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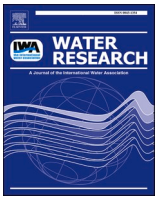

Cyanobacteria decay alters CH_4 and CO_2 produced hotspots along vertical sediment profiles in eutrophic lakes

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ABSTRACT

Cyanobacteria-derived organic carbon has been reported to intensify greenhouse gas emissions from lacustrine sediments. However, the specific processes of CH_4 and CO_2 production and release from sediments into the atmosphere remain unclear, especially in eutrophic lakes. To investigate the influence of severe cyanobacteria accumulation on the production and migration of sedimentary CH_4 and CO_2, this study examined the different trophic level lakes along the middle and lower reaches of the Yangtze River. The results demonstrated that eutrophication amplified CH_4 and CO_2 emissions, notably in Lake Taihu, where fluxes peaked at 929.9 and 7222.5 μmol/m^2·h, mirroring dissolved gas levels in overlying waters. Increased sedimentary organic carbon raised dissolved CH_4 and CO_2 concentrations in pore-water, with isotopic tracking showing cyanobacteria-derived carbon specifically elevated CH_4 and CO_2 in surface sediment pore-water more than in deeper layers. Cyanobacteria-derived carbon deposition on surface sediment boosted organic carbon and moisture levels, fostering an anaerobic microenvironment conducive to enhanced biogenic CH_4 and CO_2 production in surface sediments. In the microcosm systems with the most severe cyanobacteria accumulation, average CH_4 and CO_2 concentrations in surface sediments reached 6.9 and 2.3 mol/L, respectively, surpassing the 4.7 and 1.4 mol/L observed in bottom sediments, indicating upward migration of CH_4 and CO_2 hotspots from deeper to surface layers. These findings enhance our understanding of the mechanisms underlying lake sediment carbon emissions induced by eutrophication and provide a more accurate assessment of lake carbon emissions.

1. Introduction

Lakes are recognized as significant natural contributors to global greenhouse gas emissions. It is estimated that lakes worldwide annually emit 8–48 Tg of methane (CH_4) and 60–840 Tg of carbon dioxide (CO_2) annually into the atmosphere (Bastviken et al., 2004, 2008; Raymond et al., 2014). Previously, it has been identified bottom sediments as key zones for CH_4 and CO_2 production, primarily due to anaerobic conditions and the substantial accumulation of organic carbon (Einzmann et al., 2022). However, recent studies suggest that the decomposition of cyanobacteria induced by eutrophication significantly alters the physical and chemical properties of surface sediments (Zhou et al., 2022a). Changes in the characteristics of lake surface sediments, particularly resulting from eutrophic processes, have emerged as important factors that affect the accurate estimation of lake carbon emissions (Qi et al., 2020).

Surface sediments conventionally exhibit relatively higher oxygen concentrations compared to bottom sediments and are not traditionally considered primary zones for CH_4 production (Einzmann et al., 2022). However, several studies have proposed that eutrophication-induced cyanobacterial blooms lead to a significant accumulation of cyanobacterial residues on the sediment surface. This accumulation forms a "cyanobacteria detritus mat", creating a suitable environment for methanogenic archaea to thrive on the surface sediments (Qi et al.,

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2020). Importantly, in comparison to decomposition processes involving aquatic plants, cyanobacterial residues typically contain more easily accessible forms of organic carbon, including low molecular weight organic acids, sugars, amino acids, and lipids. These forms provide resources for methanogenic archaea, leading to a faster decomposition rate (Villacorte et al., 2015; Bao et al., 2023). When cyanobacteria decompose, the introduction of cyanobacteria-derived carbon into lakes triggers co-metabolic effects, accelerating the breakdown of recalcitrant carbon, particularly in surface sediments where interactions occur between cyanobacteria-derived carbon and recalcitrant carbon (Deng et al., 2022). This co-metabolism markedly increases the mineralization rate of organic carbon, contributing substantially to CH_4 and CO_2 emissions from lakes (Ma et al., 2020; Deng et al., 2023). Furthermore, the accelerated decomposition of organic carbon, driven by microbial activity, leads to a reduction in oxygen concentrations and significantly intensifies the rate of carbon metabolism in surface sediment (Qi et al., 2020; Ma et al., 2024). Therefore, surface sediments may exhibit heightened activity in CH_4 and CO_2 production processes.

The emission of CH_4 from lakes into the atmosphere is influenced by both CH_4 production and oxidation processes (Verpoorter et al., 2014; Zhou et al., 2022b). CH_4 and CO_2 generated through the mineralization of organic carbon in sediments are emitted into the atmosphere through various pathways, including ebullition, water column release, diffusive emission, and plant-mediated emission (Bastviken et al., 2004; Davidson et al., 2015). In lake ecosystems, as CH_4 produced in bottom sediments moves towards the surface sediments, between 50 % and 90 % of it is consumed through oxidation processes. This reduces the CH_4 concentration by the time it reaches the surface sediments (Alanna et al., 2017). The presence of increasing oxygen concentrations during its upward movement in sediments is a crucial factor that promotes methane oxidation (Hu et al., 2024). Methane oxidation plays a vital role in mitigating the greenhouse effect in lakes, as it converts most of the CH_4 into CO_2, resulting in increased CO_2 emissions (Miller et al., 2016; Yan et al., 2023). However, the formation of the cyanobacteria detritus mat on the surface sediment creates an anaerobic environment that inhibits the methane oxidation process in the surface sediments (Emerson et al., 2021; Perez-Coronel et al., 2022). While some research suggests anaerobic oxidation as a potential pathway for methane oxidation, aerobic oxidation processes primarily govern this mechanism in eutrophic freshwater lakes (Yang et al., 2019). Cyanobacteria residues consume and deplete oxygen from the surface sediments, potentially reducing methane oxidation losses (Cerbin et al., 2022). Traditionally, bottom sediments have been identified as hotspots for CH_4 production, as evidenced by in-situ experiments showing significantly higher CH_4 concentrations compared to the surface (Einzmann et al., 2022). Nevertheless, changes in the lake's environmental conditions have led to surface sediments also being recognized as important sites for CH_4 production, indicating increased transmission efficiency (Murase et al., 2005; Xiao et al., 2017). Factors such as temperature and pressure, which are influenced by depth, play a role in determining the efficiency of gas transport (Gudasz et al., 2010; Emilson et al., 2018). Therefore, variations in the depth of areas with high CH_4 and CO_2 production can significantly alter the capacity to emit carbon in lakes.

This study examines the influence of eutrophication on sediment carbon pools and explores the underlying mechanisms. The study collected water, sediment, and gas samples from seven lakes with varying trophic levels in the highly developed regions of the middle and lower reaches of the Yangtze River. Field investigations were conducted to measure the concentrations of dissolved CH_4 and CO_2, as well as their release fluxes in the overlying water. In addition, measurements of dissolved CH_4 and CO_2 concentrations were taken at different depths in the sediment pore-water. Furthermore, a series of microcosms were established using cyanobacteria, water, and sediment samples collected from the typical eutrophic Lake Taihu, to evaluate the impact of cyanobacterial carbon on the mineralization of organic carbon within the sediment. These findings provide valuable insights for accurately assessing the equilibrium of the lake sediment carbon pool and the associated carbon emissions in the context of increasing eutrophication conditions.

2. Materials and methods

2.1. Study site and sample collection

Seven shallow freshwater lakes (depth<7 m) located within the Yangtze River basin were selected and classified into three categories: mesotrophic (30<*TLI*<50), eutrophic (50<*TLI*<60), and hypereutrophic ((*TLI*>70)) based on the Trophic Level index (*TLI*) (Figs. S1 and S2). In July 2021, three sampling sites were designated in these lakes, all located over 300 m from the lake shore. Gas, water, and sediment samples were collected, with the water depth at each sampling point not exceeding 5 m. Additionally, to simulate a typical eutrophic lake environment, samples of water, sediment, and cyanobacteria were collected from Lake Taihu to establish microcosmic systems. Detailed information about the lakes can be found in Table S1.

The gravity core sampler was be used to collect the sediment core at a depth of 0 to 24 cm, divided into 12 layers at 2 cm intervals. Overlying water samples from each lake were systematically collected 30 cm beneath the surface, in triplicate, to assess nutrient concentrations and concentrations of dissolved CH_4 and CO_2. Cyanobacteria were harvested from the cyanobacterial accumulation area using a plankton net with a mesh size of 250. Gas samples were systematically gathered at 10-min intervals over a period of one hour using floating static chambers (38.5 cm × 30.5 cm × 18.5 cm), a method validated for delivering accurate assessments of water-gas exchange.

2.2. Microcosm system

The microcosm system consisted 156 plexiglass columns (8 cm diameter, 70 cm height), divided into four groups based on cyanobacterial density: K (no accumulation), A (4 cm), B (8 cm), and C (12 cm), each with three replicates. Each column contained in-situ lake water (20 cm) and sediment (20 cm), with varying cyanobacteria amounts. The cyanobacteria within the microcosmic system were labeled using $NaH^{13}CO_3$ (98 at.%^{13}C) inorganic salts. The $\delta^{13}C$ value of cyanobacteria before cultivation was −22.72 ‰, which decreased to −18.28 ‰ after cultivation. Before addition, cyanobacteria were washed to remove residual salts. Nitrogen gas was introduced into the headspace of the plexiglass columns for 20 min to ensure that the carbon in each treatment group originated solely from within the microcosm system. The rubber plug was sealed and further secured with silicone sealant, with a gas extraction pipe aperture reserved within the rubber plug. All microcosm systems were shielded from light, and incubated in the dark at a constant temperature of 28±1 °C in a water bath to simulate the ambient temperature in Lake Taihu during cyanobacterial blooms. Destructive sampling was conducted on days 0, 5, 10, 15, 20, 30, 40, 50, 70, 100, 140, 180, 270, and 360 over one year.

2.3. Chemical analytical methods

2.3.1. Determination of organic carbon concentration in sediment

The microcosm system utilized a gravity core sampler to collect sediment core samples from depths of 0–20 cm, which were then divided into 5 layers with intervals of 4 cm each. The sediment core samples obtained in the field and microcosm were freeze-dried using freeze-drying machines (Biosafer-10A, China). After freeze-drying, the sediment samples were acidified with 1 mol/L hydrochloric acid and subsequently dried in an oven at 60 °C for 8 h. The dried sediments were analyzed for total organic carbon (TOC) using a TOC analyzer (AnlaytikJena HT1300, Germany) in accordance with EPA 9060A guidelines, with an accuracy of TOC concentration to within 1 %.

2.3.2. Determination of CH_4 and CO_2

In this study, measurements were conducted to assess the CH_4 and CO_2 emissions at the water-gas interface, as well as to determine the concentrations of dissolved CH_4 and CO_2 in overlying water. Additionally, measurements were taken to determine the CH_4 and CO_2 concentrations in sediment pore-water of various depths. All gas samples were determined by gas chromatography (GC-2014, Shimadzu, Japan).

The emissions fluxes (F) of gas (CH_4 and CO_2) were determined by the static chamber method as follows:

$$F = \frac{V}{A} \times \frac{dC}{dt} \quad (1)$$

Where F is the gas emissions ($\mu mol \cdot m^{-2} \cdot h^{-1}$); V is the volume of the static chamber (m^3); A is the surface area of the static chamber (m^2), and dC/dt is the slope of the gas concentration changing with time during sampling ($\mu mol \cdot m^{-3} \cdot h^{-1}$).

To collect gas samples from water and measure dissolved CH_4 and CO_2 concentrations, 300 mL of water was slowly poured into an anaerobic bottle. Excess gas in the headspace was then removed by blowing N_2 for 3 min. The anaerobic bottles were agitated for 5 min before withdrawing the headspace gas using a syringe. The gas was injected into an airbag (E-Switch, China) for storage and later measured by gas chromatography.

To investigate the concentrations of dissolved CH_4 and CO_2 at various sediment depths, pore-water was extracted from sediment cores and analyzed using the static headspace method (Sun et al., 2022). Wet sediment core samples (1 g each) were collected from different depths in both in-situ and microcosms, and placed in brown bottles (30 cm^3 in volume), and each sediment layer was sampled in triplicate. Subsequently, 20 mL of ultrapure water, previously deoxygenated through 5 min of vigorous aeration by N_2, was added to each bottle. After sealing, the brown glass bottles were shaken for 5 min and left to reach water and gas diffusion equilibrium. Finally, 5 mL of gas was extracted using a syringe and its concentration was measured by gas chromatography. The pore-water concentrations of CO_2 and CH_4 were calculated according to Sun et al. (2022).

2.3.3. Measurements of $\delta^{13}C$ in sediment

The freeze-dried sediment core samples were treated with concentrated hydrochloric acid for 24 h to remove particulate inorganic carbon. After the treatment, the samples were washed extensively with deionized water to neutralize and adjust the pH to a neutral level. The $\delta^{13}C$ values of the sediment were determined using an organic elemental analyzer (FLASH 2000, Thermo Fisher, Monza, Italy) (Zhou et al., 2023a).

2.3.4. Biological analysis

To investigate the impact of cyanobacterial decomposition on microorganisms in the sediment, sequencing and real-time reverse-transcriptase quantitative polymerase chain reaction (RT-qPCR) technologies were employed. The microbial communities were quantified with sets targeting ArBa515F_806R. Sediment samples were stored at −80 °C in an ultra-low temperature freezer. Total genomic DNA was extracted using the E.Z.N.A.® Soil DNA Kit (Omega Bio-Tek, Norcross, GA, USA). The quality of nucleic acids was assessed via 1 % agarose gel electrophoresis, and concentrations were measured with a NanoDrop 2000 UV spectrophotometer (Thermo Scientific, USA). Bacterial communities were quantified through 16S rRNA gene analysis, following MIQE guidelines.

2.4. Statistical analysis

Data statistical analysis was conducted using Origin 2023 and SPSS 18.0. Prior to analysis, the normal distribution of the data was assessed to establish correlations. The Pearson correlation coefficient was employed for bivariate correlation analysis. Significant differences among variables were assessed through one-way analysis of variance (ANOVA) and independent sample t-tests.

3. Results

3.1. Trophic status and TOC concentration in the sediments of lakes

The investigated lakes in the field displayed a range of trophic state, with eutrophic lakes facing significant ecological challenges (Fig. S2). Among them, Lake Taihu, Lake Chaohu, and Lake Dianshan were in a hyper-eutrophic state, with Lake Taihu exhibiting the highest degree of eutrophication with a *TLI* of 83.1. The TOC concentration in sediments in hyper-eutrophic lakes was notably high, especially in the surface sediment layers (Fig. S3). The sediments of Lake Taihu had the highest TOC concentration, with the surface sediment reaching up to 68.4 ± 114.9 g kg^{-1}. As the sediment depth increased, the TOC concentration gradually decreased, with a more pronounced trend observed in eutrophic lakes. In Lake Taihu, the most significant variation in TOC concentration with depth occurred in the range of −10 to −14 cm, where the TOC concentration decreased from 52.8 ± 330.1 to 39.7 ± 5.5 g kg^{-1}.

3.2. Dissolved CH_4 and CO_2 in the water and their emissions in air-water fluxes of lakes

The emissions of CH_4 and CO_2 in air-water fluxes varied significantly among different lakes and displayed a positive correlation with the degree of lake eutrophication (Figs. 1 and S4). In these lakes, the CH_4 emissions in air-water fluxes ranged from 26.4 ± 5.0 to 929.9 ± 106.6 $\mu mol/m^2 \cdot h$, while CO_2 emissions ranged from 0.3 ± 0.3 to 7222.5 ± 1197.3 $\mu mol/m^2 \cdot h$. Among all investigated lakes, Lake Taihu had the highest emissions of CH_4 and CO_2 in air-water fluxes at 929.9 ± 106.6 and 7222.5 ± 1197.3 $\mu mol/m^2 \cdot h$, respectively. Conversely, the lowest emissions for CH_4 and CO_2 in air-water fluxes were observed in Lake Caizi at 26.4 ± 5.0 and 0.3 ± 0.3 $\mu mol/m^2 \cdot h$, respectively.

Dissolved CH_4 concentrations in the overlying water, ranging from 0.3 ± 0.1 to 2.1 ± 0.3 μmol/L, showed a positive correlation with the Trophic Level Index (*TLI*) of the studied lakes (Figs. 1 and S5). In a similar pattern, dissolved CO_2 concentrations varied from 26.6 ± 0.9 to 98.9 ± 3.9 μmol/L, mirroring the trends observed for CH_4. The peak concentration of dissolved CH_4, recorded at 2.4 ± 0.6 μmol/L, was found in Lake Dianshan, while Lake Taihu registered the highest dissolved CO_2 concentration at 98.9 ± 3.9 μmol/L.

3.3. Dissolved CH_4 and CO_2 in the pore-water of lakes

At a spatial scale, the dissolved CH_4 and CO_2 concentrations in pore-water from various lake sediments exhibited significant variation (Fig. 2a, b). Lake Taihu stood out as having particularly high concentrations of dissolved CH_4 and CO_2 in its pore-water. Specifically, the bottom sediment in the lake contained 2.2 ± 0.3 μmol/L of dissolved CH_4 and 160.1 ± 18.7 μmol/L of dissolved CO_2. Furthermore, the concentrations of dissolved CH_4 and CO_2 in the pore-water differed significantly at various depths in the sediment, gradually decreasing from the bottom to the surface. This decrease showed a strong negative correlation with depth (Fig. 2c). In lakes with hyper-eutrophic conditions, a slight increase in the dissolved CO_2 concentrations in the pore-water of surface sediments (−4–0 cm depth) was observed. For instance, at a depth of −4 cm in Lake Dianshan, the concentration of dissolved CO_2 measured 88.1 ± 16.7 μmol/L, while at the surface sediment, it registered at 96±16.8 μmol/L. Additionally, the TOC concentration in the sediment played a pivotal role in the production of CH_4 and CO_2. There existed a positive correlation between the TOC concentration and the concentration of dissolved CH_4 and CO_2 in the pore-water (Fig. 2d).

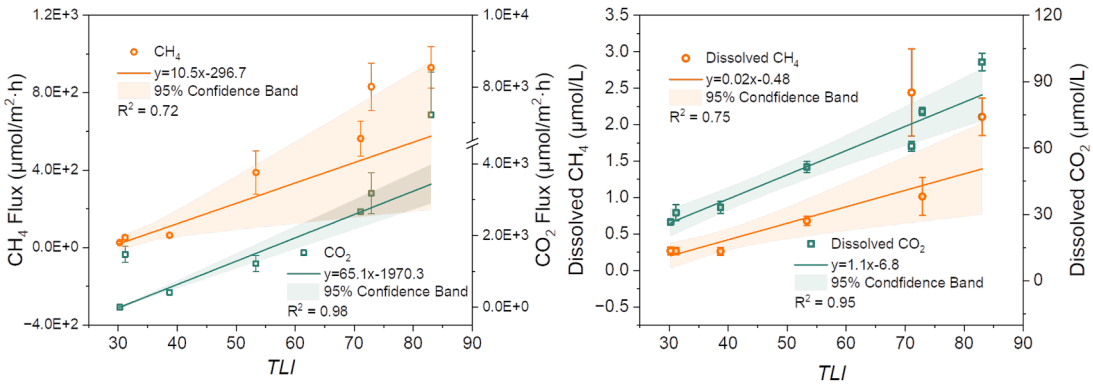

Fig. 1. Correlation analysis between Trophic Level index (*TLI*) and the CH_4, CO_2 flux (left), dissolved CH_4, CO_2 (right) of the investigated lakes along the Yangtze River, respectively.

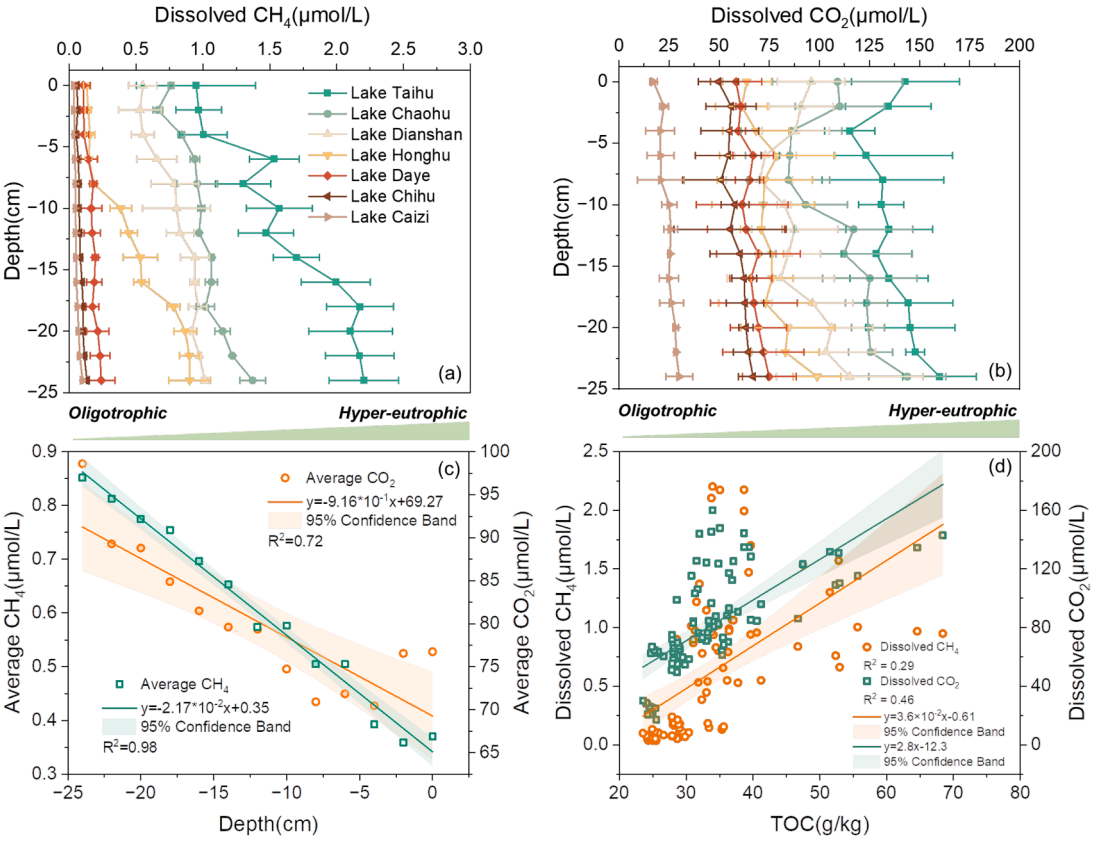

Fig. 2. The dissolved CH_4 (a) and CO_2 (b) concentrations in sediment at different depths, correlation analysis between depth and the dissolved CH_4, CO_2 in sediment (c), correlation analysis between Total Organic Carbon (TOC) and the dissolved CH_4, and CO_2 in sediment (d) of the investigated lakes along the Yangtze River.

3.4. Cumulative CH_4 and CO_2 emissions in microcosms

During the decomposition of cyanobacteria, the cumulative concentrations of CH_4 and CO_2 in the microcosm system showed a continuous increase, eventually reaching a plateau (Fig. 3). In the initial 100 days of the experiment, there was a rapid increase in CH_4 and CO_2 concentrations, with group C showing the highest increase. At 100 days, the concentrations of CH_4 reached 7.2 ± 1.5 mol/L, while the concentration of CO_2 reached 4.1 ± 0.2 mol/L. The cumulative CH_4 and CO_2 concentrations were found to be correlated with the initial cyanobacteria biomass. Specifically, the experimental group with a higher initial accumulation of cyanobacteria exhibited a greater release of CH_4 and CO_2.

3.5. TOC and $\delta^{13}C$ concentrations in sediments in microcosms

With the gradual decomposition of cyanobacteria, there was a concomitant increase in sediment TOC concentration. However, there were discernible differences among the experimental groups, indicating substantial variations in TOC concentration (Figs. 4, S6 and S7). The concentration of TOC in sediments showed a positive correlation with the magnitude of cyanobacteria accumulation, suggesting that a higher biomass of cyanobacteria led to an elevated TOC concentration in the sediment. On the 360th day, Group C displayed the highest concentration of sediment averaging 56.2 ± 14.0 g kg^{-1}. Throughout the incubation period, the average TOC concentration in sediments decreased from the initial 41.1 ± 12.3 to 22.9 ± 1.0 g kg^{-1} in Group K without cyanobacteria. The concentration of TOC in surface sediments exhibited a

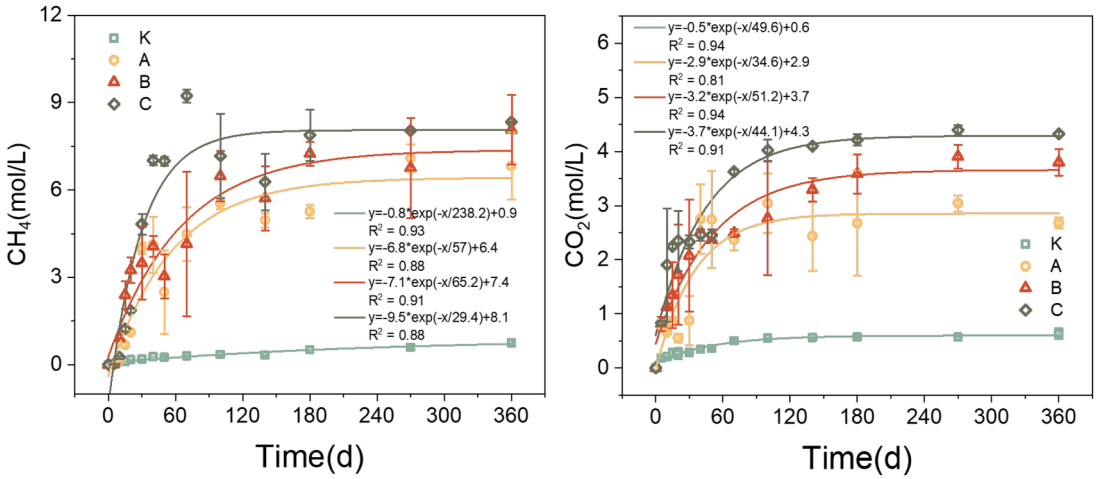

Fig. 3. Dynamics of cumulative CH_4 (left) and CO_2 (right) emissions in the microcosms during incubation under different cyanobacteria biomass. (K: without cyanobacteria accumulation, A: cyanobacteria accumulate to a height of 4 cm, B: cyanobacteria accumulate to a height of 8 cm, C: cyanobacteria accumulate to a height of 12 cm. The figures below are consistent).

notable increase. In Group C, the surface sediment exhibited an average TOC concentration of 79.3 ± 16.6 g kg^{-1}, whereas the bottom layer displayed a notably lower concentration of 23.6 ± 5.0 g kg^{-1}.

Cyanobacteria decomposition led to a notable increase in $\delta^{13}C$ in the sediment, indicating the incorporation of cyanobacteria-derived carbon into the sediment (Figs. 4 and S8). In the group characterized by cyanobacteria accumulation, there was a noticeable increase in the $\delta^{13}C$ value, demonstrating a positive correlation with the cyanobacteria biomass. On the 360th day, the average value of $\delta^{13}C$ in the sediment of Groups K, A, B, and C were −23.32±0.59 ‰, −22.48±0.44 ‰, −22.25 ±0.36 ‰, and −21.88±0.62 ‰, respectively. From 70d to 140d of incubation, there was a substantial decrease in the $\delta^{13}C$ value, reaching its lowest value in Group A at −25.05 ‰. The average $\delta^{13}C$ value showed a pronounced decrease as the sediment depth increased, as indicated by the TOC concentration in the sediment.

3.6. Dissolved CH_4 and CO_2 in the pore-water of microcosms

The dissolved CH_4 and CO_2 concentrations in pore-water exhibited a substantial increase during cyanobacteria decomposition, showing a positive correlation with the carbon derived from cyanobacteria (Figs. 5, 6, S9, and S10). However, the distribution pattern of dissolved CH_4 concentration in the sediment pore-water within the microcosm system differed from field investigations. In the microcosm system, higher concentrations of dissolved CH_4 were observed at the surface and bottom layers, while lower concentrations were found in the middle layer. In Group C, the average dissolved CH_4 concentration in the pore-water of surface sediment was 6.93±0.74 mol/L, whereas in the pore-water of bottom sediment it was 4.71±0.59 mol/L. The dissolved CH_4 concentration in the pore-water initially increased and reached a peak at 100 days of incubation. Group C displayed the highest dissolved CH_4 concentration, peaking at 8.55±1.01 mol/L when it reached equilibrium.

The cyanobacteria decomposition also resulted in a peak in the dissolved CO_2 concentration in pore-water at 100 days. The average dissolved CO_2 concentration in the pore-water of sediment for each group was 2.01±0.15, 2.23±0.47, 2.29±0.61, and 3.22±0.17 mol/L, respectively. Subsequently, the dissolved CO_2 concentration gradually decreased and eventually stabilized at a certain concentration. The pattern of dissolved CO_2 concentration in the pore-water of sediment within the microcosm system was in contrast to field observations, as the concentration decreased gradually with increasing sediment depth. The CO_2 concentration in the pore-water of surface sediment in each group ranged from 0.68±0.09 to 2.35±0.14 mol/L, with higher concentrations corresponding to higher accumulation of cyanobacteria.

3.7. Microbial communities in sediments of microcosms

The cyanobacteria decomposition caused changes in the structure of the microbial community in the sediment, resulting in a greater variety of species within these communities (Fig. 7). The composition of microbial communities in surface sediments differed markedly from those in bottom sediments.

In surface sediments, the accumulation of cyanobacteria led to a higher abundance of *Halobacterota* in the sediment, accounting for 32.3 %, 24.1 %, and 57.5 % of the microbial composition in Groups A, B, and C, respectively. In the group without cyanobacteria accumulation, there were no significant changes observed in the microbial community structure within the sediment. The predominant microorganism remained *Proteobacteria*, initially, representing 24.1 % and increasing to 28.5 % in Group K.

In bottom sediments, *Proteobacteria* was the dominant species; however, the proliferation of cyanobacteria resulted in a decrease in its abundance. The final abundance figures for *Proteobacteria* were 29.3 %, 22.3 %, 19.5 %, and 19.7 % of the microbial composition in Groups A, B, and C, respectively. Similar to surface sediments, no significant changes were observed in the microbial community structure within the bottom sediment in Group K.

4. Discussion

4.1. Status of carbon emissions in lakes

Lakes, as significant natural sources of carbon emissions, release an estimated 117–212 Tg/y of CH_4 and 60–840 Tg/y of CO_2 into the atmosphere (Rosentreter et al., 2021; Raymond et al., 2014). As vital components of freshwater ecosystems, lakes play a crucial role in counterbalancing continental carbon sinks through CH_4 emissions, accelerating climate change and altering aquatic environments (Bastviken et al., 2011; Soued et al., 2022). The increasing eutrophication of lakes is believed to be a potential factor contributing to this phenomenon (Beaulieu et al., 2019; Zhou et al., 2022b). Currently, several studies have established bidirectional positive feedback loops between the escalation of lake eutrophication and the amplification of climate warming (Yan et al., 2017; Zhou et al., 2022a). Climate warming leads to higher temperatures, which in turn boosts the growth rates of cyanobacterial blooms by enhancing water body stability and prolonging thermal stratification duration (Ho et al., 2019). As cyanobacteria

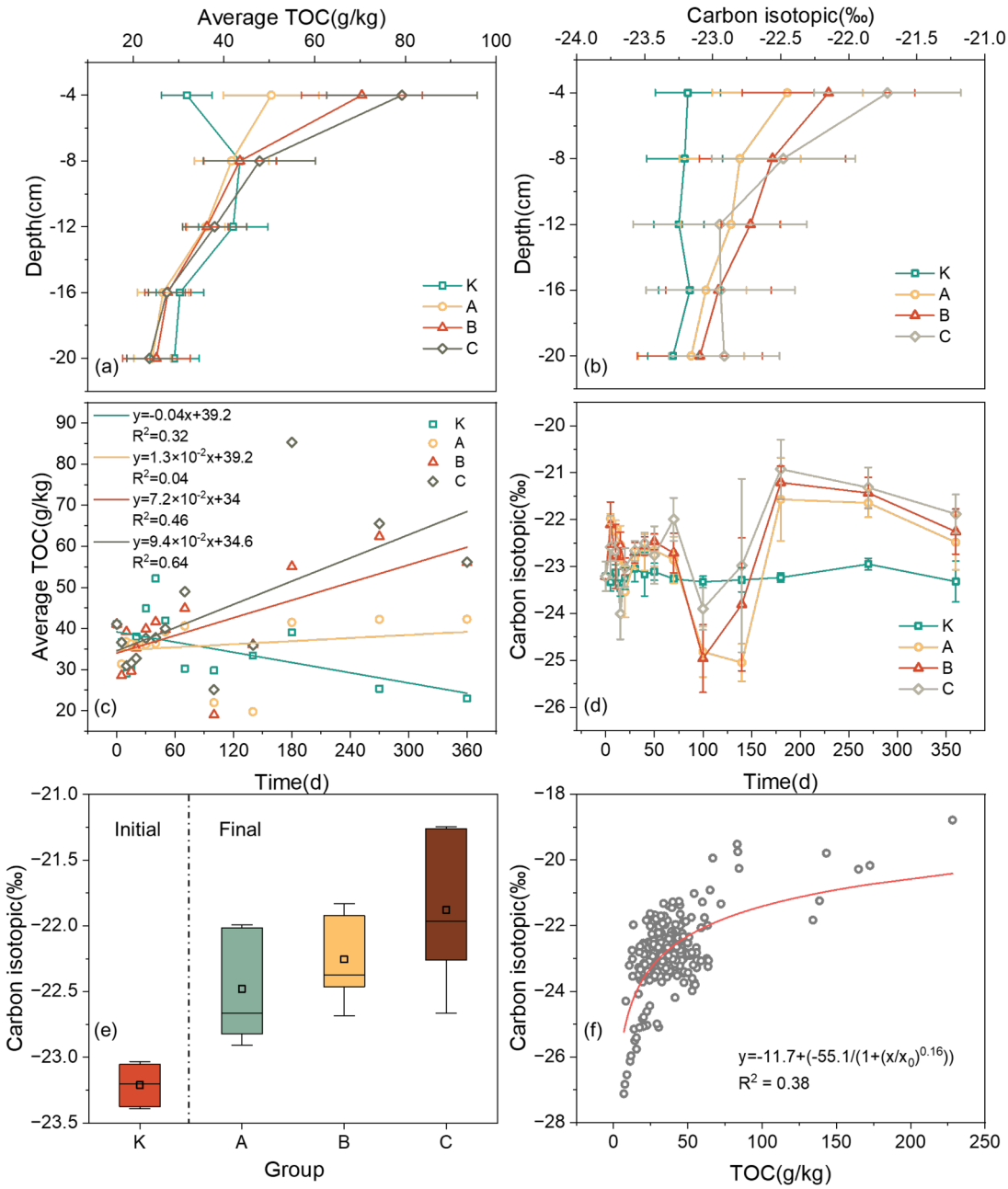

Fig. 4. Dynamics of average TOC concentration and average $\delta^{13}C$ values in different depths of sediment at temporal scale (a, b), average TOC concentration and average $\delta^{13}C$ values in sediment at temporal scale (c, d), initial and final $\delta^{13}C$ values in sediment (e), and correlation analysis between $\delta^{13}C$ values and TOC (f), during the incubation under different cyanobacteria biomass in microcosms of each group, respectively.

proliferation, their massive accumulation and subsequent decomposition accelerate CH_4 emissions by fostering an anaerobic reducing environment and enhancing the organic carbon mineralization process (Zhou et al., 2024). The average emissions of CH_4 and CO_2 from the hyper-eutrophic lakes examined in this study were 774.8 and 4357.3 μmol/m^2·h, respectively, significantly higher than the 47.7 and 30.8 μmol/m^2·h in mesotrophic lakes (Figs. 1 and S4). Elevated eutrophication levels in lakes also result in increased concentrations of dissolved CH_4 and CO_2, indicating that various sources of organic carbons contribute to more intense organic carbon mineralization processes in eutrophic lakes (Zhou et al., 2023b). Our findings verify a rise in dissolved CH_4 and CO_2 concentrations in surface waters, particularly in lakes experiencing severe eutrophication, with average dissolved concentrations of 1.9 and 78.7 μmol/L, respectively (Figs. 1 and S5).

Current comprehensive research has confirmed the significant role of carbon derived from cyanobacteria, accelerating the release of carbon emissions and likely to strengthen further in the future (Torres et al., 2011; Zhou et al., 2023a). Studies on the positive effects of cyanobacteria-derived carbon on CH_4 and CO_2 have focused on increasing the supply of organic matter, creating an anaerobic environment, and promoting more active microbial activity (Paerl et al., 2013). However, with the continuous input of cyanobacteria-derived carbon in sediments (Zhou et al., 2023b), the influence of changes in sediment carbon pool structure and the physical and chemical environment on the mechanism of CH_4 and CO_2 production from organic carbon mineralization remains unexplored. Crucially, while methane oxidation in shallow lakes is typically vigorous, recent observations reveal an unexpected high in CH_4 emissions from these environments, which was consistent with the results of this study (Figs. 1 and S4). Consequently, it is imperative to thoroughly evaluate the impact of

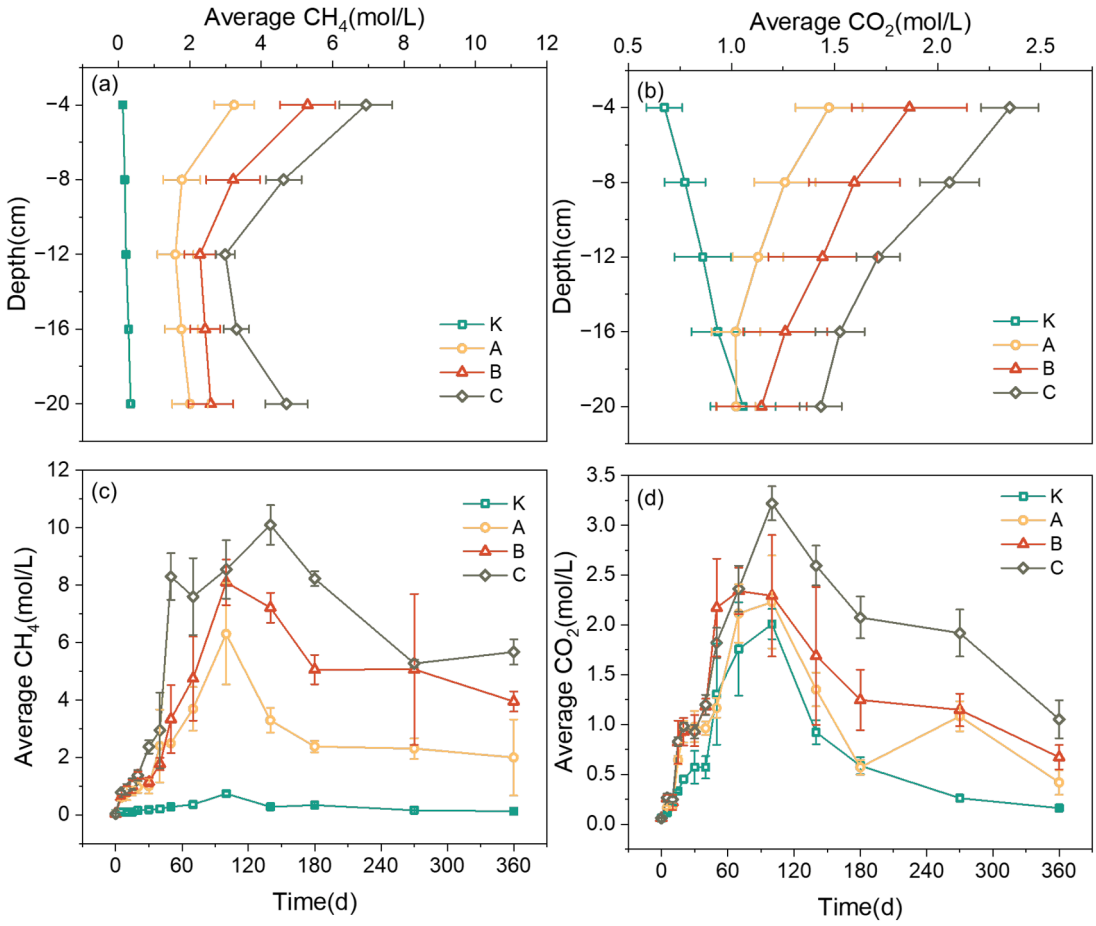

Fig. 5. Dynamics of average CH_4 and CO_2 concentration in different depths of sediment pore-water (a, b), average CH_4 and CO_2 concentration in sediment pore-water during the incubation at temporal scale (c, d) during the incubation under different cyanobacteria biomass in microcosms, respectively.

escalating eutrophication on the mechanisms of CH_4 and CO_2 production and emission during the organic carbon mineralization process.

4.2. Potential factors influencing carbon emissions in eutrophic lakes

In freshwater lakes, the transfer of CH_4 and CO_2 from sediments to the atmosphere is a complex process involving generation in sediments, release to overlying water, and eventual emission to the atmosphere (Zhou et al., 2023b). The presence of organic carbon in lake sediment's carbon pool is crucial in determining the rate and intensity of CH_4 and CO_2 production during organic matter mineralization (Wik et al., 2016; Peter et al., 2017). This study revealed a positive linear correlation between CH_4 (R^2 = 0.29) and CO_2 (R^2 = 0.46) concentrations in field sediments and the organic carbon content in sediments (Fig. 2). Sediment bottoms are well-known as hotspots for CH_4 and CO_2 production, especially CH_4, due to the combination of anaerobic conditions, stable temperature and pH, and limited CH_4 oxidation (Einzmann et al., 2022). In-situ experiments in this study demonstrated that CH_4 and CO_2 concentrations in sediments increase with depth, particularly in lakes with low nutrient levels (Fig. 2). As CH_4 moves upward, significant losses occur due to oxygen-induced oxidation processes, which are crucial for managing carbon emissions from lakes effectively (Holgerson et al., 2016). The release of CH_4 and CO_2 from sediments into overlying water elevates dissolved concentrations of these gases, playing a vital role in regulating GHGs emissions (Holgerson et al., 2016). This study noted high CH_4 and CO_2 concentrations in overlying water, positively correlated with increased fluxes of CH_4 (R^2 = 0.65) and CO_2 (R^2 = 0.98) from water to the atmosphere (Figs. 1, 3, S4 and S5).

The escalation of eutrophication is leading to a notable rise in carbon emissions from lakes, largely due to higher levels of organic carbon stemming from cyanobacteria (Shi et al., 2017; Bartosiewicz et al., 2021). The continuous input of cyanobacteria-derived carbon disrupts the sediment carbon pool, leading to higher concentrations of TOC in the sediment (Figs. 4, and S6). This study found that the elevated TOC levels in the sediment spurred the production and release of both CH_4 and CO_2 (Figs. 2, 5, and 6). Increased organic carbon levels boost the activity of anaerobic microorganisms, which are key players in CH_4 and CO_2 production in sediments, promoting the anaerobic breakdown of organic carbon (Deng et al., 2019). It is proposed that the microbial co-metabolism of the sediment carbon pool, triggered by cyanobacterial organic carbon input, results in higher sediment carbon emissions (Deng et al., 2022). This process is driven by the fact that cyanobacteria-derived organic carbon alters the composition of the sediment carbon pool (Ma et al., 2022), mainly comprising unstable and easily decomposable carbon compounds with high primary productivity (Steffenhagen et al., 2012). As a result, metabolic processes and microbial activities in the sediment carbon pool become more active (Figs. 7 and 8). The presence of dissolved organic carbon is crucial in the transport of cyanobacteria-derived carbon into sediment, influencing the carbon dynamics within the sediment (Duan et al., 2022).

It has been reported that cyanobacteria outbreaks and their subsequent accumulation not only elevate organic carbon levels in freshwater lakes but also affect the sediment carbon pool, which is essential for CH_4 and CO_2 production (Braeckman et al., 2019). This impact includes the formation of cyanobacterial detritus mats and alterations in the physicochemical environment (Martinez-Cruz et al., 2018). While surface cyanobacterial detritus mats have been found in the sediments of eutrophic lakes (Qi et al., 2020), more research is necessary to fully

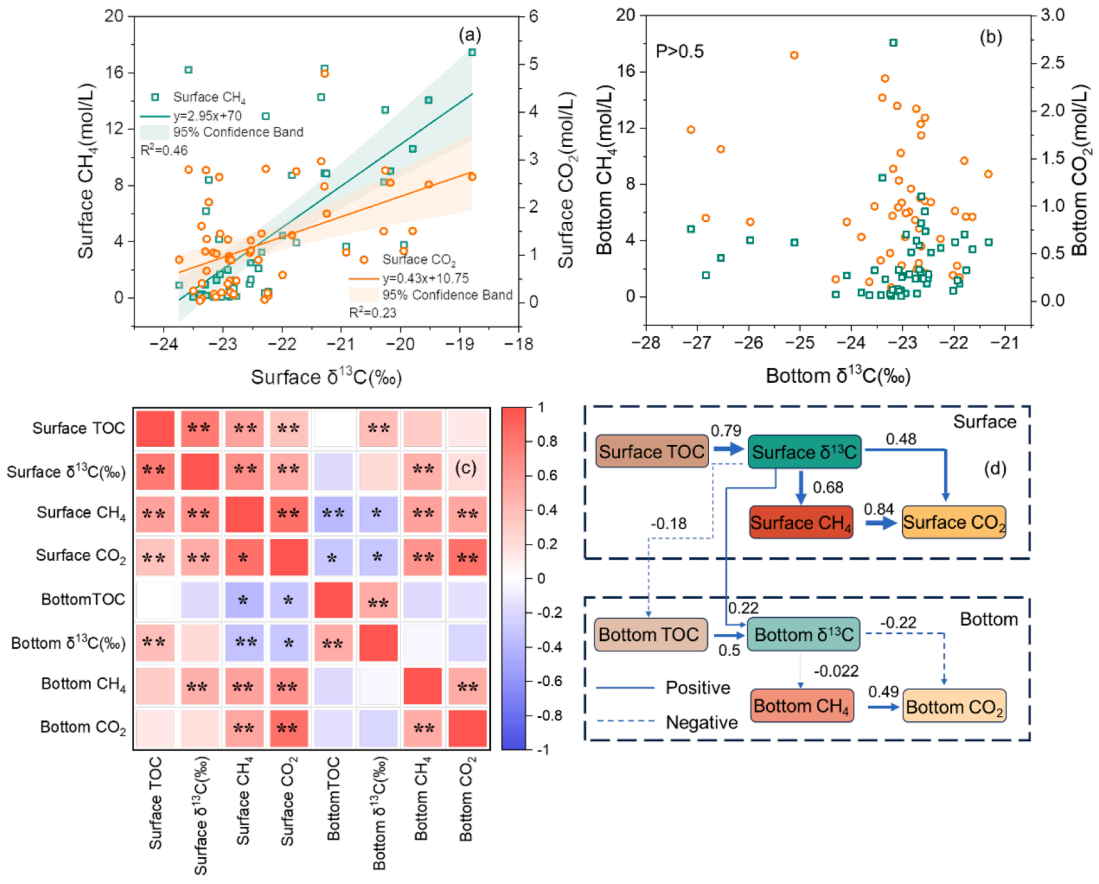

Fig. 6. Correlation analysis of dissolved CH_4 and CO_2 concentrations in surface and bottom sediments with surface $\delta^{13}C$ (a, b), correlation analysis of factors affecting dissolved CH_4 and CO_2 in surface and bottom sediment (c), and contribution of cyanobacteria-derived carbon on dissolved CH_4 and CO_2 in surface and bottom sediment (d). (* and ** indicate the significant differences between expected and observed values at $P < 0.05$ and $P < 0.01$, respectively).

Fig. 7. The initial and finial community structures of microbial in the surface (left) and bottom (right) sediment under different cyanobacteria biomass in microcosms.

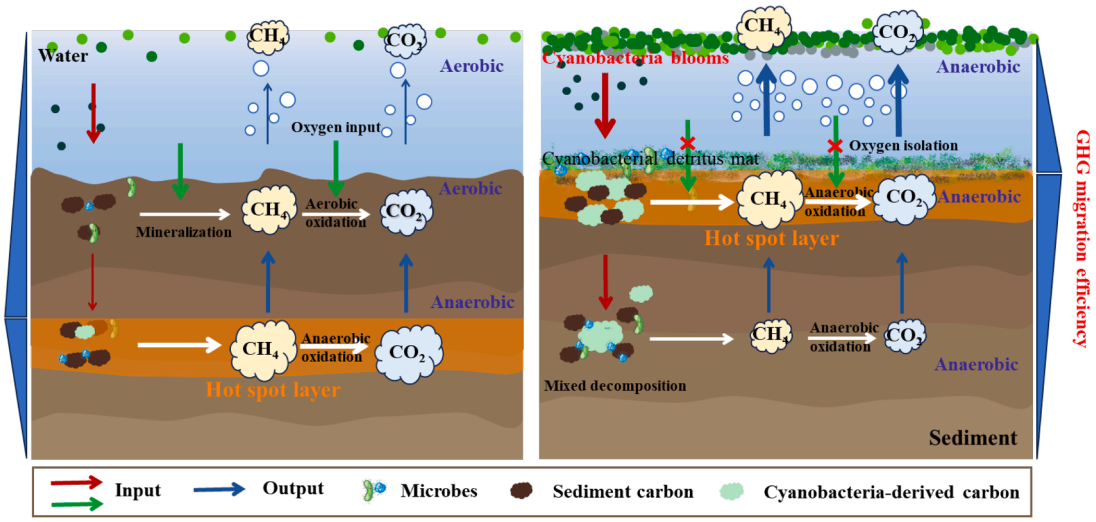

Fig. 8. A conceptual diagram of the mechanism of cyanobacteria decay changes the hot spots of carbon dioxide and methane production along vertical sediment profiles in eutrophic lakes.

comprehend their influence on the CH_4 and CO_2 production, particularly in specific areas where CH_4 and CO_2 are generated.

4.3. *Effects of cyanobacteria-derived carbon on hotspots for CH_4 and CO_2*

Eutrophication-induced cyanobacterial blooms have a significant impact on carbon emissions and the methanogenic zones in sediment. This results in the fromation of hotspots for CH_4 and CO_2 production, driven by the higher concentration of organic carbon in surface sediments and the creation of an anaerobic reducing environment (Figs. 2, 5, 6, and 8). The formation of cyanobacterial detritus mats, composed of cyanobacteria-derived carbon on sediment surfaces, plays a key role in this process (Yang et al., 2021). Using isotopic tracers, this study illustrated that the accumulation of cyanobacteria residues on sediment surfaces led to a marked rise in organic carbon concentrations (Figs. 4, S6 and S8). The cyanobacteria-derived organic carbon primarily enters the sediment carbon pool through gravitational sedimentation (Xu et al., 2015). The continuous influx and migration of cyanobacterial carbon into the sediment substantially raised the abundance of ^{13}C in the bottom sediment, accompanied by a significant increase in organic carbon concentration (Figs. 4, S6 and S8). Despite the rising concentration of organic carbon in bottom sediments, the levels and isotopic abundance of organic carbon in surface sediments remain notably higher, due to the considerable accumulation of surface cyanobacteria residues. With sediment depth increases, there was a noticeable decrease in both the concentration and isotopic abundance of organic carbon (Figs. 4, S6, S7, and S8).

The sediment is the primary site for CH_4 and CO_2 production, as evidenced by multiple field studies. These gases decrease as they move upwards from the sediment bottom (Einzmann et al., 2022). CH_4 and CO_2 production in sediment necessitates an anaerobic setting, with their production being impeded by the micro-aerobic conditions present at the water-sediment interface (Lyautey et al., 2021). Notably, CH_4 undergoes oxidation in the presence of oxygen, and prior studies suggest that lake methane oxidation could potentially mitigate the greenhouse effect by up to 30 % (Pimenov et al., 2014). However, our study challenges this concept, particularly in scenarios marked by substantial cyanobacteria accumulation (Fig. 8). Our findings demonstrate a significant link between CH_4 and CO_2 levels, and the quantities and isotopic compositions of organic carbon across various sediment depths. Surface sediments exhibited significantly higher CH_4 and CO_2 concentrations compared to bottom sediments (Figs. 4, 5, 6, S6~10). The rich organic carbon content in cyanobacterial detritus mats acts as a plentiful carbon source (Figs. 5–7), facilitating organic carbon metabolism and notably boosting CH_4 and CO_2 production in surface sediment (Figs. 4, S6, and S8). Concurrently, the decomposition of cyanobacterial detritus mats leads to low pH, and dissolved oxygen levels, establishing a distinctly anaerobic reducing environment at the water-sediment interface (Martinez-Cruz et al., 2018; Qi et al., 2020). Within this environment, anaerobic microorganisms flourish and partake in metabolic processes involving organic carbon (Figs. 7 and 8). Additionally, the anaerobic conditions further impede the oxidation process of CH_4, resulting in heightened CH_4 emissions (Steinsdottir et al., 2022).

Cyanobacterial detritus mats may enhance a more prominent co-metabolic effect in the surface layer of sediment, potentially leading to the upward movement of methanogenic hotspots within sediments (Figs. 4–6, S6–S8). Recently, the co-metabolic effect triggered by cyanobacterial carbon has been identified as a potential mechanism to increase lake carbon emissions. The breakdown of resistant organic carbon is a key component of this process (Liu et al., 2020; Deng et al., 2023). Shallow lakes tend to accumulate substantial amounts of plant debris in their surface sediments, primarily composed of resistant organic carbon, which can lead to a higher co-metabolic intensity (Deng et al., 2019). Co-metabolism involves the utilization of resistant organic carbon in sediments, facilitating the transition of the lake carbon pool from a source to a sink (Ma et al., 2020; Deng et al., 2023). This study revealed a surprising decrease in organic carbon concentration in the bottom sediments of the experimental group supplemented with cyanobacteria, as opposed to the control group without cyanobacteria, demonstrating a co-metabolic effect (Fig. S7). Moreover, a rapid reduction in $\delta^{13}C$ abundance in sediment was observed alongside with peak CH_4 and CO_2 concentrations, potentially indicating the presence of a co-metabolic effect (Figs. 3–5). The higher carbon content in algal sediments emerged as a key factor leading to elevated concentrations of CH_4 and CO_2 in the surface sediment layer, exceeding those found in deeper sediment layers (West et al., 2012). Additionally, this study observed that cyanobacteria decomposition significantly increased sediment water content, especially in surface sediments. Microcosms containing cyanobacteria had noticeably higher water content compared to those without (Fig. S11). The release of extracellular polysaccharides and mucus by cyanobacteria, followed by subsequent degradation processes, significantly contributed to the rise in sediment water content (Xu et al., 2018). This increase in water content hinders oxygen diffusion, fostering anaerobic bacterial growth and organic carbon mineralization, ultimately boosting CH_4 and CO_2 production in the sediment (Lu et al., 2021). Therefore, eutrophication-induced cyanobacteria significantly

contribute to the upward movement of CH_4 and CO_2 production hotspots in sediments, enhancing the efficiency of carbon gas emissions. These insights contribute to more accurate assessments of lake carbon emissions and provide a theoretical foundation for lake management.

5. Conclusion

Eutrophication-driven cyanobacterial blooms significantly impact the CH_4 and CO_2 emission capacity of sediments by causing the migration of production hotspots. Field investigations in hypereutrophic lakes showed an unusual rise in CH_4 and CO_2 concentrations in the surface pore-water layer, which was confirmed by microcosm experiments. Cyanobacteria-derived carbon accumulates on the sediment surface, altering its physical and chemical properties and increasing water content. This influx of organic carbon boosts microbial activity, especially in surface sediments, leading to increased CH_4 and CO_2 production. The cyanobacterial residues create an environment with high organic carbon, anaerobic conditions, and elevated water content, enhancing organic carbon mineralization. The migration of CH_4 and CO_2 hotspots towards the surface sediment reduces the travel path for carbon emissions. Additionally, the cyanobacterial deposits on the sediment surface hinder methane oxidation and may trigger microbial co-metabolism in the surface sediment, resulting in a significant increase in carbon emissions in the lake. These findings provide valuable insights into the assessment of the impact of cyanobacterial blooms on carbon emissions and the carbon budget of the sedimentary carbon pool.

CRediT authorship contribution statement

Chuanqiao Zhou: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Yu Peng:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Muchun Zhou:** Methodology, Investigation, Data curation, Conceptualization. **Ruoyu Jia:** Methodology, Investigation, Data curation. **Huazu Liu:** Methodology, Investigation, Conceptualization. **Xiaoguang Xu:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis. **Li Chen:** Methodology, Investigation. **Jie Ma:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Tsuyoshi Kinouchi:** Writing – review & editing, Funding acquisition. **Guoxiang Wang:** Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

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