

Microbial Metabolism and Flux of Methane (CH₄) in Marine Sediments and Water Columns

Ming Li, Congbiao You ✉

Hainan Tropical Agricultural Resources Research Institute, Tropical Microbial Resources Research Center, Sanya, 572025, Hainan, China

✉ Corresponding author: congbiao.you@hitar.org

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Abstract Studying the mechanisms by which microbial metabolism in marine sediments and water bodies affects methane production and consumption is of great significance for understanding global methane flux and its contribution to greenhouse effect. This study focuses on the microbial metabolism and flux of methane (CH₄) in marine sediments and water bodies, as well as its importance in the global methane cycle. With the impact of climate change and human activities, the dynamics of methane in marine systems may undergo significant changes. Therefore, in-depth exploration of the role of microbial communities in methane metabolism and the influence of environmental factors on it can help better predict future trends in methane emissions and provide scientific basis for responding to climate change.

Keywords Methane cycle; Microbial metabolism; Marine sediments; Climate change; Methane oxidation

1 Introduction

Methane (CH₄) is a potent greenhouse gas with significant implications for global climate change. In marine systems, methane is produced primarily in anoxic sediments by methanogenic archaea through the anaerobic degradation of organic matter (Conrad, 2020). The majority of this methane is oxidized before it reaches the atmosphere, primarily through sulfate-dependent anaerobic oxidation of methane (S-AOM) in the sulfate-methane transition zone (SMTZ) (Wallenius et al., 2021; Wang et al., 2021). However, methane can also be oxidized aerobically by methanotrophic bacteria in the upper layers of sediments and water columns (Taubert et al., 2019). The balance between methane production and oxidation is influenced by various biogeochemical processes and environmental factors, including the availability of electron acceptors, organic matter inputs, and redox conditions (Aromokeye et al., 2020; Rahmati-Abkenar et al., 2021).

Understanding methane metabolism in marine environments is crucial due to its role in the global carbon cycle and its impact on climate change. Methane emissions from marine systems, such as coastal sediments, methane seeps, and gas hydrates, contribute significantly to atmospheric methane levels (Dean et al., 2018; Taubert et al., 2019). The microbial processes that control methane production and oxidation are complex and involve various functional guilds of microorganisms, including methanogens, methanotrophs, and other associated microbial communities (Taenzer et al., 2020). Studying these processes helps in predicting future methane emissions and developing strategies to mitigate their impact on climate change.

This study integrates current knowledge on microbial methane metabolism and methane flux in marine sediments and water columns. It will cover key microbial processes involved in methane production and oxidation, environmental factors affecting these processes, and the impact of climate change on methane emissions. We will also focus on the latest developments in methane kinetic modeling and identification of microbial participants involved in the methane cycle. To gain a comprehensive understanding of methane metabolism in the ocean system and its importance for global methane budgeting and climate prediction.

2 Microbial Communities Involved in Methane Metabolism

2.1 Methanogens in marine sediments

Methanogens are a group of archaea responsible for the production of methane in anoxic marine sediments. These

microorganisms utilize substrates such as carbon dioxide, acetate, and methylated compounds to produce methane. In coastal sediments, methanogenic activity is influenced by the availability of organic matter and electron acceptors. For instance, in the Shenhu area of the northern South China Sea, methanogens such as *Methanococcoides* and *Methanosarcina* were found to increase slightly in abundance under certain incubation conditions, although their overall presence remained low (Kong et al., 2022). Additionally, in the Yangtze Estuary, the abundance of methanogens was significantly impacted by anthropogenic activities, with elevated levels of methane metabolism-related microbes observed in areas affected by wastewater treatment plant effluents (Guo et al., 2019).

2.2 Methanotrophs in water columns

Methanotrophs are bacteria that oxidize methane, thereby mitigating its release into the atmosphere. These microorganisms are particularly active in the water columns above methane seeps and in the upper layers of sediments. In deep oligotrophic Lake Constance, members of the *Methylococcaceae* family were found to be highly active in oxidizing methane, significantly reducing methane emissions from sediment seeps (Bornemann et al., 2016). Similarly, in shallow marine seeps near Elba, Italy, *Methylococcaceae* and *Methylophilaceae* were identified as key players in rapid aerobic methane oxidation, with *Methylococcaceae* catalyzing the initial step of methane oxidation to methanol, which was then utilized by *Methylophilaceae* (Taubert et al., 2019).

2.3 Interactions between methanogens and methanotrophs

Methanotrophs are bacteria that oxidize methane, thereby mitigating its release into the atmosphere. These microorganisms are particularly active in the water columns above methane seeps and in the upper layers of sediments. In deep oligotrophic Lake Constance, members of the *Methylococcaceae* family were found to be highly active in oxidizing methane, significantly reducing methane emissions from sediment seeps (Ruff et al., 2016). Similarly, in shallow marine seeps near Elba, Italy, *Methylococcaceae* and *Methylophilaceae* were identified as key players in rapid aerobic methane oxidation, with *Methylococcaceae* catalyzing the initial step of methane oxidation to methanol, which was then utilized by *Methylophilaceae* (Jing et al., 2020).

2.4 Influence of environmental factors on microbial activity

Environmental factors such as the availability of electron acceptors, organic matter inputs, and anthropogenic impacts play a significant role in shaping the activity and composition of methane-cycling microbial communities. In coastal sediments, the availability of sulfate, iron, and nitrate as electron acceptors can influence the pathways of methane oxidation. Pollution and eutrophication can also alter microbial community structures, as observed in small polluted ponds where high pollution levels led to significant shifts in methanogenic and methanotrophic communities (Wang et al., 2021). Additionally, global warming and climate change can enhance water column stratification and primary production, favoring methanogenesis in coastal areas (Wallenius et al., 2021).

3 Methane Production in Marine Sediments

3.1 Anaerobic methane production

3.1.1 Biochemical pathways of methanogenesis

Methanogenesis in marine sediments is primarily driven by methanogenic archaea through several biochemical pathways. The two main pathways are hydrogenotrophic methanogenesis, where methane (CH_4) is produced from hydrogen (H_2) and carbon dioxide (CO_2), and acetoclastic methanogenesis, where methane is produced from acetate (Conrad, 2020; Shuai et al., 2021). Additionally, methylotrophic methanogenesis, which involves the conversion of methylated compounds such as methanol and methylamine to methane, also plays a significant role. These pathways are tightly regulated by the availability of substrates and environmental conditions, such as the presence of electron acceptors like sulfate, nitrate, and metal oxides (Wegener et al., 2016).

3.1.2 Role of organic matter in methane production

The availability and type of organic matter are crucial in determining the rate and extent of methane production in marine sediments. Organic matter serves as the primary substrate for methanogenesis, undergoing initial fermentation to produce intermediates like acetate and H_2 , which are then utilized by methanogens. In eutrophic coastal areas, high organic matter inputs can lead to increased methanogenesis due to enhanced microbial activity

and subsequent depletion of electron acceptors (Wallenius et al., 2021). The type of organic matter also influences the methanogenic pathways, with more complex organic compounds favoring acetivlastic methanogenesis, while simpler compounds like methanol and methylamine support methylotrophic methanogenesis (Shuai et al., 2021).

3.2 Role of temperature and pressure in methane generation

Temperature and pressure significantly impact methane production in marine sediments. Higher temperatures generally enhance methanogenic activity by increasing the metabolic rates of methanogens. For instance, in sub-Antarctic lake sediments, a temperature increase from 5°C to 20°C resulted in a substantial rise in methane production rates, particularly favoring hydrogenotrophic methanogenesis at higher temperatures (Lavergne et al., 2021). Pressure, on the other hand, affects the solubility of gases and the physical properties of sediments, which can influence microbial activity and methane production. In deep-sea environments, high pressure can limit the diffusion of substrates and products, thereby affecting the overall rate of methanogenesis (Martinez-Cruz et al., 2017).

3.3 Methane fluxes in different marine sedimentary environments

Methane fluxes vary significantly across different marine sedimentary environments due to variations in microbial communities, substrate availability, and environmental conditions. Coastal sediments, characterized by lower sulfate concentrations (Figure 1), often exhibit higher methane emissions due to reduced sulfate-dependent anaerobic oxidation of methane (AOM) (Wallenius et al., 2021). In contrast, deep-sea cold seeps and hydrate-bearing sediments show complex methane dynamics, with significant contributions from both methanogenesis and AOM processes. In these environments, microbial consortia involving anaerobic methane-oxidizing archaea (ANME) and sulfate-reducing bacteria (SRB) play a crucial role in mitigating methane emissions (Kong et al., 2022). Additionally, the presence of alternative electron acceptors like nitrate and metal oxides can further influence methane fluxes by supporting different AOM pathways (Jing et al., 2020).

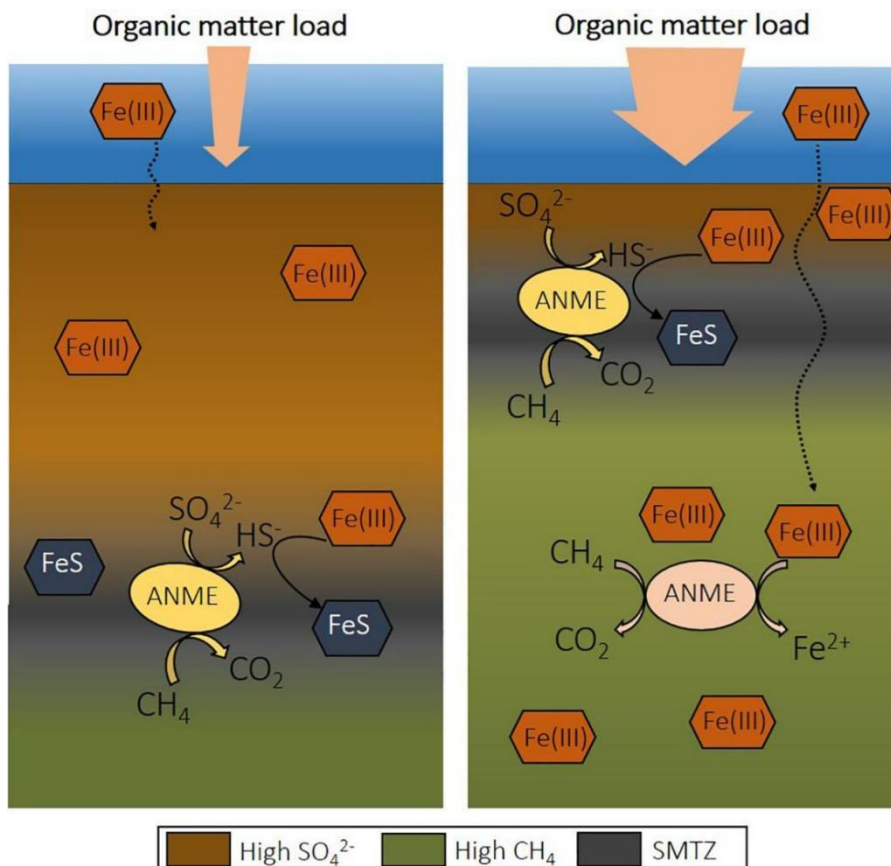


Figure 1 The effect of eutrophication on the depth of the sulfate-methane transition zone (SMTZ) in coastal sediment and the potential for Fe-AOM (Adopted from Wallenius et al., 2021)

4 Methane Oxidation in Water Columns

4.1 Aerobic methane oxidation

Aerobic methane oxidation is primarily facilitated by methanotrophic bacteria, which utilize methane as a carbon and energy source in the presence of oxygen. In marine environments, members of the *Methylococcaceae* family are key players in this process. For instance, in the sediments of a shallow seep near Elba, Italy, *Methylococcaceae* were found to catalyze the first step of methane oxidation to methanol, which was then further processed by methylotrophic *Methylophilaceae*, demonstrating a communal metabolism that significantly mitigates methane emissions (Figure 2) (Taubert et al., 2019). Additionally, aerobic methanotrophs such as *Methylobacter* have been identified in sub-Arctic lake sediments, where they assimilate carbon from methane, either directly or indirectly, contributing to the reduction of methane emissions in these regions (Nie et al., 2021).

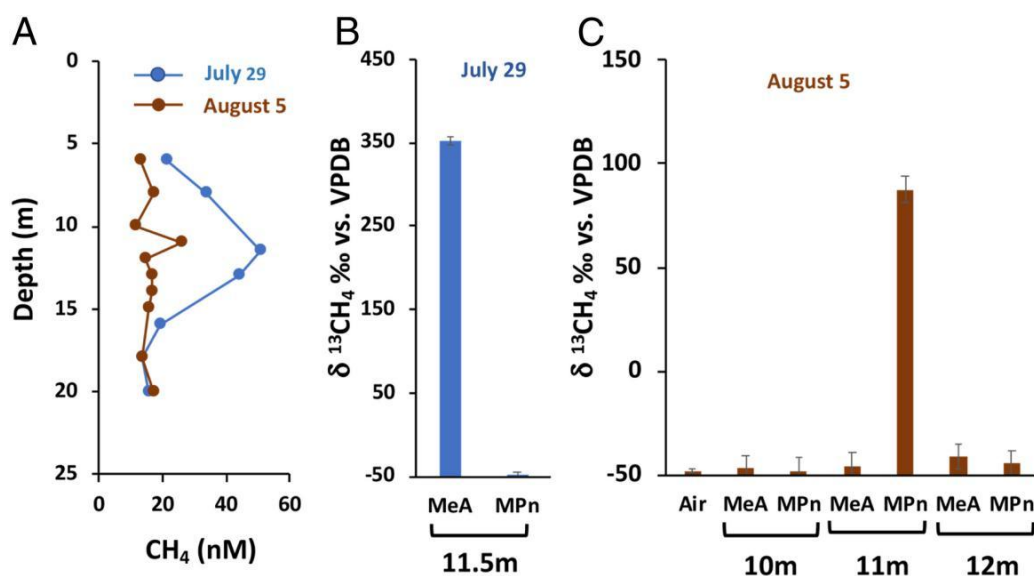


Figure 2 Characterization of the water column methane and MPn and MeA metabolism potential of the PMEZ microbial communities (Adopted from Wang et al., 2021)

4.2 Anaerobic methane oxidation

4.2.1 Coupling of methane oxidation with sulfate reduction

AOM coupled with sulfate reduction is a well-documented pathway in marine sediments. This process involves ANME archaea and their SRB partners, which together oxidize methane and reduce sulfate to sulfide. For example, in long-term incubations of sediments from the Shenhu area of the northern South China Sea, AOM was observed alongside sulfate reduction, indicating the presence of these microbial consortia (Chai et al., 2020). Similarly, in sediment-free long-term AOM enrichments from marine seeps, ANME-2 archaea and Seep-SRB2 bacteria were found to dominate, further supporting the role of sulfate reduction in AOM (Wegener et al., 2016).

4.2.2 Nitrite-dependent methane oxidation

Nitrite-dependent anaerobic methane oxidation (n-DAMO) is another significant pathway, particularly in environments where nitrite is available as an electron acceptor. This process is primarily mediated by bacteria such as "*Candidatus Methyloirabilis oxyfera*" and "*Candidatus Methyloirabilis sinica*." In deep-sea cold seeps, n-DAMO bacteria like *Methyloirabilis* and *Methanoperedens* have been identified as key performers, utilizing nitrite and nitrate, respectively, as electron acceptors. Additionally, in bioelectrochemical reactors, methane oxidation driven by nitrite reduction was observed, with *Methyloirabilis oxyfera* playing a significant role (Chai et al., 2020).

4.3 Enzymes and genes involved in methane oxidation pathways

The enzymes and genes involved in methane oxidation pathways are critical for understanding the biochemical mechanisms underlying these processes. In aerobic methane oxidation, enzymes such as methane monooxygenase (MMO) play a pivotal role. For instance, in the sediments of a shallow seep near Elba, Italy, the presence of MMO

in *Methylococcaceae* was crucial for the initial oxidation of methane to methanol (Taubert et al., 2019). In anaerobic environments, the key enzymes and genes are associated with the ANME archaea and their SRB partners. Metatranscriptomic analysis has revealed significant upregulation of genes such as *flaB* in ANME-2d and *pilA* in *Desulfococcus*, which are likely involved in the formation of nanonets for electron transfer between ANME and SRB (Nie et al., 2021). Additionally, in nitrite-dependent methane oxidation, genes related to nitrite reduction and stress response systems are critical for the niche differentiation of n-DAMO bacteria like "Candidatus *Methylomirabilis oxyfera*" and "Candidatus *Methylomirabilis sinica*" (Nie et al., 2023).

5 Factors Controlling Methane Flux

5.1 Physical factors (temperature, pressure, salinity)

Physical factors such as temperature, pressure, and salinity play crucial roles in controlling methane flux in marine environments. Temperature influences the metabolic rates of methanogenic and methanotrophic microorganisms, with higher temperatures generally enhancing microbial activity and methane production (Klasek et al., 2019). Pressure, particularly in deep-sea environments, affects the solubility of gases and the stability of methane hydrates, which can act as significant methane reservoirs (Aromokeye et al., 2020). Salinity impacts the availability of electron acceptors and the composition of microbial communities, with lower salinity environments often exhibiting reduced sulfate concentrations, thereby affecting sulfate-dependent anaerobic oxidation of methane (S-AOM) (Wallenius et al., 2021).

5.2 Biological controls (microbial activity, community composition)

Biological factors, including microbial activity and community composition, are pivotal in regulating methane flux. Methanotrophic bacteria, such as those from the *Methylococcaceae* family, play a significant role in oxidizing methane before it escapes to the atmosphere (Bornemann et al., 2016; Taubert et al., 2019). The presence and activity of anaerobic methanotrophic archaea (ANME) and their interactions with sulfate-reducing bacteria (SRB) are critical in the sulfate-methane transition zone (SMTZ), where a substantial portion of methane is oxidized. The community composition of methanotrophs, including niche separation between Alpha- and Gamma-MOB, also influences methane oxidation rates and overall methane flux (Reis et al., 2019).

5.3 Human impacts on methane emission and uptake

Human activities, such as eutrophication and climate change, significantly impact methane emissions and uptake in marine environments. Eutrophication, driven by nutrient runoff, increases organic matter inputs, leading to hypoxia and enhanced methanogenesis in coastal sediments. Climate change, through global warming, reduces oxygen solubility in surface waters, promoting water column stratification and further enhancing methanogenesis (He et al., 2019). Additionally, anthropogenic disturbances, such as gas blowouts, can create high methane flux sites, where microbial communities rapidly adapt to oxidize methane, mitigating its release to the atmosphere (Steinle et al., 2016).

6 Global Significance of Methane Flux in Marine Systems

6.1 Contribution of marine methane emissions to global greenhouse gas levels

Methane (CH₄) is a potent greenhouse gas with a global warming potential significantly higher than carbon dioxide (CO₂) over a 100-year period. Marine systems, particularly coastal areas, contribute substantially to global methane emissions. Coastal sediments are major sources of methane due to the activity of methanogenic archaea in anoxic conditions (Mai et al., 2024). However, a significant portion of this methane is oxidized before it reaches the atmosphere, primarily through sulfate-dependent anaerobic oxidation of methane (S-AOM) in the sulfate-methane transition zone (SMTZ). Vegetated coastal ecosystems (VCEs) such as mangroves, salt marshes, and seagrasses also play a critical role, contributing approximately 0.33~0.39 Tmol CH₄-C/year, which increases the global marine methane budget by more than 60% (Arnold et al., 2023). Despite the mitigation by microbial oxidation, methane emissions from marine systems remain a significant component of the global greenhouse gas inventory.

6.2 Role of marine systems in global methane cycling

Marine systems are integral to the global methane cycle, acting both as sources and sinks of methane. Methane is

produced in marine sediments through microbial methanogenesis and can be released into the water column and eventually the atmosphere. However, various microbial processes, including aerobic and anaerobic oxidation, significantly mitigate these emissions. For instance, aerobic methane-oxidizing bacteria (methanotrophs) in the water column can oxidize methane, preventing its release into the atmosphere (Bornemann et al., 2016). In eutrophic coastal areas, the interplay between methanogenesis and methane oxidation is influenced by factors such as organic matter input, oxygen availability, and the presence of alternative electron acceptors like metal oxides and nitrate (Żygadłowska et al., 2023). Additionally, microbial communities in methane seeps and pockmarks play a crucial role in methane oxidation, further highlighting the complex interactions within marine methane cycling (Taubert et al., 2019).

6.3 Impact of climate change on marine methane dynamics

Climate change has profound effects on marine methane dynamics, potentially increasing methane emissions through various mechanisms. Rising temperatures can enhance methanogenesis in marine sediments and reduce the solubility of oxygen in surface waters, leading to increased stratification and hypoxia, which favor methane production (Dean et al., 2018). Eutrophication, driven by increased nutrient inputs, can exacerbate these conditions, further promoting methane emissions (Qian et al., 2022). Additionally, sea level rise and changes in hydrology can alter the redox conditions in sediments, affecting the availability of electron acceptors for methane oxidation. The feedback loop between methane emissions and climate change is a critical area of study, as increased methane emissions can further accelerate global warming, creating a positive feedback mechanism.

7 Technological Advances in Methane Measurement

7.1 In situ sensors for methane detection

In situ sensors for methane detection have significantly advanced our ability to monitor methane concentrations directly within marine sediments and water columns. These sensors provide real-time data, which is crucial for understanding the dynamics of methane fluxes in various marine environments. For instance, the study by Wallenius et al. (2021), demonstrating the importance of accurate in situ measurements for robust carbon budget estimations. Additionally, the research conducted at a methane seep near Elba, Italy, highlighted the role of in situ sensors in measuring methane oxidation rates, which were found to be up to 871 nmol of methane per gram of sediment per day (Żygadłowska et al., 2023).

7.2 Stable isotope techniques for tracing methane sources

Stable isotope techniques have become a powerful tool for tracing the sources and processes affecting methane in marine environments. By analyzing the isotopic compositions of methane ($\delta^{13}\text{C}$ and $\delta^2\text{H}$), researchers can distinguish between different methane production and oxidation pathways. For example, the study on Lake Biwa utilized stable isotope measurements to determine that excess methane in oxic surface waters originated from the littoral zone via lateral transport (Tsunogai et al., 2020). Similarly, proteomic stable isotope probing (SIP) has been employed to track protein synthesis in methane-impacted microbial communities, revealing the active synthesis of enzymes involved in anaerobic oxidation of methane (AOM) (Marlow et al., 2016). These techniques provide detailed insights into the biogeochemical cycling of methane and the specific microbial processes involved (Meister et al., 2019).

7.3 Advancements in modeling methane fluxes

Modeling methane fluxes in marine sediments and water columns has seen significant advancements, allowing for better predictions and understanding of methane dynamics. The development of dynamic transport-reaction models, as presented in the study by (Rahmati-Abkenar et al., 2021), enables the prediction of methane concentrations without requiring initial values, thus providing a robust tool for carbon budget estimations. Another study modified a biofilm model originally developed for wastewater treatment to simulate microbial kinetics and substance conversions in aqueous surface sediments, revealing the complex interactions between different microbial communities and environmental factors (Chen, 2024). These models are crucial for explaining phenomena that are difficult to resolve experimentally, such as the alternation between atmospheric methane

sources and sinks in unstable sediments. Furthermore, the integration of isotopic data into these models helps in understanding the isotopic fractionation during microbial carbon metabolism, as demonstrated by the research on the isotopic composition of dissolved inorganic carbon and methane in marine porewater (Meister et al., 2019). These advancements in modeling are essential for predicting the impacts of environmental changes on methane fluxes and for developing strategies to mitigate methane emissions.

8 Conclusion

The research on microbial metabolism and methane flux in marine sediments and water columns has revealed several critical insights. Methanotrophic microorganisms, particularly from the families *Methylococcaceae* and *Methylophilaceae*, play a significant role in mitigating methane emissions by oxidizing methane at the sediment-water interface. In coastal sediments, sulfate-dependent anaerobic oxidation of methane (S-AOM) by consortia of anaerobic methane-oxidizing archaea (ANME) and sulfate-reducing bacteria (SRB) is a major process, although alternative electron acceptors like metal oxides or nitrate can also drive anaerobic oxidation of methane (AOM). High methane oxidation rates have been observed in both sediment and water columns, with notable contributions from aerobic methanotrophs in the water column. Additionally, dynamic modeling approaches have been developed to predict microbial methane generation and consumption, providing robust tools for carbon budget estimation in marine sediments. The interplay between microbial activity and climate change is crucial, as increased methane emissions from marine systems could induce further climate change, creating a positive feedback loop.

Future research should focus on several key areas to enhance our understanding of methane cycling in marine environments. First, there is a need for more detailed studies on the factors controlling methane emissions from coastal sediments, particularly in eutrophic areas where organic matter inputs and oxygen availability can significantly influence methane cycling. Additionally, the role of alternative electron acceptors in AOM and the specific microorganisms involved require further exploration. Long-term studies on the response of microbial communities to changes in methane and sulfate supplies are also essential, as current research suggests that active anaerobic methanotrophic populations may take years to develop. Moreover, the development and application of advanced modeling approaches to simulate methane processes in extreme marine environments, such as mud volcanic eruptions and hydrate leakage, are critical for accurate predictions of methane emissions.

Marine methane plays a dual role in the context of climate change. On one hand, methane emissions from marine sediments and water columns contribute to global warming due to methane's potency as a greenhouse gas. On the other hand, microbial communities in marine environments act as significant methane filters, mitigating the release of methane to the atmosphere. The efficiency of these microbial filters, particularly in the face of climate change and anthropogenic impacts, is a crucial area of study. Understanding the balance between methane production and consumption under future climate scenarios is essential for predicting the role of marine methane in global climate feedbacks. Enhanced knowledge of microbial pathways and geochemical processes will lead to more accurate predictions of methane emissions and help develop strategies to mitigate the impact of methane on climate change.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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