southwest of China. Though inputs of external P have decreased substantially, algal blooms still occur frequently, aggravating the oxygen deficit and causing deterioration of the water quality (Wan, 2009). The previous studies indicated that the internal P released from benthic sediment contributed greatly to the P load (Wan, 2009; Jiang et al., 2011; Wang et al., 2015). In consideration of substantial P regeneration there, Hongfeng Lake was selected for this study.

2. Materials and methods

2.1. Study site

Hongfeng Lake (N 26°26′-26°36′, E 106°19′-106°28′), located approximately 32 km west of the city of Guiyang, is an artificial reservoir that was constructed in 1960 (Fig. 1). With a catchment of 1596 km^2 and a lake area of 57.2 km^2, Hongfeng Lake has six inflow rivers and only one outflow. The average water depth is 10.5 m, and the mean residence time of water is 0.325 years (Zhu et al., 2013). It is monomictic and stratified during summer, with the anoxic hypolimnion normally below the depth of 12 m from June to September.

Fish breeding started in Hongfeng Lake in 1987, and gradually increased to the peak in 1996. The trophic status in the fish breeding area was eutrophicated, and mid- or mild-eutrophicated in other areas (Zhong et al., 2004). The Conservation Regulation of Water Quality for Hongfeng Lake was issued in 1996, and the restoration measures were carried out since then.

2.2. Sampling and analysis

Using Niskin bottles, water samples were collected from the middle layer at three sites, i.e., north central region (NC), Houwu (HW), and Xinglong (XL), in late May 2017. SPM for C, N, and P analyses were collected on glass-fiber filters (Whatman GF/C, 15 cm diameter) that had been preignited at 550 °C for 16 h. SPM in ~20 L water was collected and stored frozen until analysis. After freeze-drying, the filters were fumigated with 12 M HCl (ACS Plus grade) for 24 h to remove carbonates, and then dried again (Zigah et al., 2011). Total organic carbon and total nitrogen (TN) of SPM were analyzed via an element analyzer (PE2400-II).

Sediment cores at the corresponding sites were retrieved using a gravitational sampler and a polyethylene tube with a diameter of 59 mm. As shown in Fig. 1, water from all inflow rivers collects in the north central region of the lake. Hence, sedimentary information from NC can reflect the nutrient evolution history. Samples were collected throughout the core for the NC site, whereas only the surface 1 cm was sampled for the other two sites. The upper portion of the core (0—20 cm) from NC was sectioned in situ at 1 cm intervals, whereas the rest was sectioned at 2 cm intervals. All the samples were put into polyethylene centrifuge tubes. After freeze-drying, the sediment samples were ground to homogeneous
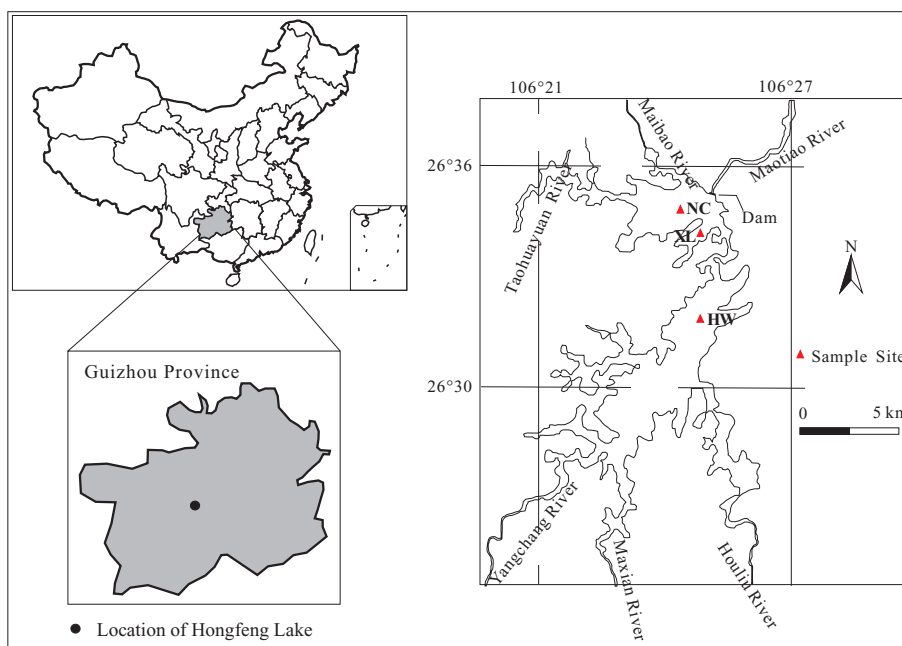

Fig. 1. Location of Hongfeng Lake and sample sites.

powders (particles smaller than 124 μm).

Before the analysis of TOC and TN, the sediment powders were soaked with 1 M HCl for 24 h at room temperature to remove carbonates, and then rinsed with clear water and dried again. TOC and TN were measured via an element analyzer (PE2400-II). TP in SPM and sediments was determined by the method harmonized and validated in the frame of standards, measurements and testing programme (generally mentioned as SMT) (Ruban et al., 1999).

3. Results

3.1. TOC, TN, and TP in SPM and surface sediments

TOC, TN, and TP, as well as the corresponding TOC/P ratio, in SPM and surface sediments from Hongfeng Lake are shown in Table 1. The contents of TOC, TN, and TP in SPM were all much higher than those of the corresponding surface sediments. TOC and TP of SPM at the three sites were similar, whereas the differences in TOC and TP of the surface sediments among the three sites were obvious, especially for TP. TOC/P ratios of SPM at NC, HW, and XL were significantly lower than those of the corresponding surface sediments. The surface sediment at XL had the lowest TOC, TN, TP, and TOC/P ratio, compared to those of the other two sites.

3.2. Profiles of TOC, TN, TP, and the TOC/P ratio in the sediment core

Significant differences occurred between the values of TOC, TN, TP, and the TOC to TN ratio (TOC/N) from the samples above 38 cm and those values from the samples below 38 cm. All the values of the samples below 38 cm were low and stable. Moreover, the colors of the samples above 38 cm and below 38 cm were significantly different. The former were dark gray, whereas the latter were yellow-gray. Therefore, it was supposed that the samples below 38 cm were not deposited lake sediments, but rather the soil formed before the dam was constructed. Accordingly, just the data from the upper 38 cm sediments were employed in this study.

As shown in Fig. 2, TOC, TN, and TP in the core from NC varied within 2.9%–8.2%, 0.28%–0.80%, and 770–3010 μg g^{-1}, respectively, with mean values of 5.80%, 0.61%, and 1815 μg g^{-1}. The molar ratios of TOC/P and TOC/N fluctuated within 44–136 and 9–17, respectively, with mean values of 87.5 and 11.4. TOC decreased from the top layer to the next several centimeters, and then fluctuated to its peak value, followed by a significant decrease to a relatively stable value. Excluding the top several centimeters, TP and TN presented relatively comparable variation patterns to that of TOC. In addition, TOC/P ratio had a significant positive correlation with TOC/N ratio ($R^2 = 0.228$, n = 29, P < 0.01) (Fig. 3).

4. Discussion

4.1. Nutrition status changes recorded by sediment chemistry

The molar ratio of TOC/N has been widely used to differentiate terrestrial (allochthonous) OM from endogenous (autochthonous) OM, because the former is typically greater than 20 and the latter is typically within the range of 4–10 (Meyers, 1997). The variations in TOC, TN, and the TOC/N ratio in the sediment core (Fig. 2) could be divided into three stages since the dam was constructed. (1) Stage 1, corresponding to the core depth from 38 cm to 26 cm: During this period, TOC gradually decreased, while TN slightly increased. The TOC/N ratio rapidly decreased from 17, when the reservoir just formed, to approximately 11, which implied that the source of OM changed from terrigenous-source dominated to endogenous-phytoplankton dominated. (2) Stage 2, corresponding to the core depth from 26 cm to 20 cm: TOC/N ratios fluctuated between 11 and 13, while TOC and TN rapidly increased, which implied that the in-lake primary production increased significantly during this period and that the lake might be changing from an oligotrophic state to a eutrophic state. (3) Stage 3, corresponding to the core depth from 20 cm to the top layer: TOC and TN remained at a high level, and their ratios fluctuated between 9 and 11, which implied that the source of OM was mainly endogenous and primary production was sustained at a high level. The lake remained in a state of eutrophication during this period.

Significant in-lake activities could be recorded by sediment chemistry, although the degradation of OM might alter the chemical compositions of sediment during the early diagenesis (Wei et al., 2005). The sudden increase of TOC, TN, and TP from 26 cm to 20 cm in the sediment core, as shown in Fig. 2 (Stage 2), is believed to reflect the burgeoning fish breeding activity in the 1990s. The higher contents of TOC, TN, and TP in sediments from HW and NC (Table 1) indicate higher algal productivity there.

4.2. Preferential regeneration of P relative to C

4.2.1. Comparison of the TOC/P ratio in SPM and surface sediments

To verify the hypothesis of preferential regeneration of P relative to C, the ratio of TOC/P was employed. If P was preferentially regenerated relative to C during the degradation of OM, an increase in TOC/P from SPM in the water column to the surface sediment should be observed (Emeis et al., 2000). As shown in Table 1, the ratio of TOC/P in SPM (90) was less than that in the surface sediment at NC (115), and the same was true for HW (119 *vs.* 154) and XL (116 *vs.* 131). This indicated that the preferential release of P from settling seston and sediment did occur.

A similar phenomenon has been extensively observed in marine system, e.g., TOC/organic-P ratios at the sediment surface were much higher than those in planktonic OM in the continental margin off Namibia (Kuester-Heins et al., 2010). An increase in the TOC/P ratio from about 100 in sediment trap material to 157 in surface sediment was observed in the Gotland Basin of the Baltic Sea (Emeis et al., 2000). Meng et al. (2014) also found that the TOC/organic-P ratio in sediment was much higher than in SPM in the Changjiang Estuary. All these studies showed that P was lost from the material during the transformation from sinking matter to sediment. However, without relevant data of SPM from bottom water, it cannot be distinguished where the main depletion process takes place, i.e., during particle transport in the water column or

Table 1
TOC, TON, and TP in SPM and surface sediments.

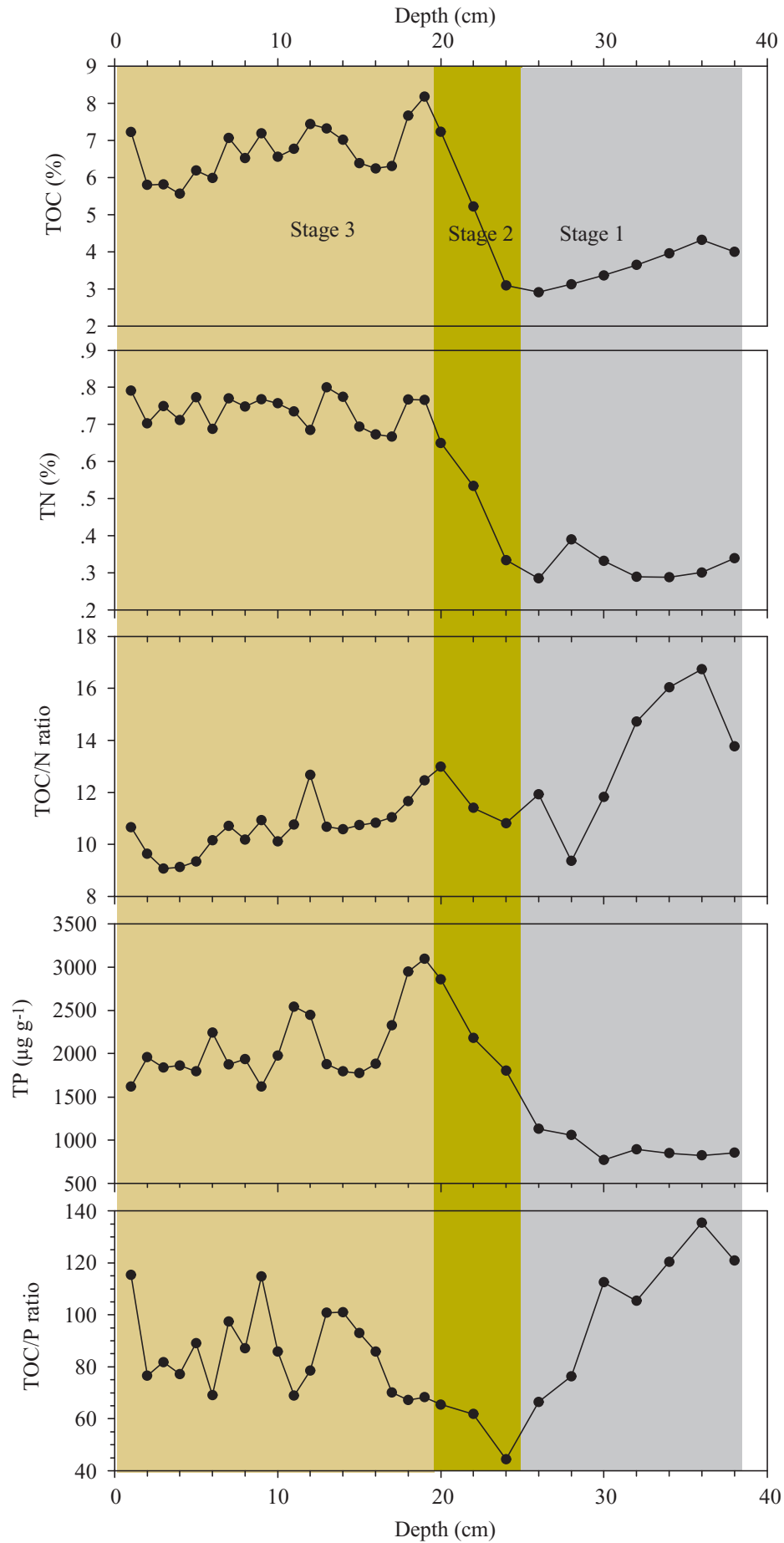|	Sample site	TOC (%)	TN (%)	TP (μg g^{-1})	TOC/P molar ratio
SPM	NC	9.11	1.74	2610	90
	HW	11.1	2.63	2400	119
	XL	10.6	1.64	2350	116
Surface sediments	NC	7.23	0.79	1620	115
	HW	7.68	0.52	1290	154
	XL	4.10	0.50	805	132

Fig. 2. Profiles of TOC, TN, TP, TOC/P ratio, and TOC/N ratio of the sediment core at NC site.
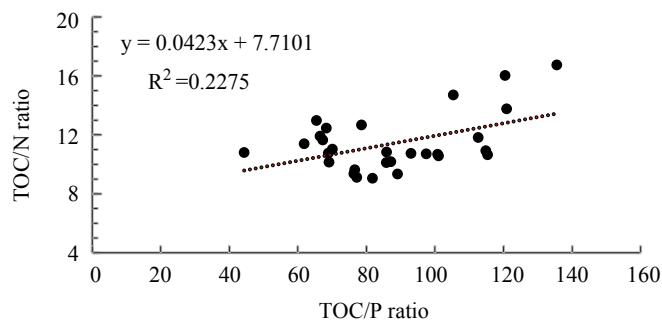
Fig. 3. Relationship between TOC/P and TOC/N ratio.

after deposition on the lake floor.

Although the change of TOC/organic-P ratios was widely used to reflect the preferential release of P relative to C in previous studies (Kuester-Heins et al., 2010; Meng et al., 2014), it may over-estimate the P release, because a portion of P released from the organic matter would precipitate or be absorbed in situ. Therefore, TOC/P ratios in particulate matter are expected to reflect the net release difference of P relative to C during the degradation of OM more accurately than TOC/organic-P ratios. In this study, variations in the TOC/P ratios between SPM and surface sediment are used to estimate the preferential release of P relative to C.

4.2.2. Variations of the TOC/P ratios in the sediment core

Several studies have shown that preferential P release relative to organic C during early diagenesis resulted in high TOC/P ratios in marine and coastal environments (Krom and Berner, 1981; Ruttenberg, 1990; Ingall and Jahnke, 1997). Ingall and Vancappellen (1990) proposed that the TOC/P ratio of incompletely decomposed OM is higher than that of primary OM and almost completely decomposed OM. As shown in Fig. 2, the TOC/P ratio in the top 1 cm sediment was much higher than that of the next several cm sediment. It is well known that starch, glycogen, and maltose, all of which are important components of OM, are composed of α-glucosidase bonded together (Liang et al., 2003). Thus, the activity of α-glucosidase enzymes can reflect to some extent the degradation intensity of OM. In the top sediment layer of Hongfeng Lake, the activity of α-glucosidase was the highest, up to 0.75 mol min^{-1}g^{-1} dry sediment (Liang et al., 2003), suggesting that the degradation of starch, glycogen, and other substances in the OM was the most intense, and a large proportion of OM could be degraded there. As sediment depth increased, α-glucosidase activity decreased sharply. Thus, the high TOC/P ratios in the top sediment layer of Hongfeng Lake are most likely resulted from the intense diagenesis of OM.

The variations in sources of OM may also have important influence on the TOC/P ratios in the sediment core. The TOC/N ratios in sediments from NC varied from 9 to 17 (Fig. 2), indicating both terrestrial and autochthonous OM are the probability. TOC/P is significantly correlated with TOC/N (Fig. 3), implying that the nature of the OM has important influence on the TOC/P ratios in the sediment core. The higher TOC/N and TOC/P ratios reflected greater contribution percentage of terrestrial-derived OM. Thus it can be seen, the TOC/P ratios in the sediment core are affected by both the OM source and early diagenesis in Hongfeng Lake. During the period when the source of OM changes from terrigenous-source dominated to in-lake-source dominated, the TOC/P ratios should decrease, accompanied by a decrease in the TOC/N ratios. During the period when OM is dominated by endogenous phytoplankton while the lake was still oligotrophic, the lake water is normally enriched in oxygen, which allows the OM to decompose much

more completely, resulting in much lower TOC/P ratios in the sediments. As the lake develops to eutrophic stage, anoxia occurs seasonally, especially in the hypolimnion of sub-deep lakes (Chen et al., 2018b). P was preferentially regenerated relative to C during the degradation of OM under anoxic conditions, resulting in higher TOC/P ratios in the sediments.

4.3. Mechanisms of the preferential regeneration of P

The regeneration of P is decoupled from that of C and N under hypoxic/anoxic conditions (Ingall et al., 1993; Ingall and Jahnke, 1994, 1997; Hupfer and Gachter, 1995; Golterman, 2001; Slomp et al., 2002; Jilbert et al., 2011). The possible explanation of enhanced P regeneration under anoxic conditions involves the reductive dissolution of iron oxyhydroxides. Under oxic conditions, Fe oxyhydroxides provide efficient surfaces for P adsorption and therefore act as a sink for dissolved P. Under anoxic conditions, however, Fe oxyhydroxides are unstable, resulting in the release of dissolved P. Wang et al. (2016) found that hypoxia significantly promoted the release of P from sediments, especially the release of redox-sensitive P (mainly bound to Fe hydroxides and Mn compounds) in Hongfeng Lake. Although this mechanism is well-documented (Mortimer, 1941; Froelich et al., 1979; Sundby et al., 1992; McManus et al., 1997), its contribution to the enhanced hypoxic/anoxic regeneration of P remains poorly understood on the global scale (Diaz et al., 2012). In fact, Fe-linked P cycling is insufficient to account for the preferential regeneration of P (Golterman, 2001; Ingall et al., 2005; Turnewitsch and Pohl, 2010; Jilbert et al., 2011). Polyphosphate (poly-P) cycling, via microorganisms, is supposed to be another mechanism for the preferential regeneration of P in aquatic environments (Diaz et al., 2012).

Poly-P is a linear polymer of at least three orthophosphates linked via high-energy phosphoanhydride bonds (Kornberg, 1995; Brown and Kornberg, 2004). In biological cells, poly-P can be organic (such as ATP) or inorganic. Inorganic poly-P is a common and multifunctional biomolecule in cells, typically ranging in size from three to several hundreds of P atoms (Kornberg, 1995; Rao et al., 2009). In ocean environments, both bacteria and phytoplankton are sources of inorganic poly-P (Diaz et al., 2012). Bacteria are well-known for their ability to remineralize inorganic poly-P in a redox-sensitive manner (Nielsen et al., 2010; Diaz et al., 2012). The work by Diaz et al. (2012) indicated that particulate inorganic poly-P was present at concentrations ranging from 1 to 9 nM within several meters above the total particulate phosphorus maximum. Below the depth with 1% oxygen saturation, however, particulate inorganic poly-P was undetectable (<0.8 nM in situ) and assumed to be remineralized to soluble reactive phosphorus. The occurrence of poly-P in lakes with different redox concentrations also confirmed that inorganic poly-P is redox sensitive. High poly-P contents were detected in Lake Gommaren, which has well oxidized sediments; smaller contents of poly-P were detected in Lake Langsjon, which has oscillating aerobic-anaerobic conditions; and no poly-P was detected in Lake Flaten, which has constant anoxic conditions (Torres et al., 2014). No poly-P was detected in the sediments of Hongfeng Lake (Zhang et al., 2009), which resulted most likely from the remineralization of poly-P in the hypoxic/anoxic benthic water and sediments. Poly-P metabolism may play an important role in P release from particulate matter in lacustrine system, but the processes and mechanisms remain to be further investigated.

4.4. P release flux

Based on the difference in TOC/P ratios between SPM and surface sediment, the amount of P missing in settling seston and

sediments in Hongfeng Lake was calculated using the following equation (Emeis et al., 2000):

$$M_{P-reg} = A \times B \times C \times (1/D - 1/E)$$

M_{P-reg}: the amount of P missing from settling seston and sediments

A: average sediment accumulation rate, $0.17 \pm 0.1\,g\,cm^{-2}a^{-1}$ (Wan, 1999)

B: area of the sediment surface

C: TOC of the settling particulate matter

D: mass ratio of TOC/P of the settling particulate matter

E: mass ratio of TOC/P of the surface sediment

The results showed that the average release flux of P was $0.78 \pm 0.28\,t\,km^{-2}a^{-1}$. The average water area of Hongfeng Lake is $32.15\,km^2$ (Shang et al., 2011). About 25.1 ± 9.0 t P is released from settling seston and sediments in Hongfeng Lake each year. Zhang et al. (2015) have estimated that 8.58 t P was lost during the thermal stratification of the lake. The study from Luo et al. (2015) showed that about 6.27–8.00 t P was lost in summer. Shang et al. (2011) indicated that 5.0 ± 5.6 t P was released annually. These estimations were based on sediment core incubation experiment or P concentration gradient in sediment porewater, and focused only on the release from sediment. The P release flux obtained in the current study, contains both the P release from settling seston in water column and from sediment, and is much higher than the previous results. This indicates that a significant percentage of P may be lost during particulate matter transport in the water column of Hongfeng Lake, thus providing new insight into the P regeneration in lake system. Besides the two mechanisms mentioned above, zooplankton P excretion may be a nonnegligible factor for P loss from particulate matter in water column (Kowalczewska-Madura et al., 2007).

4.5. Positive feedback loop among bottom water anoxia, enhanced P regeneration, and algal bloom in sub-deep lakes

In marine system, benthic regeneration of reactive P is more extensive when sediments are overlain by waters with low dissolved oxygen concentrations (Ingall and Jahnke, 1997). The significance of this finding is that a positive feedback may develop between hypoxia in bottom water and P regeneration from sediment. More efficient release of reactive P from sediments caused by hypoxia in bottom-water may result in higher primary productivity. Enhanced primary production and respiration rates below the euphotic zone intensify water-column anoxia, which further stimulates benthic P release, hence creating a positive feedback loop (Ingall and Jahnke, 1997). Ingall and Jahnke (1997) proposed that the key to this positive feedback is the transfer of P regenerated in anoxic deep waters to the euphotic zone. In sub-deep lakes with water depths of 10–50 m, seasonal stratification is the most important factor influencing the physicochemical and biological processes, material cycling and evolution of eco-environment (Chen et al., 2018b). As the ambient temperature increased from late spring to early summer, a temporary thermal stratification will come into being, resulting in the significant decrease in mass transfer between the upper and deeper layers, and the hypoxia in the hypolimnion. Hypoxia accelerates the release of P from sediment (Wang et al., 2016). Once the temporary stratification is broken, a large amount of P enriched in anoxic deep waters would be taken to the upper euphotic zone, resulting in elevated primary productivity in the epilimnion, even algal bloom. This will further intensify water anoxia, accelerate the P release, and promote algal primary productivity, thus forming a positive feedback loop among bottom water anoxia, enhanced P regeneration, and algal bloom in

sub-deep lakes. The positive feedback loop should not exist either in deep water lakes or shallow lakes, because permanent thermal stratification cuts off the mass transfer between the upper water and the hypolimnion in deep lakes while the water body is not deep enough to form stratification in shallow lakes. By this token, sub-deep lakes are more vulnerable than deep or shallow lakes once if the eutrophication happens. This highlights not only the significance of probing into the positive feedback loop, but also the extreme value of early prevention of eutrophication in sub-deep lakes, similar to Hongfeng Lake.

5. Conclusions

In this study, contents of C, N, and P in SPM and surface sediments of Hongfeng Lake were systematically investigated in order to characterize the regeneration behaviors of C and P in lake system. The TOC/P ratios were obviously lower in SPM than surface sediments, demonstrating the preferential regeneration of P relative to C in lake system for the first time. Possible mechanisms for such include reductive dissolution of Fe oxyhydroxide and poly-P remineralization under hypoxic/anoxic conditions. The TOC/P ratios in SPM reflect the net release difference of P relative to C during the degradation of OM more accurately than the TOC/organic-P ratios, because a portion of P released from the OM would precipitate or be absorbed in situ. Based on the difference in the TOC/P ratios between SPM and surface sediments, about 25.1 t P was estimated to be released annually from settling seston and sediments, which is much higher than the previous results on the P release flux from sediment in Hongfeng Lake. This indicates that a significant percentage of P may be regenerated during particulate matter transport in the water column, thus providing new insight into the P regeneration in lake system. The preferential regeneration of P may result in a positive feedback loop among bottom water anoxia, enhanced P regeneration, and algal bloom in sub-deep lakes. This highlights not only the significance of probing into the positive feedback loop, but also the extreme value of early prevention of eutrophication in sub-deep lakes. Further studies on the mechanism and environmental effect of the P regeneration in sub-deep lakes are desirable.

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