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Eutrophication Heterogeneously Enhances Organic Matter and Phosphorus Exchanges among Dissolved, Particulate, and Sedimentary Phases in a Large Shallow Lake

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in the suspended particles and surface sediments of eutrophic regions. As the trophic state increased, interactions between dissolved and particulate subsystems and between particulate and sedimentary subsystems strengthened, whereas few changes occurred in the interaction between dissolved and sedimentary subsystems. This suggests that particle release and sediment resuspension are more significant pathways for internal nutrient loading in eutrophic regions. These findings provide a comprehensive understanding of how eutrophication affects lake subsystems and their interactions, offering potential ecological restoration references for eutrophic shallow lakes.

KEYWORDS: eutrophication, organic matter, phosphorus, shallow lakes, internal nutrient cycling

1. INTRODUCTION

Eutrophication is a major environmental issue for most freshwater ecosystems, including lakes, rivers, and ponds, which reduces biodiversity and impairs ecological functions worldwide.¹ Despite numerous studies and whole-lake experiments, systematically evaluating the eutrophication-related changes in these ecosystems remains a significant challenge.²⁻ Water, suspended particulate matter (SPM), and sediments are fundamental substrates or subsystems for lakes. The chemical composition and flows of organic matter (OM) and phosphorus (P) among these three subsystems determine ecological functions such as primary production and nutrient remineralization, as well as the health state of lakes.⁵ A comprehensive assessment of how eutrophication affects both OM and P pools in lakes is complicated but crucial for ecologists to understand the underlying mechanisms of lake state shifts and to implement effective management measures.

higher trophic states. High mobile P and low inert P were observed

Eutrophication has significantly impacted OM pools in lakes, including the contents and chemical compositions of dissolved (DOM) and particulate (POM) fractions. In eutrophic lakes, for example, algal-derived substances and the microbial decomposition of plankton and macrophyte detritus serve as significant sources of autochthonous DOM.⁶ Specifically, protein-like compounds⁷ and microbial-derived humic-like compounds⁸ increased notably with eutrophication. Sedimentary OM (SOM) may also vary with lake trophic states because eutrophication often increases the burial rate of algal-derived organic carbon in the lakebed.^{9,10} Moreover, components of OM pools in water, SPM, and sediments are highly exchangeable.¹¹ POM in SPM can be released as DOM through dissolution or desorption.¹² Reversely, DOM can be converted into POM by combining oxidized metal elements or through the adsorption of existing SPM.¹³ Both DOM and POM can influence the SOM composition through gradient diffusion and sinking, respectively. Debris of algal organic particles in the surface sediments is easily resuspended in

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shallow lakes as well.¹⁴ Exchangeable OM in sediments can also directly desorb at the sediment–water interface (SWI). Understanding the complex exchanges of OM among DOM, POM, and SOM may provide insights into the processes of lake state shifts.¹¹ Despite this, few studies have explicitly evaluated the effects of eutrophication on the exchange patterns of OM pools among the three lake subsystems.

Phosphorus overloading is a primary contributor to eutrophication, leading to harmful algal blooms in numerous lakes.¹ Phosphorus stocks include the dissolved and particulate forms in the overlying water (i.e., dissolved and particulate P fractions) and the sedimentary P fraction. The exchange and transformation of P among these pools are the main processes of internal P cycling, supporting the proliferation of cyanobacterial blooms in eutrophic lakes. For instance, the release of P from sediments or sediment resuspension is a significant mechanism for maintaining high total P concentrations in the overlying water and cyanobacterial biomass in shallow lakes.¹⁴ The composition of P species in SPM and sediments, as well as the exchanges between these pools, is closely related to eutrophication.¹⁵ Specifically, sedimentary iron-bound P is often released into the overlying water during cyanobacterial blooms due to the depletion of dissolved oxygen and reduced Fe³⁺ at the SWI.¹⁶ Moreover, cyanobacterial-derived extracellular polymeric substances (EPS) can adsorb significant quantities of inorganic P forms,¹⁷ and humic acid-like DOM can aggregate with orthophosphate as well.¹⁸ These processes transfer dissolved P into particulate forms, which may settle into the lakebed. Eutrophication may also affect the diffusion rate of P in pore water at the SWI, altering the sedimentary P loading process.⁹ Nevertheless, prior investigations have not comprehensively established connections between P pool dynamics across all the subsystems, despite frequent quantification of P fractions or empirical assessments of sedimentary P mobilization at the SWI through laboratory-based sediment incubation protocols and high-resolution microscale analytical techniques.^{15,19,20} It is challenging to understand P interaction patterns under varying trophic states based on laboratory-based or local information, especially in shallow lakes where biotic and abiotic processes involved in P exchanges are more complicated.¹⁴ Therefore, new approaches are needed to assess the P exchanges across all of the subsystems under different trophic states, which may illuminate the crucial mechanisms of internal P cycling during lake state shifts.

In this study, OM and P pools were assessed in dissolved, particulate, and sedimentary phases in Lake Taihu, which is the third-largest freshwater lake in China. The exchanges of both pools among different phases were evaluated using "3subsystem" interaction statistical algorithms to elucidate how eutrophication affects the potential pathways of internal nutrient cycling (e.g., SPM release, sediment resuspension, and sediment nutrient diffusion). We hypothesized that eutrophication increases the labile fractions in the OM and P pools and promotes their exchanges among the three subsystems. It is anticipated that stronger interactions occur between water and the SPM, and SPM releases are expected to be more pronounced than sediment resuspension or sediment nutrient diffusion. This study provides new insights into how eutrophication regulates shifts in lake ecosystems and internal nutrient cycling based on the "3-subsystem" theoretical framework.

2. METHODS AND MATERIALS

2.1. Study Area and Sample Collection. Lake Taihu is the research area of the current study. This lake has a total area of 2338 km² with an average depth of approximately 2.0 m and has experienced cyanobacterial blooms for decades in the northwest regions.¹⁴ We collected samples during a sampling campaign with 58 sites (Figure S1a) over several days from October 15 to October 18, 2020. Notably, few changes in the water temperature occurred during the sampling period (Figure S2). Therefore, the temperature variable was not included in further analyses. We summarized sampling sites with different sample types in Table S1. We collected SPM into three sample types: the total, large fraction (>100 μ m), and small fraction (<100 μ m) SPM, according to the method in the Supporting Information. We also sampled sediment cores using a gravity corer with a diameter of 90 mm and a length of 500 mm (Rigo Co., Ltd., Japan). We divided the sediment cores into four depth levels: the surface (0-5 cm), the upper mid (5-10 cm), the mid-late (10-15 cm), and the deep (15-20 cm) sediments. Other details on the sampling processes and methods for water samples and SPM can be found in a previous study.¹¹

2.2. Determination of Physicochemical Parameters and OM Extraction and Analysis. The water physicochemical parameters measured in this study included total nitrogen (TN), total phosphorus (TP), dissolved total nitrogen (DTN), dissolved total phosphorus (DTP), ammonia (NH₄–N), chlorophyll *a* (Chl *a*), total organic carbon (TOC), turbidity, and pH. We further calculated the TN:TP molar ratio. To estimate the potential effect of terrestrial sources on both OM and P pools, we measured the distance of each sampling site from the shore (DFS, km) using a digital map in Omap software V10.0 (https://www.ovital.com). We filtered the lake water using GF/F filters and collected the filtrate for DOM determination. The extraction protocols for POM and SOM can be found in a previous study.¹¹ The total sample numbers of DOM, POM, and SOM were 49, 42, and 119, respectively.

We measured the absorption spectra of DOM, POM, and SOM samples following a previous method.²¹ We further computed an absorption coefficient (i.e., a(350)) and coefficient-based ratios such as spectral slope ratio (SR) and a(250):a(365) following previous methods.²² Generally, autochthonous DOM sources have high values of SR, while terrestrially dominated sources are lower.²² In addition, a(350) was positively correlated with the concentration of OM, while a(250):a(365) was inversely linked to DOM molecular size and aromaticity.²³

Excitation emission matrix (EEM) fluorescence spectra of the DOM, POM, and SOM were assayed, and the fluorescence intensity was normalized.^{11,24} Correction for inner filter effects on EEM measurements was performed by adjusting for OM absorbance at the corresponding wavelengths.¹¹ A data set containing 210 EEM samples was decomposed using PARAFAC analysis coupled with the DOMFluor toolbox (http://www.models.life.ku.dk/) in MATLAB 12.0 (Math-Works, Natick, MA).²⁵

2.3. Determination of P Fractions in SPM and Sediments. We divided P forms in SPM and sediments into four species: labile P (NH₄Cl-extracted P), Fe/Al-P (NaOH-extracted P), Ca-P (HCl-extracted P), and Re-P (H₂SO₄-extracted P). Labile P and Fe/Al-P are highly bioavailable and named mobile P, and both have been known to supply internal

loading in lake sediments.²⁶ Refractory P fractions included Ca–P and Re–P, and both have low biological availability and have been known as "permanently bound" P.²⁶ We extracted these P species successively from the SPM and sediment samples according to a previous method.²⁷ The percentages of P species (P_i) in a particular size sort of SPM or a given sampling depth of sediments were calculated as P_i (%) P_i/ (total-P) × 100%, where total-P indicates the sum of the four P species in the size sort or the sampling depth. We used this percentage to evaluate the composition of P pools in the SPM and sediments.

2.4. Theoretical Basis of Interaction Conceptual Model and Quantitative Assessment. Here, we used a "3-subsystem" interaction conceptual model to quantify the interaction intensity of different lake subsystems. This conceptual model has a solid theoretical basis.⁵ In brief, this conceptual model simplified a lake system into three subsystems (Figure 1): water (dissolved phase), SPM



Figure 1. An interaction scheme of the three lake subsystems.

(particulate phase), and sediment (sedimentary phase). These subsystems interact complexly with physicochemical and biological processes. This conceptual model includes three interaction modules: dissolved-particulate (W–P interaction), dissolved-sedimentary (W–S interaction), and sedimentary-particulate (S–P interaction) modules. Here, we merely considered the surface sediments in the W–S and S–P interactions because the main exchange processes of sediments with water or SPM occurred in the surface layer.²⁰

Quantifying all of the interaction processes among these subsystems is difficult. For a quantitative estimate, we made two assumptions according to the different exchange patterns. First, physical interactions (i.e., adsorption, coaggregation, diffusion, settling, and resuspension) do not change the chemical species. Second, organism-derived exchanges between phases (i.e., uptake, secretion, excretion, degradation, etc.) are relatively delayed compared with physicochemical interactions. Thereby, specific OM compounds or P species could simultaneously appear or exist in the interacting phases, which presumably increases the similarity or connection of OM or P pools in both phases.¹¹ Based on these assumptions, we evaluated the interaction intensities between subsystems by establishing quantitative relationships using OM and P pool data sets from Lake Taihu. Details can be found in the Supporting Information.

2.5. Determination of Trophic States and Statistical Analysis. We employed a comprehensive trophic state index to assess the trophic states of each sampling site according to a previous method.²⁸ We added the detailed calculation process in the Supporting Information. Moreover, we calculated the relative percentage of each species in OM or P pools (i.e., EEM-PARAFAC-derived components or P species) according to the method described above to assess the potential effects of eutrophication on the compositions. We displayed the concentrations of OM and P species in SPM as per volume rather than per dry weight. This treatment provides a more accurate and scaled-up estimation of the influences of eutrophication because it also considers the variation in the suspended particle concentration.

We conducted all statistical analyses in R version 4.3.2.²⁹ We employed Student's t-test to determine significant differences in OM and P pools between trophic states with p-values of <0.05 (*), < 0.01 (**), and <0.001 (***). We assessed the relationships between the trophic state index and the concentration and composition of OM or P pools using linear and nonlinear regressions. We also tested the correlations between the trophic state index and the interaction intensities of the lake subsystems through nonlinear regression. The nonlinear regression arose from a nonparametric regression that was based on the statistical algorithm of locally estimated scatterplot smoothing (LOESS). We performed this nonlinear regression using the "geom_smooth" function in the "ggplot2" package of R. Exploring the potential correlations between trophic state and each OM or P pool in the three subsystems, we performed principal component analysis (PCA) using the "prcomp" function in the "stats" package of R. Moreover, we tried to understand the potential relationships between OM or P pools and environmental variables. Due to both OM and P pools including a diversity of compounds or forms, each pool includes two matrices (i.e., content and composition data). Therefore, we needed to test the relationships between OM or P matrices and environmental matrices. The Mantel test is a convincing tool to examine correlations between matrices and has been used intensively, 30-32 although it may lead to misleading results in spatial analyses.³³ Here, we did not explicitly test the geospatial variation of OM or P pools, and thereby, it should be suitable to employ the Mantel test. We conducted the Mantel test using the "linkET" package in R.34

3. RESULTS

3.1. Environmental Factor Variations and Trophic States of Different Sampling Regions. Environmental factors varied significantly across different sampling regions (Table S2). Lower concentrations of TN, TP, and Chl a were observed in East Taihu Bay, Xuhu Bay, and the South region. The trophic state indices varied significantly from 37.3 to 82.8 $(56.6 \pm 10.9, n = 58)$, suggesting considerable spatial heterogeneity in Lake Taihu (Figure S1b). Specifically, Xuhu Bay $(42.1 \pm 1.5, n = 3)$, Eastern Taihu Bay $(44.4 \pm 4.7, n = 6)$, and the Southern region (48.2 \pm 6.2, n = 11) were mesotrophic, though four sampling sites (E2, S9-S11) had high trophic state indices (51.2-58.1). Most sites in Gonghu Bay $(55.5 \pm 8.6, n = 7)$, Lihu Bay $(56.2 \pm 3.8, n = 3)$, Zhushan Bay $(60.9 \pm 7.2, n = 6)$, Lake center $(63.4 \pm 5.4, n = 10)$, Meiliang Bay (64.2 \pm 8.0, *n* = 5), and the Western region (68.6 \pm 11.7, n = 7) were eutrophic. Seven sites in Gonghu Bay (G6), Lake center (LC3), Meiliang Bay (M2, M4), and the Western region (W3, W5, and W7) were hypertrophic.

3.2. Characteristics of OM Pools in the Three Lake Subsystems. Nonsignificant changes in SR were observed in the DOM and POM pools, while SR in SOM increased by 12.3% from mesotrophic to eutrophic states (p < 0.01; Figure S3). High a(350) in DOM and POM occurred in the hypertrophic state, but not in SOM (Figure S3). Moreover, a(350) significantly correlated with the trophic state index in

DOM ($R^2 = 0.23$, p < 0.001, n = 49; Figure S4a) and in POM ($R^2 = 0.15$, p = 0.006, n = 42; Figure S4b).

Four PARAFAC-derived components were extracted from the EEM data sets (Figures S5 and S6). Component 1 (C1) is characterized by a peak at Ex/Em of 280/318 nm and is assigned to tyrosine-like substances.²¹ Component 2 (C2) is similar to a microbial reworked humic-like fluorophore or products of microbial degradation,²¹ showing broad Ex and Em spectra with peaks at <250 and 416 nm, respectively. Component 3 (C3, Ex/Em = 280/354) is identified as protein-like substances. Component 4 (C4, Ex/Em = (270, 370)/460) represents terrestrial humic-like substances with a high molecular size and is composed of highly aromatic compounds.³⁵ The total content of DOM or POM elevated rapidly with the trophic state (Figure 2a,b), and both were positively related to the trophic state index (DOM vs $\Sigma T_{LI,j\nu}$



Figure 2. Changes in the content of EEM-PARAFAC-derived components in DOM (a), POM (b), and SOM (c) pools under a gradient of trophic states. Total OM is the sum of four EEM-PARAFAC-derived components (C1-C4) in different OM pools.

 $R^2 = 0.15$, p = 0.003, n = 49; POM vs $\sum T_{LI,p}$, $R^2 = 0.55$, p < 0.001, n = 42; Figure S4a,b). Protein-like C3 and humic-like substances (C2 and C4) in the DOM increased with the trophic state, while the levels of tyrosine-like substances (C1) remained largely unchanged (Figure S7a). In POM, tyrosine-and humic-like substances were great at high trophic states, whereas protein-like C3 showed stability (Figure S7b). Overall, the trophic state caused slight shifts in the fluorescent compositions of DOM and POM pools (Figure S7a,b), and nonconsiderable changes existed in SOM content and composition (Figures 2c and S7c). Despite this, a positive relationship between total SOM content and the trophic state index existed ($R^2 = 0.03$, p = 0.05, n = 119; Figure S4c).

3.3. Characteristics of P Fractions in SPM and Sediments. The P concentration in total SPM increased remarkably in eutrophic waters (Figure S8a). Relationships between particulate P concentration and the trophic state index depended on P species and size sorting (Figure 3a). In SPM, mobile P fractions (NH₄Cl-P and Fe/Al-P) positively correlated with the trophic state index ($R^2 > 0.23$, p < 0.001, n= 42), while refractory P fractions (Ca-P and Re-P) did not vary ($R^2 < 0.06$, p > 0.07, n = 42). NH₄Cl-P of the large particles (>100 μ m) dominated that of the total particles (>80%) and elevated faster than that of the small particles (<100 μ m). In contrast, the small particles contained more Fe/ Al-P (>60% of the total particles) than the large particles at high trophic states. Eutrophication also altered particulate P composition, indicated by the percentages of different P species (Figure 3a). In the total SPM, the trophic state index negatively correlated with Ca-P% ($R^2 = 0.14$, p = 0.008, n =42) and Re–P% ($R^2 = 0.12$, p = 0.02, n = 42). Similarly, Ca–P % in the large particles declined remarkably with the trophic state index ($R^2 = 0.15$, p = 0.006, n = 42). Variation was not noted in the P composition of the small particles ($R^2 < 0.01$, p > 0.28, n = 42).

The effects of the trophic state on P pools in sediments depended on P species and sampling depth (Figure 3b), although the total content of sediment P did not significantly change (Figure S8b). Specifically, Fe/Al-P content lifted rapidly at both the surface ($R^2 = 0.11$, p = 0.024, n = 38) and up-mid ($R^2 = 0.10$, p = 0.04, n = 34) sediments. Fe/Al-P% in the surface sediments correlated with the trophic state index ($R^2 = 0.14$, p = 0.013, n = 38). In contrast, Ca-P% in the surface was reduced at high trophic states ($R^2 = 0.12$, p = 0.017, n = 38).

3.4. Environmental Factors Affecting OM and P Pools. In the DOM pool, samples from different trophic states were separated by the first two PCA axes, which explained 59.5% of the variation (Figure S9a). DOM species, especially C2, C4, and a(350), positively contributed to the second axis, while SR and a(250):a(365) showed negative contributions. DOM content was significantly linked to the trophic state index (Mantel's r > 0.3, p < 0.01), nitrogen (Mantel's r > 0.2, p < 0.05), Chl a (Mantel's r > 0.3, p < 0.01), TP (Mantel's r > 0.2, p < 0.05), and turbidity (Mantel's r > 0.2, p < 0.05), whereas DOM composition was related to nitrogen concentrations (Mantel's r > 0.2, p < 0.01; Figure 4a). Samples in the POM pool were also clearly separated by the first PCA axis, which contributed to 44.6% of the total variation, which was mainly attributed to the POM concentration (Figure S9b). POM composition contributed to the second PCA axis, which explained 29.7% of the total variation. This was consistent with the Mantel test, showing that trophic state (Mantel's r > 0.1, p



Figure 3. Changes in the content and composition of P fractions in SPM (a) and sediments (b) under a gradient of the trophic state index.

< 0.05) affected both POM concentration and composition (Figure 4b). The PCA plots failed to distinguish the SOM samples collected from different trophic states (Figure S9c). Correlations between the total SOM content and environmental factors were not found (Figure 4c). However, SOM content in the surface sediments significantly correlated with the trophic state index (Mantel's r > 0.1, p < 0.05; Figure S10a), while SOM contents in the up-mid sediments and the deep sediments were related to DFS and pH, respectively (Mantel's r > 0.1, p < 0.05; Figure S10b,d). Sampling depth (Mantel's r > 0.1, p < 0.01) and nitrogen concentrations in the overlying water (Mantel's r > 0.1, p < 0.05) determined SOM composition (Figures 4c and S10b,d).

In SPM, P concentrations in the hypertrophic state differed from those in the mesotrophic state owing to differences in NH₄Cl-P and Fe/Al-P concentrations (Figure S9d). Regardless of the size sorts, P content in SPM was determined by the trophic state (Figures 4b and S11), directly relating to Chl *a* (Mantel's r > 0.5, p < 0.01), turbidity (Mantel's r > 0.3, p< 0.01), and nutrients in the overlying water (Mantel's r > 0.3, p < 0.01). Trophic state (Mantel's r > 0.1, p < 0.05) and DTP concentration (Mantel's r > 0.1, p < 0.05) affected the particulate P composition (Figure 4b), although such relationships disappeared in each size sort (Figure S11). Similar to the SOM, P pools in the sediments did not separate under the trophic state (Figure S9e) but significantly relied on sampling depth (Mantel's r > 0.1, p < 0.01; Figure 4c). Nitrogen (DTN and NH₄-N) and DFS were the major factors affecting P pools in the surface and mid-late sediments (Mantel's r > 0.1, p < 0.05; Figure S10a,c).

3.5. Interactions among the Three Lake Subsystems for OM and P Exchanges. The interaction between water and SPM (W–P interaction) increased remarkably at high trophic states in both OM ($R^2 = 0.56$, p < 0.001, n = 36) and P pools ($R^2 = 0.46$, p = 0.003, n = 15). Specifically, the effect size

of the W–P interaction increased by almost three times from mesotrophic to hypertrophic states in both OM and P pools (Figure 5). The average effect sizes for the P pool were 0.25, 0.39, and 0.69 in the mesotrophic, eutrophic, and hypertrophic states, respectively (Table S3). Eutrophication promoted the interaction between sediments and SPM (S–P interaction) as well, especially considering the OM pools ($R^2 = 0.44$, p < 0.001, n = 36; Figure 5a). However, nonsignificant changes in the interaction between water and sediments (W–S interaction) were existed considering both OM ($R^2 < 0.01$, p = 0.51, n = 36) and P pools ($R^2 = 0.08$, p = 0.16, n = 15).

4. DISCUSSION

Eutrophication affects lake ecosystems completely, but few studies have simultaneously integrated dissolved, particulate, and sedimentary phases concerning OM and P pools to understand the underlying mechanisms of lake state shifts. Our results demonstrated that eutrophication dramatically affected both OM and P pools in Lake Taihu, especially in the dissolved and particulate subsystems. The interaction patterns between the subsystems varied with the trophic states.

4.1. Effects of Eutrophication on the Three OM Pools. Nutrient enrichment often boosts phytoplankton growth, especially the formation of harmful cyanobacterial blooms in lakes.¹ This could cause the DOM and POM to sharply increase with the eutrophication process (Figures 2a,b and S4a,b) and the positive relationships between Chl *a* and the two OM pools (Figure 4a,b). Similar patterns showed high DOM concentrations with cyanobacterial blooms in Lake Taihu and eutrophic saline lakes.^{21,36} Specifically, eutrophication promoted the concentrations of humic acid-like substances (i.e., C2 and C4) in both OM pools (Figure S7a,b), similar to the observations of high humic-DOM pools in eutrophic waters.⁸ The accumulation of humic substances may be due to allochthonous DOM overloading from sewage



Figure 4. Mantel tests of the relationships among OM and P pools, the trophic state index $(\sum T_{LL_j})$, nutrients (TN, DTN, NH₄–N, TP, DTP, TOC, and TN:TP ratio), phytoplankton biomass (Chl *a*), suspended particle size (PS), water physicochemical parameters (turbidity and pH), sampling depth, and the distance of sampling site from the shore (DFS). The tested OM and P pools included dissolved (a), particulate (b), and sedimentary (c) phases.



Figure 5. Effects of eutrophication on the interactions of water, SPM, and sediments concerning OM (a) and P pool (b) exchanges. S–P, W–P, and W–S indicate the interactions between sediments and SPM, water and SPM, and water and sediments, respectively.

discharge and autochthonous DOM, such as carboxylic-rich alicyclic compounds (CRAMs) from microbial degradation of algal-derived OM.³⁷ The dominant cyanobacterial species in the eutrophic regions of Lake Taihu was *Microcystis*, which can secrete soluble EPS with abundant proteins,^{14,38} presumably surging the protein-like C3 content in DOM at high trophic states (Figure S7a).

Eutrophication appeared to slightly affect the compositions of DOM and POM pools, considering the spectral parameters (Figure S3) and the fluorescent component percentages (Figure S7a,b), although the trophic state index was related to POM composition (Figures 4b and S9b) and DOM molecular formulas.³⁷ Nitrogen concentrations (TN, DTN, and NH₄-N) were the major factors affecting DOM composition (Figure 4a), presumably owing to the strong nitrogen limitation in the eutrophic bays of Lake Taihu during summer and fall.³⁹ Nitrogen limitation can remarkably increase proteinous compounds in the soluble EPS of Microcystis colonies.^{38,40} This is consistent with the increased protein-like C3% in DOM with the trophic state (Figure S7a). Attached bacteria can rapidly decompose algal-secreted proteinous matter and synthesize humic-like substances,²¹ which might be responsible for the high humic-like and low protein-like substances in POM at eutrophic states (Figure S7b). In addition, as EPS content and composition were strainspecific,⁴¹ eutrophication-induced changes in the dominant species of the phytoplankton community could also shape OM properties directly.

Sedimentary OM accumulation can indicate historical eutrophication in lakes.⁴² Eutrophication often promotes OC preservation and burial in the lakebed through DOM and POM deposition and their aerobic catabolism,¹⁰ which affects the SOM content and composition. However, we found only a weak relationship between the total SOM content and the trophic state index in Lake Taihu (Figure S4c). The SOM content and composition were comparable in all of the sediment cores regardless of the trophic state (Figures 2c and S7c). Sampling depth rather than trophic state determined the SOM composition in the sediment cores (Figure 4c). The low sensitivity of fluorescent EEM and spectrum techniques for OM chemistry²⁴ presumably underestimated eutrophication's effects on the SOM pools. For example, the EEM techniques are disabled to detect nonfluorescent matters, such as hydroxylic-rich polysaccharides, which are dominant compounds in cyanobacterial EPS (>75% DW).⁴⁰ Such hydroxylicrich compounds were frequently found in the sediments during cyanobacterial blooms.9 More importantly, the low sensitivity of the SOM pools to the trophic state might be attributed to the history of the eutrophication process in Lake Taihu. Before 1960, Lake Taihu was oligotrophic, followed by mesotrophic in 1981, and the northern bays of this lake entered the eutrophic state after 1987.43 The sediment depth in the northern bays of this lake was estimated to accumulate approximately 7-10 cmsince the beginning of eutrophication.⁴⁴ This suggests that eutrophication might merely affect the SOM pool in the surface layers (<10 cm) rather than the whole tested sediment cores (0-20 cm). Our observations confirmed that the SOM content in the surface sediments (0-5 cm) was significantly related to the trophic state index (Figure S10a), which is consistent with the high burial rates of organic carbon in eutrophic lakes.9,10

4.2. Effects of Eutrophication on P Fractions in SPM and Sediments. Eutrophication affected the P concentration and composition in the SPM (Figure 4b). The P concentration in the total SPM increased with the trophic state elevation (Figure S8a), which was mainly due to the increase of Chl a concentration or phytoplankton biomass (Figure 4b). In eutrophic lakes, most of the P content in SPM was inorganic P, such as orthophosphate.¹⁵ Our results confirmed that the concentration and percentage of the labile P forms in SPM increased sharply at high trophic states (Figure 3a), owing to the marked increase in NH₄Cl-P in the large SPM, which mainly consisted of Microcystis colonies in the eutrophic areas (Figure S12a). Colonies of Microcystis have a great capacity to adsorb orthophosphate stored in their EPS¹⁷ through complexing with quaternary ammonium of the EPS-contained proteins⁴⁵ or combining with EPS-contained humic substances by the bridging effect of metal ions.¹⁸ Inorganic P also exists in *Microcystis* cells, such as orthophosphate, pyrophosphate, and polyphosphate.^{15,46} Both extracellular and intracellular stores of labile P in Microcystis colonies might contribute to the increase in NH₄Cl-P in the large particles at a high trophic state. In contrast, the larger particles in the eastern bays with lower trophic states (e.g., Xuhu Bay and Eastern Taihu Bay) were dominated by aquatic plant fragments coupled with a small portion of green algae (e.g., Volvox) and microbial aggregates (Figure S12b). These particles contained lower labile P fractions.47 Eutrophication also promoted the concentration of Fe/Al-P in the SPM regardless of the particle size (Figure 3a). The extracted Fe/Al-P also included the fraction of organic $P(P_0)$ compared to Rydin's extraction method,³⁴ although P_o was not explicitly identified here.² Therefore, the high Fe/Al-P in SPM presumably resulted from the accumulation of cyanobacterial OM and cyanobacterial debris, as P_o accounted for approximately 45% of the extracted total content of P in cyanobacterial aggregates.¹⁷ Our results demonstrated that eutrophication promotes the

concentration of mobile P in SPM (Figure 3a), which may sustain cyanobacterial blooms after they are released or reproduced through concentration gradient diffusion, redox conditions, or microbial degradation.²⁷

The percentage of Ca-P in SPM, particularly in the large particles, reduced with the trophic state increase, while there were no significant changes in the concentrations of Ca-P and Re-P (Figure 3a). The Ca-P extracted by HCl was assumed to consist of P-calcite compounds likely deriving from the transformation of calcite into apatite or hydroxyapatite after P combination.^{26,48} Coprecipitation of Ca and P through calcite crusts in submerged macrophytes⁴⁹ might be responsible for the high Ca-P% in SPM under low trophic states. Cyanobacteria such as Synechocystis sp. PCC7942 could also induce the formation of calcite precipitation in hard-water lakes or under high Ca²⁺-treated cultures in the laboratory.⁵⁰ However, Microcystis often demands abundant Ca2+ to link their negatively charged EPS molecules for forming large colonies,⁵¹ perhaps reducing the Ca²⁺ concentration in the ambient water and the following production of apatite.⁴⁹ This coincides with the low Ca-P contents (<1% of the total cellular P) in Microcystis colonies.⁴⁶ Our findings suggested that eutrophication hindered the formation of inert P fractions in SPM, especially the Ca-P fraction (Figure 3a), which may slow the sinking and sedimentation rates of P, thus retaining more P in ambient water and consequently sustaining cyanobacterial blooms.

Like the SOM variation, P content and composition in the whole sediment cores depended on sampling depth rather than the trophic state (Figures 4c and S8b). According to the history of Lake Taihu mentioned above, eutrophication might merely affect P pools in the surface sediments (0-10 cm), where we indeed found converse trends in Fe/Al-P% and Ca-P% responding to the increase in trophic state (Figure 3b). Previous observations also showed high mobile P fractions (including Fe/Al–P) in the sediments of eutrophic lakes, but high Ca-P in oligotrophic and mesotrophic lakes.^{20,47} The high sedimentary Ca-P% in mesotrophic states has been attributed to the macrophyte-derived transformation of mobile P (especially Fe/Al–P) into the inert P fractions because high Ca²⁺ concentrations in the porewater existed, facilitating the formation of Ca-P precipitation.^{48,52} In this study, we found consistent Fe/Al-P and Ca-P patterns in both SPM and sediments (Figure 3), which suggests that SPM deposition could be a prominent mechanism in constructing sedimentary P pools.⁴⁷ In eutrophic regions, for example, the deposition of cyanobacterial aggregates and their debris to the lake bottom might be responsible for the high sedimentary Fe/Al-P%, as both contained large amounts of mobile P fractions (Figure 3). In contrast, abundant P-calcite crusts in submerged macrophytes and their debris could support the high sedimentary Ca-P% at the mesotrophic sites when they settled into the sediments. The relative contributions of the pathways to the distribution patterns of Fe/Al-P and Ca-P in the surface sediments require further estimates.

4.3. Effects of Eutrophication on Interactions between Lake Subsystems: Implications for Internal Nutrient Loading. Internal nutrient cycling significantly contributes to sustaining cyanobacterial blooms in eutrophic lakes. For example, internal P release contributed 23–90% of the P demand of cyanobacterial blooms in Lake Taihu.³⁹ Internal nutrient release normally includes SPM and sediment sources, and the sediment nutrient release can be further

divided into sediment resuspension and nutrient diffusion at the SWI. However, quantifying the processes of the internal nutrient loading in a whole lake system is quite difficult. To achieve a quantitative estimate on each pathway, a "3subsystem" interaction conceptual model was employed in the current study (Figure 1). Based on the conceptual model hypothesis, the main processes of internal nutrient loading (i.e., SPM release, sediment resuspension, and sediment nutrient diffusion) are inherently related to the model-derived interaction intensities among the dissolved, particulate, and sedimentary phases.

Specifically, our data showed that eutrophication significantly enhanced the interaction intensity between dissolved and particulate phases, indicated by both the OM and P pools (Figure 5). This suggested that SPM release was the most important source of internal nutrient loading, perhaps through physicochemical desorption/dissolution of labile P and microbial degradation of P_o from algal-derived OM.¹⁵ Cyanobacteria and macrophyte debris functioned as predominant internal sources of SPM in Lake Taihu, dominating in eutrophic and mesotrophic zones (Figure S12), respectively. Cyanobacterial debris typically underwent rapid degradation within approximately 2–7 days,⁵³ whereas macrophyte debris degradation proceeded over substantially longer time scales (>50 days).⁵⁴ This rapid degradation of cyanobacterial debris facilitates the release of dissolved nutrients and labile organic matter, ultimately enhancing the biogeochemical cycling rates of essential elements in eutrophic zones.

We also found an increased interaction between particulate and sedimentary phases in both pools under high trophic states (Figure 5). Prior investigations in Lake Taihu demonstrated significantly elevated SPM deposition rates within eutrophic regions. Annual mean deposition rates (April 2018-March 2019) reached 426.6 \pm 281.8 g dw m^{-2} d^{-1} in eutrophic regions versus 58.0 \pm 75.9 g dw m⁻² d⁻¹ in mesotrophic regions.⁹ Wind-induced sediment resuspension occurred frequently in the eutrophic bays of this large shallow lake.¹⁴ Abundant cyanobacterial debris or undigested cyanobacterial residues (such as polysaccharides and lipids) accumulated on the surface of the sediments in the eutrophic bays, such as Zhushan Bay and Meiliang Bay.^{34,55} These cyanobacterial leavings had low mass densities (~1.4 g $\rm cm^{-3})$ and were easily resuspended under wind disturbances,56 which might imply the significant contribution of sediment resuspension to internal nutrient cycling in the eutrophic areas of Lake Taihu. In comparison, the sediments were covered by bushy macrophytes in the mesotrophic regions of this lake, such as Xuhu Bay and Eastern Taihu Bay,⁹ preventing wind-induced resuspension of the surface sediments.

In contrast to what we expected, eutrophication did not result in significant changes in the interaction between the dissolved and sedimentary phases from mesotrophic to hypereutrophic states in both OM and P pools (Figure 5). This suggests similar nutrient diffusion intensities between dissolved and sedimentary phases or comparable diffusion effects of the dissolved nutrient species (e.g., SRP) at the SWI, regardless of the lake trophic state. The P species determination also showed comparable labile P contents in the surface sediments under different trophic states (Figure 3b). A field investigation observed comparable SRP fluxes across the SWI in mesotrophic (i.e., Eastern Taihu Bay) and eutrophic (i.e., Zhushan Bay) areas of Lake Taihu.⁴⁷ Moreover, sediment incubation experiments confirmed a higher TP flux at

the SWI in mesotrophic Eastern Taihu Bay (4.83 mg m⁻² d⁻¹) than those in eutrophic areas, such as Meiliang Bay (0.05 mg $m^{-2} d^{-1}$) and Gonghu Bay (-0.2 mg $m^{-2} d^{-1}$).²⁰ In the macrophyte-dominated areas, traditional Fe-P dissolution processes coupled with sulfur cycling generally control the P release at the SWI.⁵⁷ High reduced sulfur concentrations have been observed in these areas,⁴⁷ which might compete with the iron from Fe-P complexes by forming iron sulfides and lead to P release.⁵⁷ In addition, compared with the eutrophic areas, the lower concentrations of P in the overlying water created a greater diffusion gradient at the SWI in the mesotrophic areas, which could contribute to the high P fluxes. These together confirmed that the intensity of direct nutrient diffusion at the SWI was weakly related to the trophic state and thus might not play a determining role in internal nutrient release. Therefore, eutrophication may retain more nutrients, such as P in the water column via SPM release and sediment resuspension rather than direct nutrient diffusion at the SWI. This suggests that ecological restoration measures in eutrophic shallow lakes should strive to reduce SPM release and sediment resuspension (e.g., cultivating aquatic macrophytes, 58,59 in situ remediation techniques of sediments,⁶⁰ lake bottom trap technology to capture nutrient-rich sediments,^{61,62} etc.) for a low level of internal nutrient loading.

Our results demonstrate how OM and P pools respond to eutrophication in the shallow lake by simultaneously characterizing the chemical contents of both pools in water, the SPM, and sediments in Lake Taihu. Through the "3-subsystem" interaction conceptual model, we established a quantitative methodology for assessing intersubsystem interactions via analyses of both OM and P pool dynamics. Our findings confirm that eutrophication dramatically enhanced the interactions of lake subsystems, except for negligible changes in the interaction between dissolved and sedimentary phases. This offers new insights into the potential pathways of internal nutrient cycling across a gradient of lake trophic states. Notably, these patterns were derived from a single-sampling campaign data set that did not incorporate temperature variables, suggesting the need for future investigations addressing seasonal variation. Nevertheless, our findings represent a significant advance in understanding the underlying mechanisms of trophic shifts in lake ecosystems, particularly in shallow lakes.

ASSOCIATED CONTENT

Data Availability Statement

The data are available from the corresponding author upon reasonable request.

Supporting Information

The Supporting Information is available free of charge at https://pubs.acs.org/doi/10.1021/acs.est.4c12091.

The SPM fractioning method, the determination method of trophic states, quantitative assessments of interaction intensities between subsystems, a summary of sample types, variation of environmental factors, correlation coefficients between interacting phases, a map of sampling sites, variation of water temperature, optical parameters of OM pools, the relationships between the trophic state index and OM pools, sum of squared error of the EEM-PARAFAC model, PARAF-AC-derived components, P contents in suspended particles and sediments, PCA analysis of OM and P

pool dynamics, Mantel tests of the relationships between environment and SOM or sedimentary P or particulate P, microphotographs of the large suspended particles (PDF)

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Z.D.: conceptualization, investigation, data curation, funding acquisition, writing-original draft, writing-review and editing. J.L.: data curation, writing-review and editing. L.S.: investigation. Y.X.: investigation. W.G.: investigation. X.T.: writing-review and editing, funding acquisition, supervision.

Notes

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The authors declare no competing financial interest.

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