

Impacts of cyanobacterial blooms outbreak and decline on Feammox in the sediments of Taihu Lake*

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Abstract Microbial mediated anaerobic ammonium oxidation coupled to ferric iron reduction (Feammox) represents a potentially crucial nitrogen removal pathway in eutrophic lakes. However, its response to cyanobacterial blooms in sediment environments remains unclear. In this study, the microcosms containing fresh cyanobacteria particles were cultured under natural conditions, and techniques of X-ray absorption fine structure spectrum (XAFS), high-throughput sequencing, and ^{15}N isotope tracing were utilized to examine the impacts of outbreak and decline of cyanobacterial bloom on the iron forms, iron-reducing bacteria (FeRB) and Feammox potential rates in the surface sediment. The XAFS results revealed that cyanobacterial blooms promoted the formation of FeOOH , which theoretically favors Feammox. Surprisingly, the potential rate of Feammox was significantly suppressed during the active bloom phase compared to the control ($P < 0.05$), likely due to the inhibition of FeRB growth under bloom-induced high dissolved oxygen and alkaline conditions, as evidenced by a lower relative abundance of FeRB. In contrast, after an 80-d cultivation under natural conditions, the degradation of cyanobacteria led to substantial accumulation of hydrochloric acid-extractable Fe(III) , humic acid, along with a recovery in the relative abundance of FeRB, resulting in a significantly increase in the potential Feammox rate. These findings demonstrate that cyanobacterial blooms modulate sediment Feammox activity in opposite directions during distinct phases of outbreak and decline, by altering key substrates and microenvironments. This study highlights the complex role of cyanobacterial blooms in nitrogen cycling and advances our understanding of ecological nitrogen removal in eutrophic lakes.

Keyword: cyanobacterial bloom; Feammox; iron-reducing bacteria (FeRB); sediment; Taihu Lake

1 INTRODUCTION

Nitrogen, an indispensable element for life, is also a major driver of eutrophication in aquatic environments. In recent decades, the escalating input of anthropogenic reactive nitrogen from agricultural and industrial activities has led to severe eutrophication in numerous rivers and lakes, posing a serious environmental threat worldwide (Akinawo, 2023). Sediments play a dual role in the aquatic nitrogen cycle. They can act as internal sources, in which organic nitrogen undergoes mineralization, and the resulting ammonium diffuses into the water column (Ding et al., 2022b). Conversely, sediments can also function as nitrogen sinks by converting nitrogen in various forms into

nitrogen gas (N_2) through microbial-mediated processes like nitrification-denitrification or anaerobic ammonium oxidation, thereby permanently removing it from aquatic ecosystems (Zhang et al., 2022).

Anaerobic ammonia oxidation coupled to ferric iron [Fe(III)] reduction, known as Feammox, is an innovative microbial nitrogen removal pathway first identified in wetland sediments (Clément et al., 2005). Since its discovery, Feammox has been found in diverse habitats, including activated sludge (Wang et al., 2013), riparian zones (Ding et al., 2017), mangrove sediments (Guan et al., 2019), and

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paddy soils (Ding et al., 2021). In this process, microorganisms oxidize ammonium (NH_4^+) to N_2 , nitrite (NO_2^-), or nitrate (NO_3^-) while reducing Fe (III) under anaerobic conditions. Thermodynamic calculations suggest that the pathway yielding N_2 is more favorable than those producing NO_2^- or NO_3^- (Yang et al., 2012). In persistently anaerobic environments, the generation of NO_2^- or NO_3^- is limited, thereby restricting the conventional nitrogen removal processes such as denitrification or anaerobic ammonium oxidation (Anammox). In this case, Feammox may become the dominant pathway for NH_4^+ removal (Ding et al., 2022a). Therefore, Feammox may have an undeniable role in nitrogen removal within aquatic ecosystems.

Feammox activity is influenced by a range of environmental factors, such as pH levels, redox potential (Eh), and the availability of organic carbon, iron, and nitrogen (Huang et al., 2016). Differences in these factors among various ecosystems lead to varying contributions of Feammox to nitrogen removal. For instance, reported Feammox rates reach 0.48 mg N/(kg·d) in mangrove sediment (Guan et al., 2019), but remain below 0.13 mg N/(kg·d) in the sediments of the Huanghe (Yellow) River wetland (Guan et al., 2023). Vegetation distribution may also have a significant effect on Feammox. Ding et al. (2017) observed higher potential rates of Feammox in soil with vegetation (0.32–0.37 mg N/(kg·d)) than in non-vegetated soil. In contrast, She et al. (2023) reported significantly lower Feammox rates in rhizosphere soil compared to non-rhizosphere soil.

Taihu Lake is the third largest freshwater lake in China, covering an area of 2 338 km². Due to the increase in anthropogenic pollutants caused by human activities, Taihu Lake has been plagued by eutrophication and algal blooms in recent decades (Yan et al., 2024). Every summer and autumn, driven by the southeast monsoon, extensive cyanobacteria accumulate on the water surface of Meiliang Bay. During these blooms, notable diurnal fluctuations in dissolved oxygen (DO) occur in the water column (Chen et al., 2021). Such dynamic oxygen environments, like those in riparian zones and tidal zones, are typically regarded as hotspots for iron-nitrogen coupled cycling (Li et al., 2015; Ding et al., 2017). However, it is currently unclear whether the outbreak and decline of cyanobacterial bloom can enhance Feammox in sediments. On one hand, the organic matters derived from cyanobacterial decomposition can promote the

release of Fe(III) from sediments and act as the electron shuttles to facilitate electron transfer, thereby potentially enhancing the Feammox rate (Yao et al., 2020). On the other hand, the same organic matter may preferentially stimulate dissimilatory Fe(III) reduction, depleting the bioavailable Fe(III) pool for Feammox related microorganisms, and thus suppressing the process (She et al., 2023). To elucidate the precise effects of cyanobacterial blooms on Feammox, changes in iron speciation, microbial community structure, and potential Feammox rates were investigated in a microcosm system consisting of sediments, overlying water, and fresh cyanobacteria particles, using X-ray absorption fine structure spectroscopy (XAFS), high-throughput sequencing, and isotope tracing techniques.

2 MATERIAL AND METHOD

2.1 Sample collection

The sampling was carried out on a sunny day in August 2024. Influenced by the southeast monsoon, substantial cyanobacterial accumulation was observed on the water surface along the western coast of Meiliang Bay. The fresh cyanobacteria particles were accordingly collected using a plankton net at Station 1 (Supplementary Fig.S1). Microscopic examination showed that *Microcystis* comprised up to 97% of the total phytoplankton population in the algal samples (Supplementary Table S1). The mouth of Meiliang Bay, which connects the open lake with the bay proper, serves as a transitional zone where cyanobacteria are transported into the bay by southeast monsoon-driven currents. Monitoring data indicates that the nitrogen content and cyanobacterial density at the entrance of Meiliang Bay are intermediate between those in the central lake and the inner bay (Yin et al., 2023). Accordingly, surface sediments and overlying water were sampled at Station 2 using a Peterson dredge and a water sampler, respectively. All samples were placed in a 4-°C cooler, transported immediately to the laboratory, and processed without delay.

2.2 Experimental design

The sediments were sieved, thoroughly blended, and then loaded into simulation devices to a depth of approximately 10 cm (Supplementary Fig.S2). In-situ overlying water, passed through a 5-μm membrane (Millipore), was gently introduced along

the inner wall of the columns to a height of about 60 cm without disturbing the sediment. To investigate the impact of cyanobacterial bloom on Feammox in sediments, cyanobacterial particles were added to the overlying water to achieve a chlorophyll-*a* (Chl-*a*) content of approximately 250 mg/m³ (Shi et al., 2022). A set of columns without cyanobacterial addition was used as the control. All treatments were performed in triplicate. The columns were fixed in a pond to minimize the effect of high temperatures from direct sunlight on cyanobacterial growth. Throughout the incubation process, the overlying water was regularly replenished to maintain a water level consistent with that of the pond. DO and pH were measured on-site every day at 8 am. After the measurement of the DO, the overlying water was thoroughly mixed, and a 20-mL water sample was collected for Chl-*a* content determination. To ensure that the sediment samples were collected during the cyanobacterial bloom outbreak, surface sediments (0–2 cm) were sampled in the afternoon using a mini column sediment sampler, whenever a significant decrease in Chl-*a* concentration was observed relative to the previous day. A portion of these sediments was used for the determination of the potential rate of Feammox, while the remaining samples were freeze-dried for high-throughput sequencing and XAFS characterization.

To establish a uniform sediment surface and eliminate sampling-induced holes during cyanobacterial blooms, the surface sediment was rehomogenized. This mixed condition of cyanobacteria and sediment also simulated the natural wind-wave mixing observed in Taihu Lake. After homogenization, the microcosms were maintained in the pond to examine the impact of cyanobacterial degradation on Feammox processes within surface sediments. Given that the microcosms were closed systems, the overlying water could not exchange O₂ with the surrounding water body in the absence of wind and wave disturbances, leading to prolonged anaerobic conditions in the cyanobacteria-amended treatments. To address this, aeration was provided for 2 h daily above the sediment-water interface. On rainy days, transparent acrylic covers were used to shield the system from the impact of atmospheric wet deposition. To ensure complete degradation of cyanobacteria, the incubation period was set to 80 d (Chen et al., 2025). At the end of the incubation, surface sediment samples (0–2 cm) were collected for the analysis of pH, total organic carbon (TOC),

humic acid-like substances, and hydrochloric acid-extractable Fe(II) and Fe(III) contents. High-throughput sequencing and isotope tracing methods were also utilized to investigate the bacterial community structure and sediments Feammox potential, respectively.

2.3 DNA extraction and PCR amplification

DNA was extracted from sediment samples using the E.Z.N.A.[®] Soil DNA Kit (Omega Bio-tek, Norcross, GA, U.S.). Subsequently, the V3–V4 region of the 16S rRNA gene within the extracted DNA was amplified via PCR for high-throughput sequencing, employing the primer pair 338F and 806R. Sequencing and analysis were performed by Shanghai Biozeron Biotech Co., Ltd.

2.4 XAFS measurement

The freeze-dried sediments were ground in a nitrogen glove box and sealed with Kapton tape to prevent air oxidation for XAFS measurement. Fe *K*-edge XAFS measurements were performed at beamline BL20U of the Shanghai Synchrotron Radiation Facility (SSRF) in China, which operates a 3.5-GeV storage ring in a top-up mode with a constant current of 300 mA. The resulting X-ray beam was then monochromatized using a Si (111) double-crystal monochromator, which was calibrated using a Fe foil before the measurements. A 30% detuning of the monochromator was implemented to eliminate higher-order harmonics. Three scans were collected for each sample in the fluorescence mode using a Lytle detector. Data processing and curve-fitting were performed using the ATHENA and Artemis modules implemented in the IFEFFIT package, respectively.

2.5 Measurement of potential rate of Feammox

The potential rate of Feammox was determined following the method of Ding et al. (2021). In brief, surface sediments were mixed with sterile, helium-purged deionized water at a ratio of 1:3 to form a homogeneous slurry. Twelve grams of this slurry were weighed into a 140-mL serum bottle, followed by the addition of 80 mL of anaerobic deionized water. After purging with helium for 20 min, 0.14-mL 0.1-mol/L ¹⁵N-NH₄Cl solution was added. The bottle was then filled completely with anaerobic deionized water and immediately sealed. Incubation was carried out for 24 h in the dark inside an anaerobic glove box. Afterwards, microbial activity was terminated by injecting 0.1 mL of 7-μmol/L

ZnCl₂ solution. The concentrations of ²⁹N₂ and ³⁰N₂ were quantified utilizing a Membrane Inlet Mass Spectrometer (MIMA-200, Bay Instruments, USA), and the production rate of ³⁰N₂ was taken as the potential rate of Feammox (Yang et al., 2012).

2.6 Analysis of physicochemical properties of overlying water and sediments

Five grams of sediment were weighed and dried to constant weight at 60 °C, and the moisture content of the sediment was determined by the mass difference method. The TOC content in the air-dried and sieved sediment was measured using a TOC-6000 Total Organic Carbon Analyzer (Shimadzu, Japan). The concentration of Chl *a* was determined by spectrophotometry after extraction with acetone. The concentration of nitrate, nitrite, and ammonia were measured using ultraviolet spectrophotometry, diazotization-coupling spectrophotometry, and salicylate spectrophotometry, respectively. The pH and DO in the overlying water were measured using a multi-parameter analyzer (Hach HQ40D, USA). Following the method of Lai et al. (2025), the sediment pH was measured with a pH meter (INESA, China) in a slurry prepared by mixing freeze-dried sediment with CO₂-free deionized water at a ratio of 1:2.5 (g/mL). The active Fe(II) and Fe(III) in the sediment were determined by the orthophenanthroline spectrophotometric method after extraction with 0.5-mol/L HCl solution (Ding et al., 2017). Humic acid-like substances were extracted using a mixed solution of 0.1-mol/L sodium pyrophosphate and 0.1-mol/L sodium hydroxide, purified by acid precipitation and alkali dissolution, and the three-dimensional fluorescence spectra of the humic acid-like substances were measured using a Hitachi fluorescence spectrophotometer (F-7000, Japan).

2.7 Statistical analysis

The data were processed and analyzed using SPSS 18.0 software. Pearson correlation coefficient analysis and one-way analysis of variance (ANOVA) were employed to assess the correlation or differences in physicochemical properties and Feammox potential rates among different treatment groups.

3 RESULT

3.1 Effect of algae bloom and decline on the speciation and content of iron in Taihu Lake sediments

On day 4 of the experiment, the Chl-*a*

concentration decreased from 260.9±9.3 mg/m³ the previous day to 221.9±28.8 mg/m³ (Supplementary Fig.S3), indicating the onset of cyanobacterial decline. In light of this change, and to ensure the collected samples represented the algal bloom period, samples from the treatment (T_{4d}) and control (C_{4d}) groups were collected that afternoon. The valence state and coordination environment of iron in these samples were then assessed using XAFS spectroscopy. Wavelet transform (WT) EXAFS analysis showed that the *R*/*k*-values corresponding to the first neighboring peak of T_{4d} and C_{4d} were close, both exhibiting peak positions at around *R*=1.5 Å/*k*=4.9/Å, which is a typical characteristic of O coordination (Supplementary Fig.S4). Comparison of the Fe *K*-edge XANES spectra of the sediments with those of numerous standard substances indicates that amorphous FeOOH and/or Fe₂O₃ may be the main species of Fe(III) in the sediments (Fig.1a). To quantify the proportions of FeOOH and Fe₂O₃ species in the sample of T_{4d}, linear combination fitting (LCF) of the XANES spectrum was conducted. It turned out that amorphous FeOOH is the dominant species of Fe(III) in the sediment, accounting for a percentage of approximately 90% (Supplementary Fig.S5). The XANES peak shapes of T_{4d} and C_{4d} are basically the same, but there are differences in the peak intensities in the EXAFS spectra (Fig.1b). For both T_{4d} and C_{4d} samples, the quantitative least-squares EXAFS curve-fittings were conducted, with the extracted structural parameters summarized in Table 1.

The obtained coordination number (*N*) and bond length (*R*) of the Fe-O bonds in T_{4d} and C_{4d} were used to estimate the difference of the Fe valency according to valence bond theory (Brese and O'Keeffe, 1991). Following this theory, the formal valence *V* of Fe is relevant to *N* and *R* by (Brese and O'Keeffe, 1991):

$$V = N \cdot e^{\frac{R_0 - R}{B}}, \quad (1)$$

where *B*=0.37 Å and *R*₀=1.759 Å or 1.734 Å for Fe(III)-O and Fe(II)-O bonds, respectively. For the T_{4d} sample, using the parameters *N*=5.8 and *R*=1.998 Å from Table 1 and setting *R*₀=1.759 Å (for Fe(III)-O), Eq.1 yields a formal valence of 3.04, which is consistent with the Fe(III) valence state. Conversely, if we hypothetically assume Fe to be primarily in the Fe(II) state and apply *R*₀=1.734 Å (for Fe(II)-O) with the same *N* and *R* values, the calculated

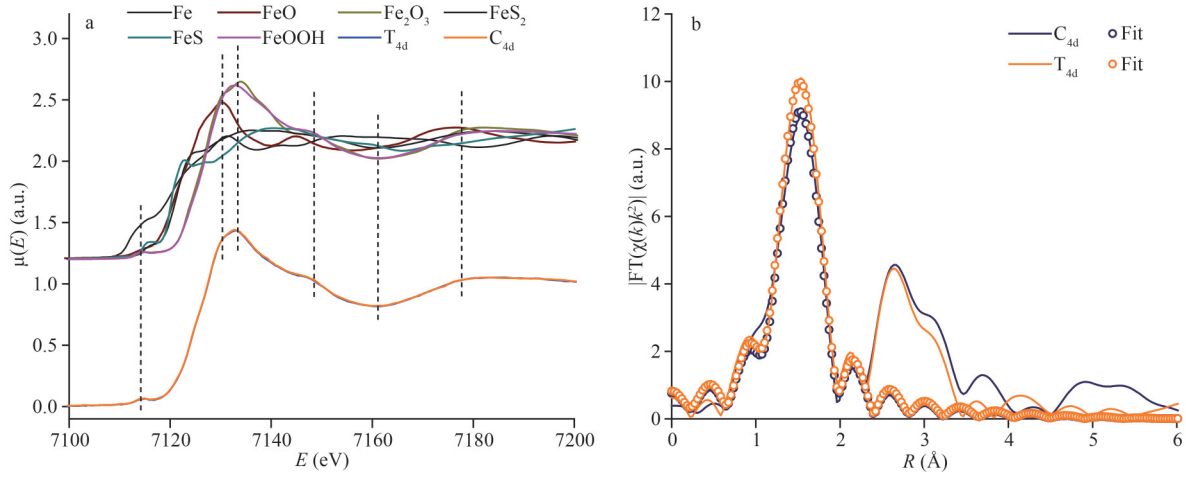


Fig.1 Normalized XANES spectra (a) and the FT curves of the k^3 -weighted $\chi(k)$ functions (b) for T_{4d} and C_{4d}

In (b), the solid lines and open circles represent the experimental data and fitting curves, respectively.

Table 1 Structure parameters of Fe-O bonds extracted from quantitative curve-fittings of the Fe K -edge EXAFS data

Sample	Coordination	N	R (Å)	σ^2 (10^{-3}Å^2)	ΔE_0 (eV)
C_{4d}	Fe-O	5.5 ± 0.4	1.997 ± 0.007	3.6 ± 0.8	-0.8 ± 0.8
T_{4d}	Fe-O	5.8 ± 0.4	1.998 ± 0.006	3.6 ± 0.8	-0.8 ± 0.8

$V=2.84$ substantially exceeds the expected value of 2, contradicting the Fe(II) assumption. Therefore, the use of the Fe(III)-O R_0 value is validated for the valence bond analysis of our samples.

Next, we use the derivative form of Eq.1, as shown as Eq.2, to estimate the difference of Fe valence in T_{4d} and C_{4d} samples.

$$\frac{\delta V}{V} = \frac{\delta N_{\text{Fe-O}}}{N_{\text{Fe-O}}} - \frac{\delta R_{\text{Fe-O}}}{R} \quad (2)$$

As showing in Table 1, the difference in the Fe-O bond length (R) between the T_{4d} and C_{4d} samples is negligible. According to Eq.2, the lower coordination number in C_{4d} thus implies a lower valence state of Fe. Substituting the $\delta N_{\text{Fe-O}} = -0.3$ (Table 1) and the Fe(III) valence in T_{4d} into the equation, we obtained a valence decrease of $\delta V = -0.18$ for C_{4d} relative to T_{4d} . This means that the average valence of Fe in C_{4d} is 0.18 lower compared to T_{4d} , that is, a certain percentage of Fe atoms in C_{4d} is in the Fe(II) state. The lower valence δV enables us to estimate the Fe(II)/Fe(III) ratio in C_{4d} via a sum-weighted calculation of the average valence. This involves an adjustable parameter p denoting

the percentage of Fe(II) to total Fe atoms through the equation $2 \times p + 3 \times (1-p) = 3 - 0.18$. Solving this equation yields $p = 0.18$, corresponding to an Fe(II)/Fe(III) ratio in C_{4d} of 0.18/0.82.

After 80 d of incubation, the surface sediments in the treatment amended with cyanobacterial particles (T_{80d}) exhibited significant differences in multiple physicochemical properties compared to the control group (C_{80d}) (Table 2). The pH of the sediments of T_{80d} was 7.12, lower than the value of 7.46 of the C_{80d} . Moreover, the contents of hydrochloric acid-extractable Fe(II) and Fe(III) in the sediments of T_{80d} reached 406.1 and 37.0 mg/kg, respectively, both significantly higher than those in C_{80d} ($P < 0.05$). These results suggest that the decline and decomposition of cyanobacteria facilitate the acidification of sediments and the generation of active Fe(II) and Fe(III). In addition, the T_{80d} sediments showed significantly higher contents of nitrate plus nitrite nitrogen ($\text{NO}_x\text{-N}$) and TOC ($P < 0.05$), but lower $\text{NH}_4^+\text{-N}$ content, compared to C_{80d} , which may be attributed to the enhanced ammonia oxidation activity induced by cyanobacteria addition.

Table 2 Physical and chemical properties of the sediments after 80-d cultivation

	pH	TOC (mg/kg)	Fe(II) (mg/kg)	Fe(III) (mg/kg)	$\text{NH}_4^+\text{-N}$ (mg/kg)	$\text{NO}_x\text{-N}$ (mg/kg)
T_{80d}	7.12 ± 0.02	9.52 ± 0.42	406.1 ± 21.1	37.0 ± 7.4	15.3 ± 2.5	22.5 ± 1.5
C_{80d}	7.46 ± 0.04	8.87 ± 0.62	346.4 ± 10.4	16.9 ± 0.9	24.4 ± 1.2	13.9 ± 1.8

3.2 Effect of cyanobacterial bloom and decline on the bacterial community in the sediments

Surface sediments were sampled after 4 and 80 d of incubation for bacterial community structure analysis. A total of 653 983 high-quality sequences were obtained, with an average length of 417 bp. The Shannon-Wiener curves of all samples reached a plateau (Supplementary Fig.S6), indicating that the sequencing depth adequately captured the microbial diversity present. The Divisive Amplicon Denoising Algorithm (DADA2) was used to obtain biological sequences free of amplification and sequencing errors, and these sequences were then taxonomically analyzed using the uclust algorithm, resulting in 6 689 and 8 053 OTUs, respectively, belonging to 44 phyla, 100 classes, 245 orders, 360 families, and 848 genera.

After 4 d of incubation, bacterial communities at the phylum level showed minimal difference between the treatment and control groups, with the dominant phyla being Pseudomonadota, Chloroflexi, Bacteroidota, and Thermodesulfobacteriota. In addition, Acidobacteriota and Actinomycetota were also present in high relative abundance (Supplementary Fig.S7). The relative abundance of Cyanobacteriota in T_{4d} sediments was 6.2%, significantly higher than the 1.2% observed in the C_{4d} , indicating that a portion of cyanobacteria had settled during the incubation process. By day 80, Pseudomonadota, Chloroflexi, and Bacteroidota remained the dominant phyla in all sediment samples, but the relative abundance of Chloroflexi in C_{80d} increased significantly, surpassing Pseudomonadota to become the most dominant phylum. Furthermore, the relative abundance of Cyanobacteriota in T_{80d} was 0.90%,

which was close to that of C_{80d} , indicating that the added cyanobacteria had completely degraded.

At the genus level, *RBG-16-58-14* was the most dominant genus in the surface sediments of both T_{4d} and C_{4d} , with relative abundances ranging from 6.4% to 20.0%. Other genera such as *Malikia*, *Desulfatiglans*, and *Vibrionimonas* were also relatively abundant (Supplementary Fig.S8). Compared to the control group's 0.94%, the relative abundance of *Malikia* in the surface sediment samples of T_{4d} was significantly higher, reaching 7.50%, indicating that the cyanobacterial blooms may favor the growth of this genera. Furthermore, the relative abundance of *Microcystis* PCC-7914 in the sediments of T_{4d} was 3.4%, notably higher than that of other cyanobacteria, which was consistent with the microscopic examination results showing that *Microcystis* was the primary genus among the cyanobacteria added. After 80 d of incubation under natural conditions, although *RBG-16-58-14* remained the dominant genus in the treatment group, its relative abundance had decreased. In addition, the relative abundance of *Malikia* also decreased substantially, while that of *Vibrionimonas* increased to 3.77%. In contrast, the control group (C_{80d}) showed a notable increase in the relative abundances of *RBG-16-58-14* and *Luteitalea*, whereas other major genera remained relatively stable.

3.3 Impact of cyanobacterial bloom and decline on potential Feammox rates in the sediments

Isotope tracing incubation experiments were performed to assess the potential rate of Feammox in the sediments. As shown in Fig.2a, the production rate of $^{30}N_2$ in sediments of T_{4d} was 0.34 mg N/(kg·d),

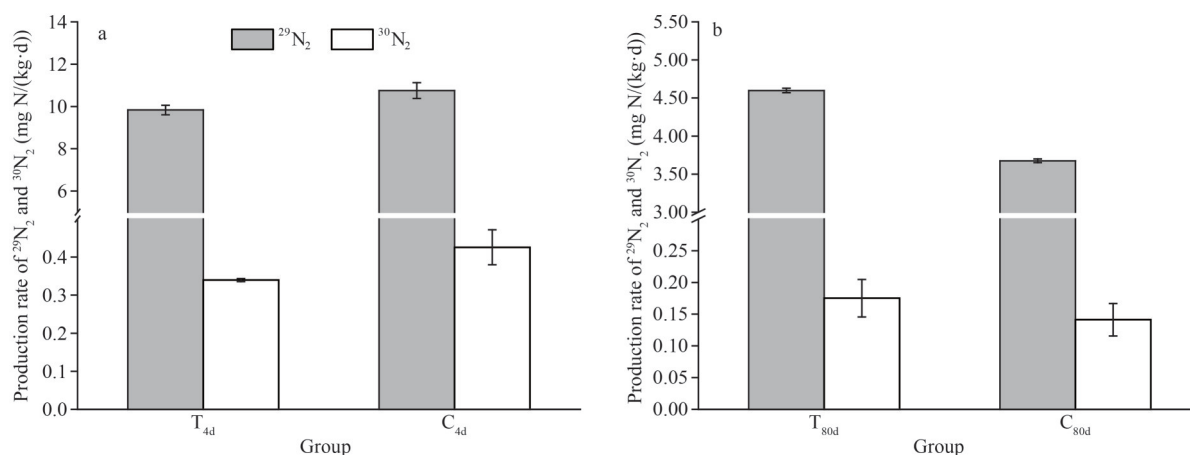


Fig.2 Production rates of $^{29}N_2$ and $^{30}N_2$

significantly lower than that of the control group ($0.43 \text{ mg N}/(\text{kg}\cdot\text{d})$, $P<0.05$), indicating that the environment created by the bloom may have suppressed the Feammox process in the sediments. After 80 d of incubation, the potential rate of Feammox in the surface sediments was much lower than that measured after 4-d incubation. This difference may be attributed to seasonal variations affecting the activity of Feammox bacteria. However, under the same seasonal conditions, the potential rate of Feammox in the surface sediments of $T_{80\text{d}}$ was $0.18 \text{ mg N}/(\text{kg}\cdot\text{d})$, higher than the control value of $0.14 \text{ mg N}/(\text{kg}\cdot\text{d})$ (Fig.2b), suggesting that the decline and decomposition of cyanobacteria likely enhanced the Feammox activity in the sediments.

4 DISCUSSION

4.1 Outbreak of cyanobacterial bloom can inhibit the progression of Feammox

Prior to the experiment, sediment samples were sieved and thoroughly homogenized before being allocated to the treatment and control devices. This ensures that the initial iron speciation and content in both groups can be considered essentially identical. XAFS analysis further revealed that the treatment group sediments exhibit a higher proportion of Fe(III) compared to controls, indicating that cyanobacterial blooms promote Fe(II) oxidation in surface sediments, with amorphous FeOOH identified as the primary product (Supplementary Fig.S5). In wastewater treatment, various forms of Fe(III) compounds, including FeOOH and Fe_2O_3 , can serve as iron sources for Feammox process (Yang et al., 2018; Qin et al., 2024), among which amorphous Fe(III) is more easily reduced (Zhu et al., 2021). In this study, the alkaline conditions induced by cyanobacterial blooms suppressed the release of ferrous iron from the sediment, thereby maintaining relatively stable total iron content. Thus, theoretically, a higher proportion of amorphous FeOOH in the treatment group should lead to an increased Feammox process (Zhu et al., 2022). However, the experimental results were unexpectedly opposite to this prediction (Fig.2a). In the isotope tracing experiment, the treatment group, despite its higher amorphous FeOOH content and the identical environmental conditions and $^{15}\text{NH}_4^+$ addition levels, showed a lower Feammox rate, indicating a potential inhibition of the relevant microorganisms.

Iron-reducing bacteria (FeRB) are a group of microorganisms capable of utilizing Fe(III) as an electron acceptor and oxidizing electron donors such as ammonia, acetate, and lactate to obtain the energy needed for their life activities. Although only one independent Feammox-performing strain, *Acidimicrobiaceae* bacterium A6, has been isolated so far due to the difficulty in culturing Feammox-related microorganisms (Huang and Jaffé, 2018), previous reports have indicated that FeRB may participate in the Feammox process (Li et al., 2015). Statistical results indicate that after 4 d of cultivation with added cyanobacterial particles, the relative abundance of the genera related to FeRB in surface sediment samples was 4.60%, lower than the 5.40% observed in the control group (Fig.3). It is worth noting that DNA extraction and high-throughput sequencing cannot eliminate the dead bacteria, so the actual relative abundance of active FeRB in the treatment with added cyanobacteria may be even lower. The decreased relative abundance of FeRB in the treatment group indicates that the environmental conditions created by cyanobacterial blooms may be unfavorable for the growth of FeRB.

pH is a key environmental factor regulating the growth and metabolism of FeRB. From the thermodynamic perspective, acidic conditions are more favorable for Feammox (Zhu et al., 2021), although the reaction has also been observed in neutral or alkaline environments (Li et al., 2015). During blooms, intensive photosynthesis of cyanobacteria absorbs substantial CO_2 , leading to a sharp increase in water pH, which can exceed 10 (Supplementary Fig.S3a). Under such conditions, the pH in the surface sediment layer can reach 7.5–9.3 (Chen et al., 2018). These alkaline conditions are likely to inhibit the growth of acidophilic FeRB such as *Thiobacillus* (relative abundance 0.30%–0.48%) and *Acidiferrimicrobium* (relative abundance 0.66%–0.87%), consequently leading to a decrease in the overall activity of FeRB.

The concentrations of DO is another key factor influencing FeRB in sediments. Feammox typically occur under microaerobic or anaerobic conditions (Xia et al., 2022). Studies have shown that the relative abundance of *Geothrix*, a genus linked to Feammox, decreases sharply with rising DO level, and the Feammox process is gradually suppressed when DO exceeds 2.0 mg/L (Li et al., 2024). During cyanobacterial blooms, the intense photosynthesis activity not only absorbs CO_2 but also causes a rapid

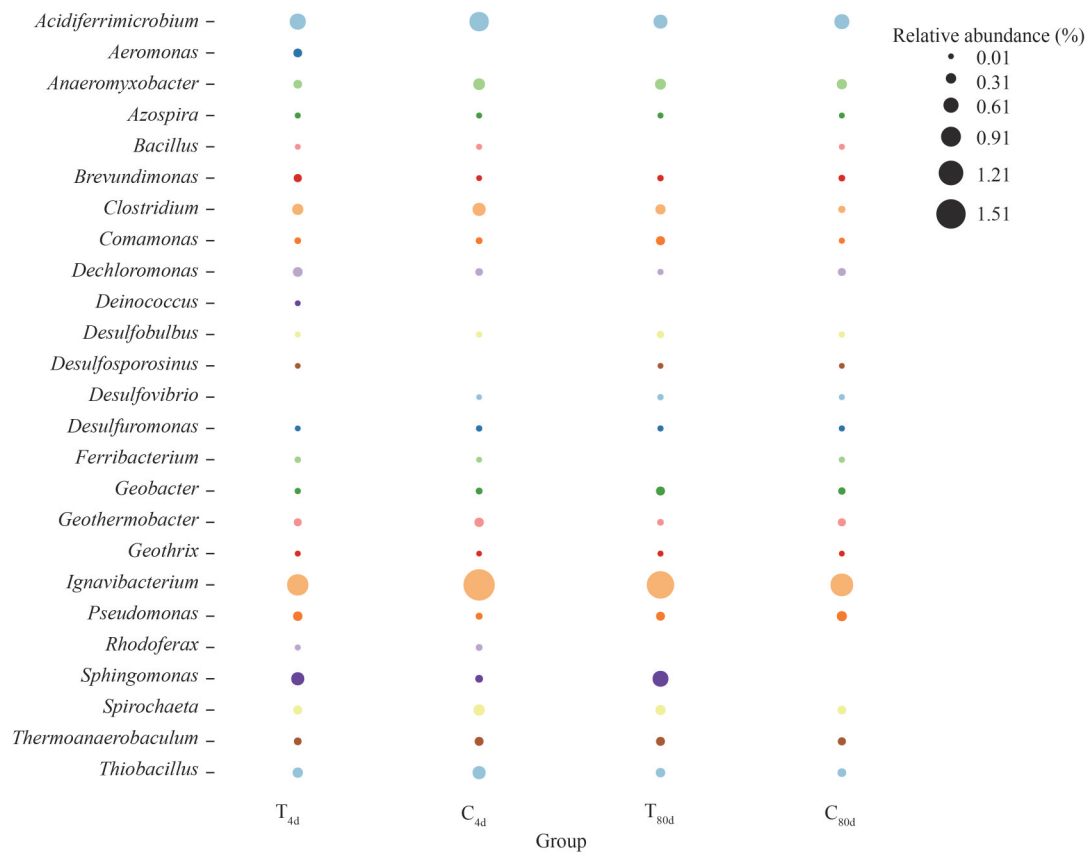


Fig.3 Relative abundance of FeRB at the genus level in sediments

increase in DO (Supplementary Fig.S3). This oxygen gradually infiltrates into the sediment, reaching penetration depth of up to 4 cm (Cui et al., 2024), which likely reduces or even eliminates the activity of FeRB. As a result, the relative abundance of *Ignavibacterium*, a ubiquitous heterotrophic anaerobe often found in anaerobic bioreactors that is closely associated with Feammox, declined from 1.63% to 0.99% (Fig.3).

In paddy soil, the 20–30-cm depth is recognized as the active zone for Feammox (Qin et al., 2019). In contrast, the primary depth at which Feammox occurrence in lake sediments remains unreported, with most current studies focusing on the surface sediments within the top 10 cm. Under alkaline conditions, the Fe(III) such as FeOOH or Fe₂O₃, formed during cyanobacterial bloom, tend to be immobilized in the surface sediment layers, thus having a minimal impact on the Feammox process in deeper sediments. Taihu Lake is a shallow lake with an average depth of about 1.9 m, where wind and waves actions frequently cause aperiodic sediment resuspension (Ding et al., 2018). It has been suggested that hydrological storms can potentially enhance the Feammox activity in

sediments by redistributing Fe(III) (Sherman et al., 2023). Thus, further research is required to evaluate how such sediment resuspension promotes Feammox during cyanobacterial bloom in Taihu Lake.

4.2 The decline and decomposition of cyanobacteria facilitate the coupled cycling of iron and nitrogen

The microbial degradation of decaying cyanobacteria would consume substantial DO, leading to a sharp decrease in Eh within the surface sediments (Chen et al., 2025). Furthermore, cyanobacteria-derived organic matter can serve as an electron donor, facilitating the microbial reduction of oxidized substances such as nitrates (Shen et al., 2020), which further lowers the sediment Eh. Under these low-Eh conditions, dissolved iron in deeper sediments will migrate upwards (Wang et al., 2023), likely explaining why the ferrous iron content in the surface sediments of T_{80d} was significantly higher than in the control (Table 2). Iron is a crucial micronutrient supporting the outbreak of cyanobacterial blooms in lake ecosystems (Qiu et al., 2022). During the decay

process of cyanobacterial blooms, these iron elements can be converted into Fe(II) through microbial activity, further increasing the pool of oxidizable iron in the surface sediments (Wang et al., 2021). Over 80-d incubation, the reoxygenation of sediments promoted the oxidation of a portion of the ferrous iron. This process, sustained by stabilized microbial activity, supplies additional electron acceptors, thereby facilitating Feammox.

From the thermodynamic perspective, the reduction of Fe(III) using organics as electron donors may be more favorable than Feammox (Liang et al., 2022). Nevertheless, evidence suggests that high concentrations of organic matter can enhance the abundance of Feammox-functional bacteria such as *Anaeromyxobacter*, *Pseudomonas*, and *Geobacter*, with soil or sediment TOC showing a significant positive correlation with the potential Feammox rate ($P < 0.01$) (Ding et al., 2017). The decomposition of senescent cyanobacteria can also provide microorganisms with abundant organic compounds, many of which are humic substances (Leloup et al., 2013). These humic substances derived from cyanobacteria can also function as electron acceptors for FeRB, facilitating the reduction of insoluble iron minerals (Tang et al., 2014). As depicted in Supplementary Fig.S9, the fluorescence intensity of humic acid-like substances in the extract of T_{80d} samples is much higher than in C_{80d} . This mechanism likely contributed to the increase in the relative abundance of FeRB to 4.96% (Fig.3), even with a decline in temperature.

The degradation of algal biomass can release protons, thereby lowering sediment pH (Chen et al., 2025). This mechanism could explain the notably decreased pH in the sediment with added cyanobacteria compared to the control (Table 2). A decreased pH is thermodynamically more favorable for the Feammox reaction and also enhances iron mobility (Wang et al., 2021). Therefore, the decay and degradation of cyanobacteria can create a more suitable pH environment for the Feammox process. Consequently, the relatively high contents of Fe(III) and humic acid, the relative abundance of FeRB, and the suitable pH conditions in the surface sediments of T_{80d} promoted the occurrence of the Feammox reaction in the sediments (Fig.2b).

Nitrate-dependent ferrous oxidation (NDFO) is a microbial process in which ferrous iron serves as an electron donor for nitrate reduction under anaerobic conditions (Straub et al., 1996), primarily producing N_2 as the end product (Liu et al., 2018). The decay

of cyanobacteria has a significant impact on NDFO-related bacteria. In a study by Chen et al. (2025), the addition of a substantial quantity of cyanobacteria led to a marked increase in the populations of *Gallionellaceae*, a typical NDFO bacterium. In this study, high-throughput sequencing revealed that the relative abundance of NDFO-related bacterial genera in the sediment of T_{80d} reached 2.94%, compared to 2.47% in the control group (Supplementary Fig.S10). Moreover, the cyanobacterial decomposition can also promote the increase in nitrate content (Table 2), indicating that the decaying cyanobacteria can also enhance NDFO activity. After 80 d of incubation, the total inorganic nitrogen ($NH_4^+-N + NO_3^--N$) content was similar in the sediments of both treatment and control groups (Table 2), suggesting that most algal-derived nitrogen was removed via denitrification and other pathways, potentially involving NDFO. Although not yet confirmed in actual lake sediments, the coupling of NDFO and Feammox has been achieved in wastewater treatment systems for simultaneous removal of NO_3^- and NH_4^+ (Li et al., 2018). Therefore, the contribution of the coupling cycle of Fe-N promoted by the decomposition of cyanobacteria to nitrogen removal in lakes may be substantially greater than the measured potential rate of Feammox alone.

5 CONCLUSION

This study demonstrates that cyanobacterial blooms exert stage-dependent effects on the Feammox process. The initial outbreak phase of cyanobacteria blooms promotes the oxidation of ferrous iron to amorphous $FeOOH$ and Fe_2O_3 , yet this oxidation process suppresses the growth of FeRB and consequently lowers the potential rate of Feammox. Conversely, the subsequent degradation phase of decaying cyanobacteria enriches sediments with humic acid and Fe(III) while reducing of the pH, thereby creating a favorable environment for FeRB, and promoting the Feammox activity. These findings highlight the contrasting roles of cyanobacterial bloom dynamics in regulating iron and nitrogen cycling in shallow eutrophic lakes.

6 DATA AVAILABILITY STATEMENT

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Electronic supplementary material

Supplementary material (Supplementary Table S1 and Figs.S1–S10) is available in the online version of this article at <https://doi.org/10.1007/s00343-026-5247-9>.