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Significance of anaerobic oxidation of methane (AOM) in mitigating methane emission from major natural and anthropogenic sources: a review of AOM rates in recent publications†

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Methane is estimated to have contributed 20% of postindustrial global warming. Methanotrophs oxidize methane and curb methane emissions into the atmosphere. Anaerobic oxidation of methane (AOM) has been recognized as an important methane sink. Sulfate is the primary electron acceptor of AOM in the marine environment, while nitrite/nitrate is encountered more often in terrestrial water-logged systems, such as rice paddy and wetlands. A key aspect of AOM is the reaction rate, which influences methane fluxes to the oxic zones and eventually the atmosphere. We collated the AOM rates from major natural and anthropogenic sources in recent publications and found that AOM rates are generally lower than the corresponding aerobic methane oxidation rates in wetlands and rice paddy, while the AOM rates are often higher than the corresponding aerobic oxidation rates in freshwater systems and marine environments. Based on the median reaction rates and estimated aerobic and anoxic zone coverages, AOM consumes approximately 71%, 8%, 5%, 13%, and 3% of the methane entering the anoxic zones in oceans, wetlands, paddy systems, lakes/reservoirs, rivers, respectively. These analyses suggest that AOM is a key methane sink in oceans, while aerobic methanotrophs consume more methane in the other studied ecosystems. Finally, the controlling factors of AOM and some issues in the rate quantification were discussed. It is believed that more comprehensive studies of AOM and improved rate quantification would assist in forecasting methane emission, which fosters scientific debate over global warming and eventually affects climate policymaking.

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Environmental significance

Anaerobic oxidation of methane (AOM) has been a focus of study for a few decades but there is still a lack of comparison of AOM rates across different methane sources. Besides, the current methane budget and global methane cycling analyses often do not consider AOM as a methane sink due to insufficient information on the distribution of AOM activity. The simplified analysis of methanotrophic rates in this study showed that anaerobic methanotrophs are sometimes more efficient than aerobic methanotrophs. A generalized model for AOM rate prediction does not exist, and the usually slow growth of anaerobic methanotrophs may be a key reason behind these low rates. A more systematic AOM study and improved AOM rate quantification will help us better understand the cycling of methane in nature and better control the emission of this greenhouse gas.

1. Introduction

Methane is a potent greenhouse gas that has 25 to 35 times the global warming potential of CO_2 over a century timescale.[1] Methane can be released from both natural (*e.g.*, wetlands, lakes/ponds, rivers, and oceans) and anthropogenic sources (*e.g.*, rice paddy).[1] The amount of methane entering the atmosphere usually depends on not only methanogenesis (*i.e.*, the microbial formation of methane) but also methanotrophy (*i.e.*, the microbial processes that consume methane, aerobic or anoxic, as shown in Fig. 1). AOM has been reported in all the aforementioned environments as an important methane degradation pathway and a growing number of publications suggest that AOM is an integral part of the methane sink.[2–7] Although "anaerobic" is used in AOM, AOM usually occurs under anoxic conditions with common electron acceptors other than oxygen (Fig. 1). To avoid potential misunderstanding by readers from various disciplines, this review used "anoxic" if possible. For example, in marine sediments where methane

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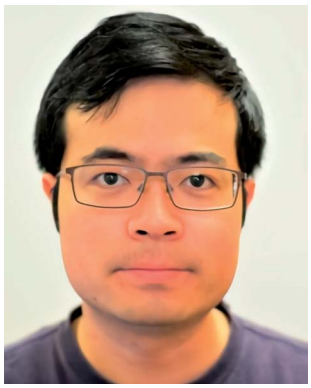
generated deep in the seabed travels upwards by diffusion, almost all the methane generated is oxidized by anaerobic methanotrophs (ANME) and their bacterial partners before entering the seawater.[8,9] The pathway by which ANME utilizes methane is commonly agreed upon to be the reversal of methanogenesis.[9] The bacterial partners are often related to sulfate-reducing bacteria (SRB), and these bacteria metabolize sulfur compounds, which serve as electron acceptors (eqn (1); eqn (2) and (3) represent one of the possible reaction pathways, and the sum of the two steps leads to eqn (1)).[10] So far, three main marine clades, ANME-1a/b, ANME-2a/b/c, and ANME-3, have been identified.[11,12] The reports of AOM coupled with denitrification around 2004 (ref. 2 and 13) imply that AOM can be coupled with the reduction of nitrate/nitrite, not just sulfate. Later, studies showed that methanotrophic bacteria and ANME can also couple the oxidation of methane to the reduction of other electron acceptors such as iron[11] and these electron acceptors sometimes decouple methane oxidation from sulfate reduction.[8]

$$CH_4 + SO_4^{2-} \rightarrow HCO_3^- + HS^- + H_2O \text{ (ref. 15)} \quad (1)$$

$$7CH_4 + 8SO_4^{2-} + 5H^+ \rightarrow 4HS_2^- + 7HCO_3^- + 11H_2O \text{ (ref. 10)} \quad (2)$$

$$4HS_2^- + 4H_2O \rightarrow SO_4^{2-} + 7HS^- + 5H^+ \text{ (ref. 10)} \quad (3)$$

AOM has also been observed in anoxic freshwater and terrestrial environments, such as lakes, rivers, wetlands, paddy systems, and even deep underground in fractured granitic rocks.[4,16–20] DAMO (denitrifying anaerobic methane oxidation) has been demonstrated as a major AOM pathway in terrestrial environments.[21–24] DAMO entails two different processes, *i.e.* nitrite-DAMO and nitrate-DAMO (eqn (4) and (5)). The former is proposed to be intracellular aerobic methane oxidation,[2] first



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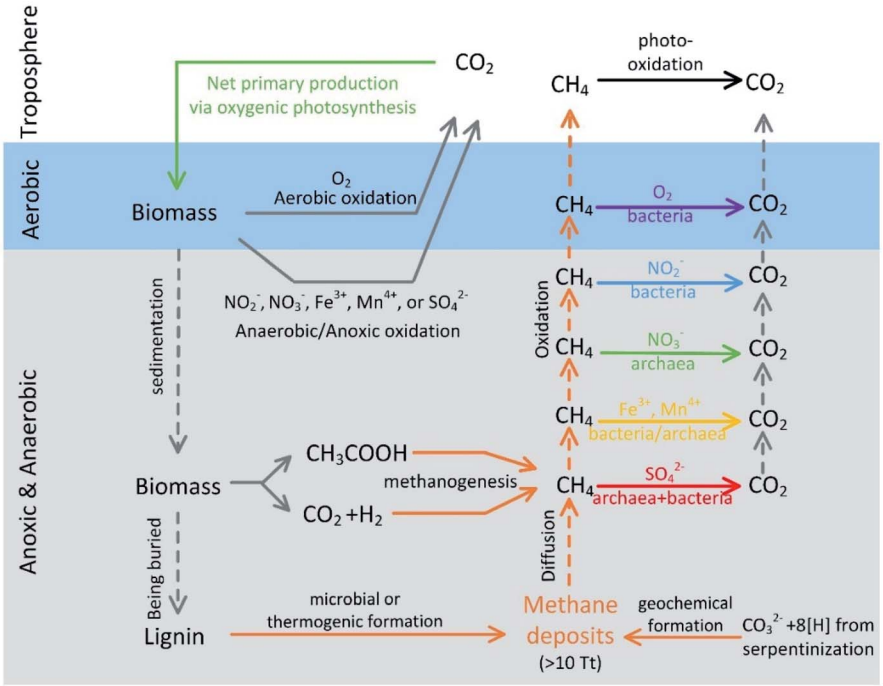

Fig. 1 A sketch of the carbon cycle with a focus on methane generation and oxidation pathways (reproduced from R. K. Thauer[14] with permission from Elsevier, copyright [2011]).

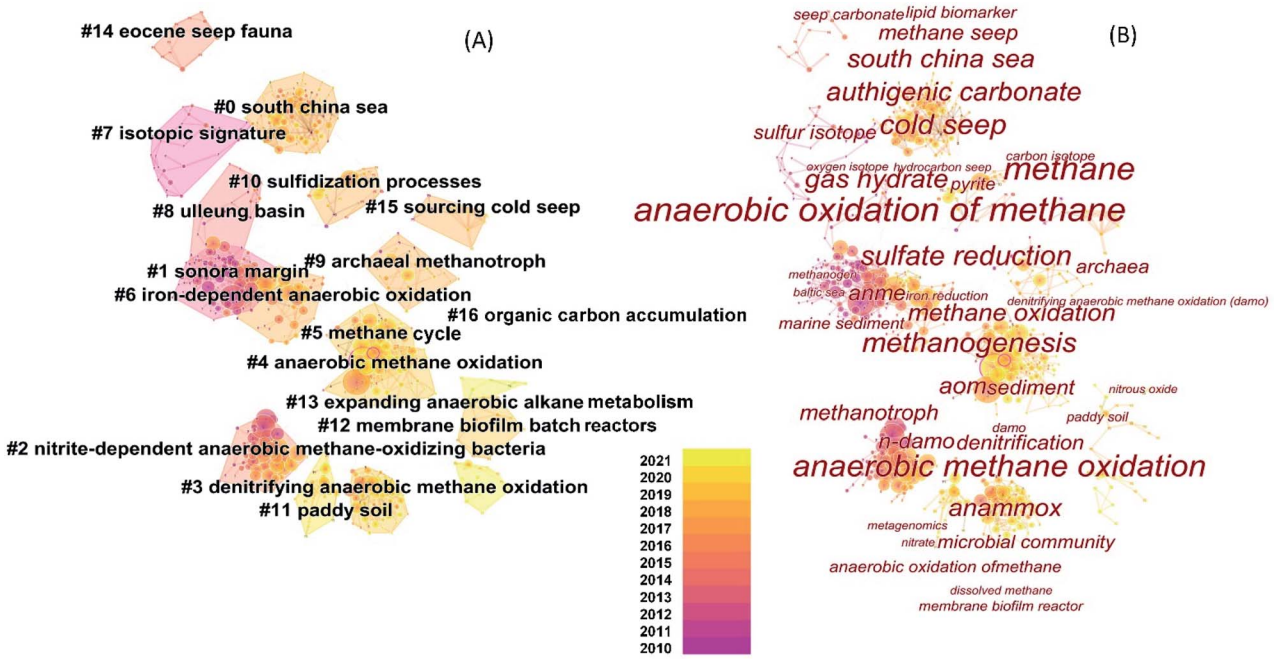

Fig. 2 Clustering analysis (CiteSpace V5.3.R11) of the anaerobic methane oxidation co-citation network (A), generated by the top 30 per slice between 2010 and 2021. In this visualization, the earliest work (*i.e.*, 2010) appeared from the left of the network (purple), whereas the most recent ones are close to the right (gold). This network is decomposed into clusters of references based on the strengths of co-citation links, and the clusters are numbered in the descending order of their size. The largest one is numbered as 0, followed by 1, and so on. Names of the clusters were based on the titles of all studied publications (1384 publications and 46 091 distinct references) with the log-likelihood ratio algorithm. (B) The network with the major nodes labeled by the extracted keywords from the titles and abstracts based on the frequency of usage. The bigger size of a keyword indicates a higher frequency of usage. A node represents an article. A larger node means a higher frequency of citation.

found to be catalyzed by the NC10 bacterium "*Candidatus Methylomirabilis oxyfera*". Later, some other species from the NC10 phylum have been identified, *i.e. M. sinica*,[25] *M. limnetica*,[26] and *M. lanthanidiphila*.[27] The nitrate-DAMO was found to be carried out by anoxic archaea belonging to the ANME-2d clade,[28] which is more prevalent in terrestrial environments than other ANME-2 clades.[28–30] A frequently reported nitrate-reducing archaeal species, named "*Candidatus Methanoperedens nitroreducens*", also applies reverse methanogenesis for AOM.[28] Besides, recent studies also indicate that DAMO archaea can couple AOM with the reduction of Fe(III) (eqn (6)) and sulfate,[31,32] implying that DAMO may also be active in environments with non-nitrogen-based electron acceptors.

$$2CH_4 + 8NO_3^- \rightarrow 2CO_2 + 8NO_2^- + 4H_2O \text{ (ref. 33)} \quad (4)$$

$$3CH_4 + 8NO_2^- + 8H^+ \rightarrow 3CO_2 + 4N_2 + 10H_2O \text{ (ref. 33)} \quad (5)$$

$$CH_4 + 8Fe^{3+} + 2H_2O \rightarrow CO_2 + 8Fe^{2+} + 8H^+ \text{ (ref. 32)} \quad (6)$$

The research of AOM has been under development for approximately five decades.[29,34] The progress and evolution in the past decade or so can be largely visualized by the co-citation network based on recently published research articles and review papers (Fig. 2). Generally, AOM studies have expanded to environments other than methane seeps or marine sediment. The research topics or keywords that could be considered central to AOM research can be found in Fig. 2B. For example, DAMO is becoming one of the prominent research areas. The interactions between carbon cycling and nitrogen cycling in freshwater ecosystems and engineered systems have been two other research focuses.

Instead of detailing the various reaction pathways, reaction thermodynamics, biochemical mechanisms, microbial physiology, and the various implications in natural and engineered systems like other reviews,[7,9,35–44] this review article concentrates on recently published AOM rates in the literature (*ca.* 2010–2021). The AOM rates were organized according to the environment where the reactions occur. In both major natural and anthropogenic methane sources, the AOM rates are compared with the corresponding aerobic rates of methane oxidation. Additionally, the AOM capabilities of various methanotrophs enriched in biological reactors, mainly DAMO microorganisms,[23,33,45–53] are summarized as references for the currently highest possible AOM rates. To reveal the significance of AOM as a methane sink, the annual rates of methane oxidation in major methane sources were estimated. Finally, the controlling factors for AOM and some issues in the rate quantification were briefly discussed.

2. AOM in major methane sources

2.1 Terrestrial and freshwater environments

2.1.1 Wetlands. Freshwater wetlands account for one-third of total methane emissions to the atmosphere.[54] Besides, the methane emission from freshwater wetlands is almost 290 times the total methane emission from coastal wetlands or coastal vegetated ecosystems (*e.g.*, mangroves, seagrasses, and salt marshes).[55] Thus, the discussion in this section mainly focused on freshwater wetlands. In addition to aerobic oxidation induced by wetland vegetation, which oxidizes 16% to over 90% of the methane at their roots and/or plant parts in the water-logged soils,[56] aerobic methanotrophs in oxic zones oxidize methane at the rates of 0.03 $nmol_{CH_4}\ cm^{-3}\ d^{-1}$ to 3.6×10^3 $\mu mol_{CH_4}\ cm^{-3}\ d^{-1}$ (median = 0.16 $\mu mol_{CH_4}\ cm^{-3}\ d^{-1}$, Q1–Q3 [first to third quartiles]: 0.04–0.7 $\mu mol_{CH_4}\ cm^{-3}\ d^{-1}$) (Fig. 4), accounting for 2–79% of the methane efflux to the atmosphere.[57–61] AOM was found to be another methane sink[20,62] in freshwater wetlands and was estimated to reduce methane emissions by around 5.7% to over 50%.[4,63] AOM in wetlands has been reported to be mainly catalyzed by DAMO microorganisms, including DAMO bacteria and DAMO archaea. For example, according to the detection of *pmoA* (the gene targeting the alpha subunit of particulate methane monooxygenase, a gene marker for DAMO bacteria[64]) and the 16S rRNA genes of DAMO bacteria, 68% and 90% of the studied wetlands in China showed DAMO activity.[65] The incubation of soils from the Zoige National Wetland Reserve, on the Tibetan Plateau, indicates

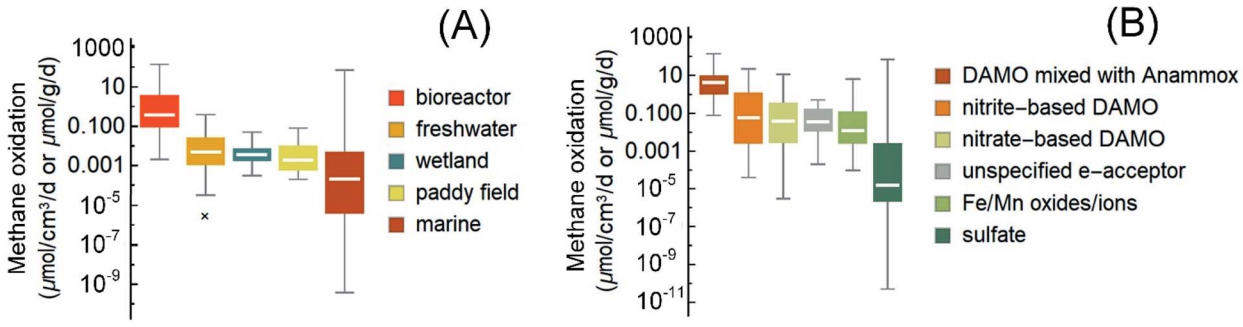

Fig. 3 Box-and-whisker plots of the reported rates of AOM in the literature (2010–2021) and the cited references therein. (A) The rates grouped according to the ecological habitats. Reaction rates in bioreactors are included as a reference for the maximum possible AOM rates. (B) The rates grouped according to reaction type/electron acceptors. In panel B, both rates from short-term incubation with natural samples and these long-term enriched cultures in bioreactors are plotted. The boxes are ranked from left to right according to the medians (marked by white horizontal lines in the boxes). Median values, instead of averages, are used for methane budget estimations in this review to avoid interference from extreme values. Most outliers were removed following a method reported elsewhere.[1] Please refer to the ESI† for the rates used in the plots.

that both DAMO bacteria and archaea were active:[63] in the warm season, nitrite reduction was high in the 10–30 cm section and nitrate reduction was high in the 30–60 cm section, ranging from 0.36 to 4.33 $nmol_{CO_2}$ g^{-1} d^{-1} and 0.89 to 9.51 $nmol_{CO_2}$ g^{-1} d^{-1} by DAMO bacteria and archaea, respectively (note: the CH_4- and CO_2-based rates are considered equivalent here, due to the often unavailable information about carbon assimilation during AOM. The reported values thus potentially underestimated the true rates). Although *M. oxyfera* and/or *M. oxyfera*-like bacteria activate methane using oxygen,[2] the proliferation of DAMO bacteria requires anoxic conditions as created in water-logged soils[65] or deep underground (*e.g.*, 50–100 cm depth).[62] The distribution of DAMO microorganisms depends on both the availability of electron acceptors and methane; the latter may be more influential as demonstrated by the difference in the depth distribution of the abundances of nitrate/nitrite and the *pmoA* gene.[66]

In addition to nitrite and nitrate, other electron acceptors such as sulfate and ferric iron have all been shown to stimulate AOM in wetland soils.[4,67,68] For instance, iron-mediated AOM may occur in freshwater sediments, where the concentrations of nitrate and sulfate are low.[69] Besides, natural organic matter, relying on its redox-active quinone moieties, has also been reported to stimulate AOM in water-logged soils in wetlands, and the enriched water-saturated soils with humic substances derived from Pahokee peat can increase AOM activity to approximately 100 $nmol_{CH_4}$ cm^{-3} d^{-1}.[70] Unclassified marine benthic group B and D families, both belonging to Euryarchaeota, were thought to have carried out AOM, whereas *Clostridia* and *Bacilli* were assumed to mediate the reduction of humic substances.[70] Humic substances may also serve as electron mediators during AOM driven by the reduction of N_2O.[71] Hence, the previously observed insignificant enhancement of AOM in several North American peatlands with nitrate/sulfate/ferric iron[20] might be explained by the interference caused by natural organic matter.

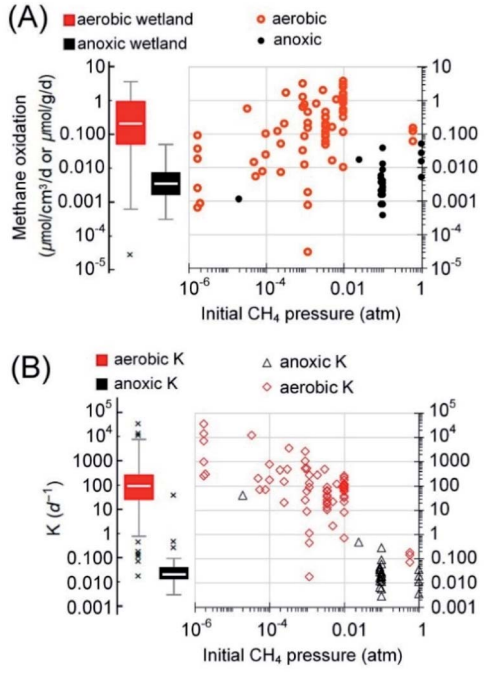

Fig. 4 Rates of aerobic methanotrophy (n = 79) and anoxic methanotrophy (n = 27) in freshwater wetlands (A). The reaction rates and the initial methane partial pressures applied/measured during rate quantification were from the cited references in the text. (B) The fractional turnover rate. The box covers the interquartile interval and the whiskers extend to 1.5 times the interquartile range above Q3 or below Q1. White horizontal line marks the median.

Recent reports indicate that the rates of AOM in different wetlands span a wide range, 0.31 to 50 $nmol_{CH_4}$ cm^{-3} d^{-1} (median = 3.4 $nmol_{CH_4}$ cm^{-3} d^{-1} and Q1–Q3: 1.8–7.0 $nmol_{CH_4}$ cm^{-3} d^{-1})[4,18,20,62,66,70,72,73] (Fig. 4). Ideally, the estimation of methanotrophic contributions to the overall methane sink should be based on depth integration because the reaction rate is not uniform along the depth. Nevertheless, detailed depth-integrated rates or rates with depth are often not available. Hence, the median of commonly reported active depths is used to estimate the areal flux of methane. Based on the commonly reported active depth of AOM, 40 [Q1–Q3: 20–100] cm,[62,63,66,74–77] the active depth of aerobic methane oxidation, 7.5 [Q1–Q3: 3.6–15.3] cm,[57,78–81] and the estimated global freshwater wetland area (5.69×10^{12} m^2),[4] the respective methane oxidation rates suggest that anoxic and aerobic methanotrophs have the capability of reducing methane emission by approximately 45 [Q1–Q3: 23–92] Tg_{CH_4} per year and 389 [Q1–Q3: 103–1854] Tg_{CH_4} per year, respectively (Table 1). The methane oxidation *via* AOM extrapolated by Segarra *et al.*[4] is 200 Tg_{CH_4} per year (data from three wetlands) and AOM solely due to the oxidation by natural organic matter was estimated to be over 1300 Tg_{CH_4} per year (data from one wetland).[70] Both these studies showed much higher AOM capacities than the estimated median value in this study. The discrepancy could be attributed to the differences in the total number of wetlands considered here (n = 42). Besides, it has to be mentioned that the reported depth of active AOM in freshwater wetlands is often dependent on the tools for core sampling. The DAMO activity has also been detected down to 12–15 m under the surface.[65] Nevertheless, such kind of analysis is scarce. The real contribution of AOM to wetland methane oxidation may be larger than the estimation provided here.

Additionally, it seems that the methane oxidation rate is methane-limited, *i.e.* a higher rate with a higher methane partial pressure (Fig. 4A). The fractional turnover per unit time,[82,83] K (per day, rate/concentration), of aerobic methanotrophs was generally four orders of magnitude higher than those under anoxic conditions (Fig. 4B and Table 1). The higher K values of aerobic methane oxidation suggest that aerobic methanotrophs are more active than methanotrophs under anoxic conditions or the abundance of aerobic methanotrophs is higher.[82]

The recent estimate of the median methane emission from freshwater wetlands is 150.1 [Q1–Q3: 138.3–164.6] Tg_{CH_4} per year.[55] Therefore, based on the estimated median capacity of anoxic and aerobic methanotrophic activities, a significant amount of methane is oxidized before entering the atmosphere. The sum of efflux to the atmosphere and the potential amount of methane oxidized leads to the estimated median methane

Table 1 Methanotrophic reaction rates and the estimated emission potential components

Habitat	Component		Reaction rate (Q1, Q3; μmol per cm^3 per day)	Area (m^2)	Median depth (Q1, Q3; m)	Oxidation/emission capacity (Q1, Q3; Tg_{CH_4} per year)
Marine	Anoxic oxidation[a]	Inner shelf (0–10 m)	1.2×10^{-3} (4.1×10^{-4}, 1.8×10^{-3})	2.6×10^{12}	0.4 (0.3, 0.8) (SMTZ[b])	7.3 (2.5, 10.6)
		Inner shelf (10–50 m)	3.5×10^{-4} (1.4×10^{-4}, 1.4×10^{-3})	9.2×10^{12}	0.9 (0.4, 2.3) (SMTZ)	16.9 (6.9, 65.7)
		Outer shelf (50–200 m)	7.1×10^{-6} (3.8×10^{-6}, 2×10^{-3})	1.3×10^{13}	0.95 (0.6, 1.8) (SMTZ)	0.5 (0.3, 140.9)
		Seep system	0.1 (1.6×10^{-2}, 1.7)	2.0×10^{10}	0.2 (0.2, 0.3) (SMTZ)	3.3 (0.4, 39.6)
		Slope (200–2000 m)	4.1×10^{-6} (1.4×10^{-6}, 9.5×10^{-5})	3.0×10^{13}	3.6 (1.4, 10.3) (SMTZ)	2.6 (0.9, 59.9)
		Rise (2000–3500 m)	6.8×10^{-8} (1.3×10^{-8}, 7.2×10^{-7})	6.3×10^{13}	14.3 (6.1, 30.3) (SMTZ)	0.4 (0.1, 3.8)
				Subtotal		30.9 (10.9, 320.5)
	Aerobic oxidation	Coastal region	4.1×10^{-8} (4.0×10^{-9}, 2.5×10^{-7})	3.2×10^{13} (9% of ocean area)	530.0 (153.5, 975.0) (aerobic surface seawater)	4.1 (0.4, 25.2)
	Emission					8.4 (4.8, 28.4)
				Total		**43.4 (16.1, 374.1)**
Freshwater wetlands	Anoxic oxidation		3.4×10^{-3} (1.7×10^{-3}, 7.0×10^{-3})	5.7×10^{12}	0.4 (0.2, 1)	45.3 (23.3, 92.4)
	Aerobic oxidation		1.6×10^{-2} (4.1×10^{-2}, 7.4×10^{-1})		7.5×10^{-2} (3.6×10^{-2}, 1.5×10^{-1})	388.8 (102.6, 1854.2)
				Subtotal		434.1 (125.8, 1946.7)
	Emission					150.1 (138.3, 164.6)
				Total		**584.2 (264.1, 2111.3)**
Rice paddy	Anoxic oxidation		1.85×10^{-3} (6.2×10^{-4}, 9.36×10^{-3})	9.7×10^{11} (60% of total)	0.5 (0.2, 0.7)	2.2 (0.7, 11.1)
	Aerobic oxidation		0.378 (0.072, 8.4)		0.01 (0.002, 0.015)	12.5 (2.4, 278.3)
				Subtotal		14.7 (3.1, 289.3)
	Emission					29.9 (24.9, 32.1)
				Total		**44.6 (28.0, 321.4)**
Lakes &reservoirs	Anoxic oxidation		1.6×10^{-2} (2.2×10^{-3}, 1.1×10^{-1})	2.7×10^{12}	0.1 (0.08, 0.2)	34.8 (4.8, 237.9)
	Aerobic oxidation		1.15×10^{-3} (3.8×10^{-5}, 5.6×10^{-3})		9.5 (5.3, 18.8)	172.2 (5.6, 831.4)
				Subtotal		207.0 (10.4, 1069.2)
	Emission					70.9 (32.1, 170.7)
				Total		**277.9 (42.5, 1239.9)**
Rivers	Anoxic oxidation		1.7×10^{-3} (4.0×10^{-4}, 5.0×10^{-3})	5.3×10^{11} (68% of total)	0.12 (0.10, 0.14)	0.6 (0.1, 1.8)
	Aerobic oxidation		0.1 (3.3×10^{-5}, 0.4)	7.7×10^{11}	—	11.3 (0.8, 591.2)[c]
				Subtotal		11.9 (0.9, 593)
	Emission					5.8 (1.8, 21)
				Total		**17.7 (2.7, 614)**

[a] Region categorization and associated areas are from Egger *et al.*;[15] the original depths from Egger *et al.* were skewed and here the outliers were removed following the method described in Section 1 (Fig. 2); the processed and expanded depth values can be found in the ESI. [b] SMTZ stands for the sulfate–methane transition zone as mentioned in the text. [c] Refer to the text for the estimation related to aerobic methane oxidation in rivers.

emission potential of global freshwater wetlands, 584 Tg_{CH_4} per year. It is worth mentioning that wetland soils, especially the section in the deep subsurface, still contain a significant amount of dissolved methane in the porewater.[84] This portion of methane is treated as the holding capacity of the wetlands, not considered in the methane emission potential.

2.1.2 Rice paddy soils. Methane released due to rice cultivation represents 10 to 25% of global methane emissions.[85] Aerobic methanotrophs in paddy soils demonstrate oxidation rates of 0.0018–17.7 $\mu mol_{CH_4}\ g^{-1}\ d^{-1}$ (median = 0.38 $\mu mol_{CH_4}\ g^{-1}\ d^{-1}$ and Q1–Q3: 0.07–8.4 $\mu mol_{CH_4}\ g^{-1}\ d^{-1}$)[86–88] (Fig. 5A). Regarding AOM in paddy soils, DAMO has been a research focus because paddy soils receive large inputs of nitrogen fertilizers, some of which can be converted to either nitrate or nitrite.[85,89–91] Paddy soils often harbor both DAMO archaea and DAMO bacteria.[53,89,92] For instance, the analysis of paddy soils in Italy showed that 16S rRNA gene copies of potential DAMO bacteria belonging to the NC10 phylum were 10^4 to 10^5 copies per g and even more AOM-associated archaea, including *M. nitroreducens*, were present.[93] Although soils collected from 10–50 cm beneath the ground are often used for AOM studies,[86,91–95] DAMO microorganisms have been demonstrated to inhabit a great depth in paddy fields.[85,89] For example, in rice paddy soil from the Yangtze River Plain, China, a high abundance of DAMO bacteria (8.5×10^7 to 1.0×10^8 copies per g dry soil) was detected in 60–140 cm soil core sections in the summertime and all soil core sections from 40 cm down to 200 cm in wintertime.[90] The reported AOM rates in paddy soils are from 0.2 to 79.9 $nmol_{CO_2}\ g^{-1}\ d^{-1}$ (median = 1.9 $nmol_{CO_2}\ g^{-1}\ d^{-1}$ and Q1–Q3: 0.6–9.4 $nmol_{CH_4}\ g^{-1}\ d^{-1}$; rates from bioreactors using paddy soils as inocula were excluded)[85,86,93,94,96–98] (Fig. 5). The probably highest reported nitrate-DAMO rate is 79.9 $nmol_{CH_4}\ g^{-1}\ d^{-1}$, observed with paddy soils at the Italian Rice Research Unit.[93] The highest nitrite-DAMO, 3.9 $\mu mol_{CH_4}\ g^{-1}\ d^{-1}$, was obtained with soils from an unspecified non-flooded rice paddy field in China.[98] Overall, the AOM rates are not significantly different with nitrate and nitrite as the electron acceptor (Mann–Whitney *U*-test, $p = 0.37$, Fig. 3B). The AOM rates are generally lower than the aerobic counterpart, so does the corresponding fractional turnover constant, K (per day), as shown in Fig. 5B. The K values of microorganisms in paddy soils are generally comparable to their counterparts in freshwater wetlands (Fig. 4B). It is noteworthy that many of the AOM studies with paddy soils applied microcosm incubation to quantify AOM rates in flooded soils; however, actual AOM rates may depend on the stage during rice cultivation, which is often not explicitly discussed. Besides, carbon assimilation by DAMO microorganisms is often not reported. Solely from the aspect of missing carbon assimilation data, the actual AOM rate should be higher than the apparent AOM rate. For instance, a recent study demonstrates that a significant amount of methane-derived carbon might be assimilated during DAMO, and the AOM rate based on CO_2 measurement underestimated the true rate by approximately 31–62%.[99]

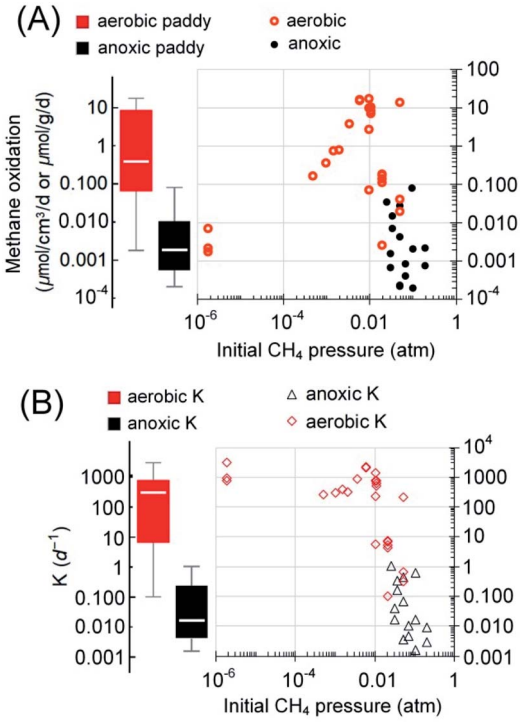

Fig. 5 Rates of aerobic methanotrophy ($n = 25$) and anoxic methanotrophy ($n = 16$) in rice paddy soils (A). The reaction rates and the initial methane partial pressures applied/measured during rate quantification were from the cited references in the text. (B) The fractional turnover rate.

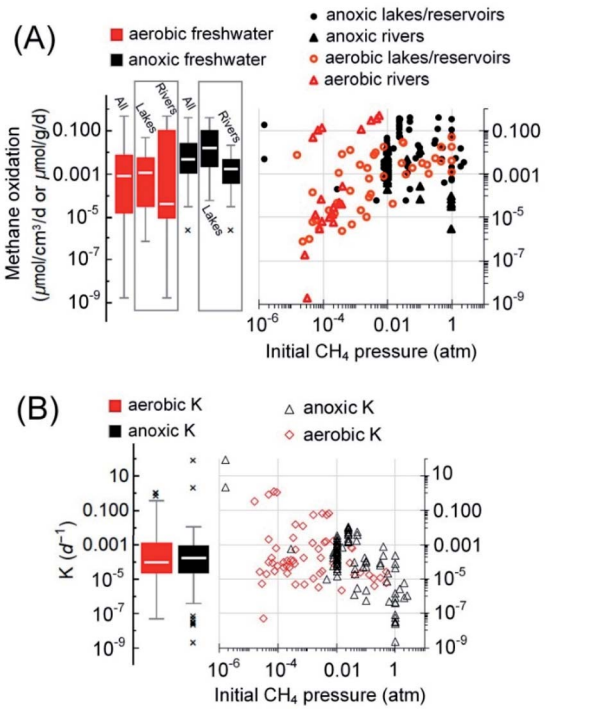

Fig. 6 Rates of aerobic methanotrophy ($n = 65$) and anoxic methanotrophy ($n = 93$) in freshwater (A). The reaction rates and the initial methane partial pressures applied/measured during rate quantification were from the cited references in the text. (B) The fractional turnover rate.

As aforementioned, the spatial distribution of DAMO microorganisms is in the decimeter to meter range below the ground in paddy soils. In contrast, active aerobic methanotrophy often exists in a millimeter-depth range at the oxic–anoxic interface.[100,101] Considering the spatiotemporal variation of both methanogenesis and methanotrophy with the rice cultivation practice, we further limit the estimation to only the irrigated area (paddy soils), which accounts for approximately 60% of the total rice cultivation area,[1] and assume that AOM is most active during the growing season (irrigated, max. 152 days[1]), while the aerobic methanotrophy dominates beyond this period. Using a 50 [Q1–Q3: 20–70] cm depth of active DAMO, 10 [Q1–Q3: 2–15] mm depth of active aerobic methane oxidation,[100] an average paddy soil density of 1.3 g cm^{-3}, and the global rice field area (1.62×10^{12} m^2),[102] AOM and aerobic methanotrophs are capable of reducing methane emission by 2.2 [Q1–Q3: 0.7–11.1] Tg_{CH_4} per year and 12.5 [Q1–Q3: 2.4–278.3] Tg_{CH_4} per year, respectively. It must be noted that the estimated 75% percentiles based on rates measured under ideal conditions may not be reached during rice cultivation due to the limitation caused by methanogenesis (often not a limiting factor in lab-scale incubations). The lower end of the currently estimated methane oxidation *via* AOM is close to the estimated values from a recent publication,[97] 2.2–5.5 Tg_{CH_4} per year. Regarding methane emission, the recently estimated efflux from paddy fields in the 2008–2017 decade is 30 [min–max: 25–38] Tg_{CH_4} per year[1] or 29.9 [Q1–Q3, 24.9–32.1] Tg_{CH_4} per year,[55] which are comparable. Therefore, based on the comparison with the methane oxidation capabilities, a significant amount of methane is oxidized before entering the atmosphere. If the median methane oxidation capacities were realized, methane oxidized *via* anoxic and aerobic pathways would be responsible for 5% and 28% of the total methane emission potential, approximately 14.7 [Q1–Q3, 3.1–289.3] Tg_{CH_4} per year.

2.1.3 Freshwater. Recent publications suggest that inland fresh water emits 159 [min–max, 117–212] Tg_{CH_4} per year, responsible for approximately 19.5–35.5% of the atmospheric methane budget,[1,55,103] much higher than that from the oceans (2–3%). The major sources include lakes/ponds, rivers/streams, and reservoirs, which account for approximately 70%, 17%, and 13% of the total average inland methane efflux from freshwater.[1,104,105] Specifically, the estimated median emission is 60.2 [Q1–Q3: 23.7–178.6] Tg_{CH_4} per year for lakes and ponds, 5.8 [Q1–Q3: 1.8–21.0] Tg_{CH_4} per year for rivers and streams, and 15.1 [Q1–Q3: 8.8–28.4] Tg_{CH_4} per year for reservoirs.[55] DAMO was found to be a major AOM pathway in freshwater ecosystems.[106,107] AOM driven by other electron acceptors has also been reported. For example, metal oxides and sulfates can also be electron acceptors,[16,69] but the rates are usually two or three orders of magnitude lower than those of the DAMO pathways.[108,109] In this section, AOM and relevant methane emissions from lakes/reservoirs/ponds and rivers/streams are discussed separately because the two water bodies are different in several aspects.

Regarding lakes/ponds, a significant amount of methane may be oxidized before entering the atmosphere, as demonstrated by the almost complete consumption of methane generated deep in the sediment of lakes in high latitudes[110] and the high assimilation of carbon derived from methane (47–90%) by microbes.[111] Sediments of reservoirs are like that of a lake, and DAMO pathways also exist in reservoir sediments.[112,113] For example, the incubation tests with methane and nitrate showed that the sediments from three reservoirs in Poland supported nitrate-DAMO with a rate ranging from 7.2 to 24.96 $nmol_{CH_4}$ g^{-1} d^{-1}.[114] AOM with unknown electron acceptors was also discovered in sediments of a small-scale dam reservoir located in Rzeszów, Poland, where the estimated AOM rate was 8.6–34.1 $nmol_{CH_4}$ g^{-1} d^{-1}.[115] Similar AOM rates were observed in Jiulonghu reservoir in China, ranging from 4.7 to 14.1 $nmol_{CO_2}$ g^{-1} d^{-1} with nitrite and 0.8 to 2.6 $nmol_{CO_2}$ g^{-1} d^{-1} with nitrate.[116] In freshwater lakes/ponds/reservoirs, the rate of aerobic methane oxidation ranges from 0.0008 to 49 $nmol_{CH_4}$ cm^{-3} d^{-1} (median = 1.2 nmol cm^{-3} d^{-1}; Q1–Q3: 0.04–5.6 $nmol_{CH_4}$ cm^{-3} d^{-1})[117–121] (Fig. 6A). AOM rates range from 0.06 to 400 nmol cm^{-3} d^{-1} (median = 16 nmol cm^{-3} d^{-1}; Q1–Q3: 2–108 $nmol_{CH_4}$ cm^{-3} d^{-1}).[6,31,106,107,110,111,119,122–125] The median AOM rate in lakes/ponds/reservoirs is higher than that of the aerobic methane oxidation (Mood's median test, $p < 0.0001$; for all freshwater systems, $p = 0.002$). The reason for this contrast is not clear because the methane oxidation catalyzed by methane monooxygenases from aerobic methanotrophic bacteria is generally 1–2 orders of magnitude higher than that catalyzed by ANME methyl coenzyme M reductase.[126]

It must be noted that AOM also exists in the water column of some lakes/reservoirs (8–23 $nmol_{CH_4}$ cm^{-3} d^{-1}),[110,119,127] but insufficient data are available for the estimation of this fraction of AOM. Therefore, only AOM in the sediments and the aerobic methane oxidation in the bulk water phase are considered here in the simplified AOM capacity estimation. The average depth of lakes on Earth is 41.8 m,[128] and the top 9.5 [Q1–Q3: 5.2–18.7] m in the water of lakes/reservoirs worldwide is usually found to be oxic.[104,117,120,129] Taking this oxic layer depth and the global area of lakes and reservoirs, 2.7×10^{12} m^2,[130] for estimation, the aerobic methanotrophs are capable of oxidizing approximately 172 [Q1–Q3: 6–831] Tg_{CH_4} per year (Table 1). Similarly, if the median thickness of sediment with active AOM in lakes/reservoirs, 14 [Q1–Q3: 8–18] cm (ref. 6, 108, 123 and 131–134), is taken for estimation, AOM solely in the sediments is capable of reducing methane emission by 35 [Q1–Q3: 5–238] Tg_{CH_4} per year. Therefore, if the median capacities of methane oxidation were realized, aerobic methane oxidation is the major methane sink (Fig. 7, approximately 62%), stronger than AOM (approximately 13%), similar to previous conclusions.[6,111]

Rivers/streams are another major freshwater body on Earth. Partly due to the difficulties in the methane flux quantification, methanotrophic activity in rivers/streams was once ignored during methane flux analysis.[135] According to recent studies, significant methanotrophic activity (at Tg per year level, mainly aerobic) exists in riverine systems such as the Amazon River.[103,136,137] The methane consumed aerobically accounts for 28–96% of the methane content in the bulk water in the Amazon basin.[103] Regarding AOM, DAMO has also been reported as a major AOM pathway in river sediments.[31,138,139] Available studies indicate that the methanotrophy in rivers depends on

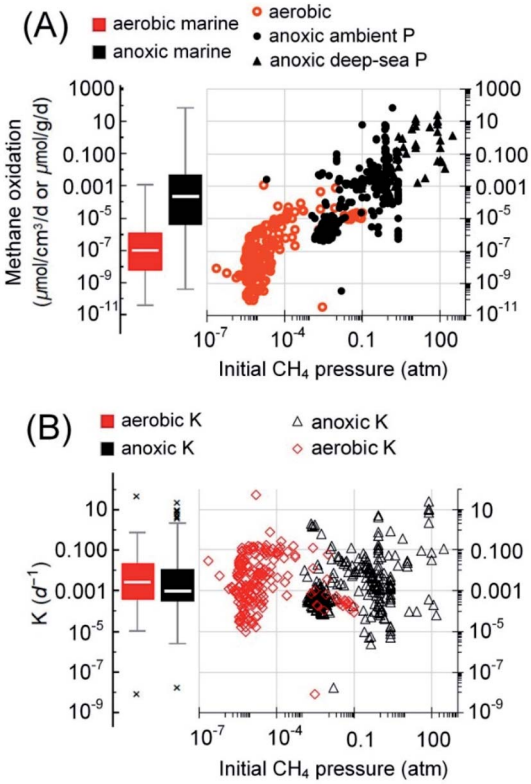

Fig. 7 Rates of anoxic methanotrophy and the rates of aerobic methanotrophy in the marine environment (A). Reaction rates of anaerobic oxidation of methane (n = 386) and aerobic methanotrophy (n = 223) and the initial methane partial pressures were collected from the cited references and online datasets. (B) The fractional turnover rate.

the riverbed sediment types. For example, a previous study of chalk rivers indicates that fine sediments can support strong methanotrophic activity that even surpasses methanogenesis,[140] and nitrate/nitrite-DAMO, ranging from 1.2 to 53.6 $nmol_{CO_2}$ g^{-1} d^{-1}, was only detected in sandy sediments of four representative rivers in southeast England but not in more oxic gravel sediments.[31] These authors further extrapolated that DAMO could account for 35% of all the methane oxidized in sandy riverbeds before entering the atmosphere in the UK.[30,31] In a study of the sediments from Jordan River in Salt Lake City, USA, DAMO activity 0.044 to 0.101 $nmol_{CH_4}$ g^{-1} d^{-1} was detected, and the rate per NC10 phylum gene copy was independent of the depth of sediment.[122] The methanotrophs are active from 2 to 15 cm in the sediment, and the rates generally peaked at 4–8 cm below the interface.[30] Overall, the AOM rates range from 0.003 to 21 $nmol_{CH_4}$ g^{-1} d^{-1} (median = 1.7 $nmol_{CH_4}$ g^{-1} d^{-1}; Q1–Q3: 0.4–5 $nmol_{CH_4}$ g^{-1} d^{-1}).[31,122,141]

Based on these previous studies, it is conceivable that for rivers contaminated by agricultural run-off, the DAMO process may be more active. However, compared with AOM in lakes and wetlands, information about the AOM rates and distribution of methanotrophs in rivers is still insufficient.[5] Taking the average global area of rivers and streams,[142] 7.73 × 10^{11} m^2, and a median depth of the active AOM zone of 12 [Q1–Q3: 10–14] cm, further restricts the estimate to only sandy riverbeds (estimated median = 68%),[31,143,144] solely AOM in the sediment of rivers/streams is capable of reducing methane emission by 0.6 [Q1–Q3: 0.1–1.8] Tg_{CH_4} per year. As for the aerobic methane oxidation in rivers and streams, the reported rates span a wide range, from 2 × 10^{-6} $nmol_{CH_4}$ g^{-1} d^{-1} to 0.48 μmol_{CH_4} g^{-1} d^{-1}.[140,145] Here, similar issues exist and hinder the estimation of methanotrophic capacity in aerobic zones, such as the lack of a suitable physical model for accurate estimation. Hence, the authors conjectured that aerobic methanotrophs are responsible for 62% (average of 28–96% in the Amazon basin[103]) of methane oxidized in the river water above the sediment on a global scale. In this case, if the median capacity potentials of methanotrophs were realized, AOM and aerobic pathways can reduce approximately 3% and 64% of the methane released from the sandy sediment globally (Table 1 and Fig. 8).

Overall, in freshwater systems, the fractional turnover per unit time, K (per day), of aerobic and anoxic methanotrophs was not significantly different (Mann–Whitney U-test, p = 0.85, Fig. 6B). Although the median AOM rate (0.0048 $nmol_{CH_4}$ g^{-1} d^{-1}) in freshwater is of the same order of magnitude as these of the wetlands (0.0034 $nmol_{CH_4}$ cm^{-3} d^{-1}) and paddy fields (0.0018 $nmol_{CH_4}$ g^{-1} d^{-1}), the median K value of AOM in freshwater (0.00016 per day) is two orders of magnitude lower than their counterparts in wetlands and paddy fields (Fig. 4B and 5B). Since DAMO is usually the dominant AOM pathway in freshwater, wetlands, and paddy fields, and the K value is assumed to be scaled with the population size of AOM microorganisms,[82] the generally smaller K value in freshwater suggests that the DAMO microorganisms are not as abundant as these in wetlands and paddy fields.

2.1.4 Terrestrial mud volcanoes, hot springs, and natural gas sites. AOM activity has also been detected in some other terrestrial environments, such as mud volcanoes, hot springs, and natural gas sites, where both methane and suitable electron acceptors are available. The microorganisms active in AOM were found to be not limited to DAMO microorganisms. For example, Methanoperedenaceae (5.7% in total archaea), ANME-3 (0.6%), ANME-2a/b (0.5%), and ANME-1 (0.3%) were identified as the main anoxic methanotrophs in a terrestrial mud volcano from the Bulganak mud volcano in Crimea.[146] Furthermore, a recently enriched microorganism, named "*Candidatus Methanodesulfokores washburnensis*", was found to carry genes for both methane oxidation and sulfur reduction in the thermal sediments from Washburn Hot Springs.[19] In addition, sulfate-driven AOM has been detected in freshwater natural gas sources with ANME-2a/b and AOM-associated archaea as methane oxidizers.[147] However, the rates ($pmol_{CH_4}$ cm^{-3} d^{-1} to $nmol_{CH_4}$ cm^{-3} d^{-1}) are generally much lower than the rates compiled in previous sections or the rates were not reported.[19,148,149] Since the research evidence of AOM in these terrestrial environments is still scarce, the reported AOM rates are incorporated in Fig. 3, but the AOM capacities in these environments are not calculated.

2.2 Marine environment

2.2.1 Overall significance of AOM in the marine environment. The AOM activity has been shown to primarily occur in

sediments,[29] and the overall rates of AOM in marine sediments, including those driven by major reported electron acceptors (*i.e.*, sulfate, metal oxides, and nitrate/nitrite), range from 5.1×10^{-8} to 7.0×10^{4} $nmol_{CH_4}$ cm^{-3} d^{-1} ($n = 387$, median = 0.2 $nmol_{CH_4}$ cm^{-3} d^{-1}, and rates obtained after prolonged incubation were excluded) (Fig. 7).[150–167] Sulfate-AOM is the dominant methane oxidation pathway because sulfate is the major reactive anion in seawater. Recent data suggest that iron/manganese oxides are only responsible for approximately 2–3% of the methane oxidized around and below the sulfate–methane transition zones (SMTZ),[165] where the sulfate-driven AOM is usually detected. Besides, within the SMTZ, sulfate-AOM is usually more significant than the background organoclastic sulfate reduction.[168] Since the data regarding the depth of sediment harboring metal oxides and nitrate/nitrite that are actively involved in AOM are not as abundant as that for sulfate-AOM,[154,169] and the coverage of these non-sulfate-dominant niches is also likely to be limited, as mentioned in Section 2.2.2, the estimation of the contribution of AOM in the marine environment is therefore based solely on sulfate-AOM in the sediment. It is thus obvious that the estimate will be conservative.

Note that the so-called cryptic sulfur cycle (*i.e.*, sulfate-AOM and sulfide oxidation occur simultaneously in a confined space) is a special phenomenon because other electron acceptors, often metal oxides, are thought to be involved in the cycling of sulfur (*i.e.*, sulfate replenishment *via* sulfide oxidation).[131] For example, a study of marine sediment on the Alaskan Beaufort Sea continental margin indicates that AOM, involving the cryptic sulfur cycle, occurs below the SMTZ, and the rates were 2.4–8 $nmol_{CH_4}$ cm^{-3} d^{-1}.[170] Rates from this kind of reaction or suspected reaction were considered sulfate-AOM because the details of sulfur cycling reactions are often unclear.

Specifically, the reported rate of sulfate-AOM from the SMTZ ranges from 5.1×10^{-8} to 7.0×10^{4} $nmol_{CH_4}$ cm^{-3} d^{-1} ($n = 370$ and median = 0.15 $nmol_{CH_4}$ cm^{-3} d^{-1}).[150,152,153,160,171–176] Based on the reported depth of the SMTZ in different regions and the corresponding area of each (Table 1),[12,15,161,165,171,177] solely sulfate mediated AOM in the SMTZ is capable of reducing the methane emission by approximately 28 [Q1–Q3: 11–281] Tg_{CH_4} per year (Table 1). Additionally, the analysis of the AOM at simulated ocean bottom pressures with samples collected from various cold seep systems and coastal marine basins suggests that AOM is capable of oxidizing 3 [Q1–Q3: 0.4–39.6] Tg_{CH_4} per year (Table 1) in cold seep systems (refer to the ESI for details†). In total, AOM in the SMTZ and cold seep systems can reduce approximately 31 [11–321] Tg_{CH_4} per year of methane from the seabed. Although the estimation here is only a rough

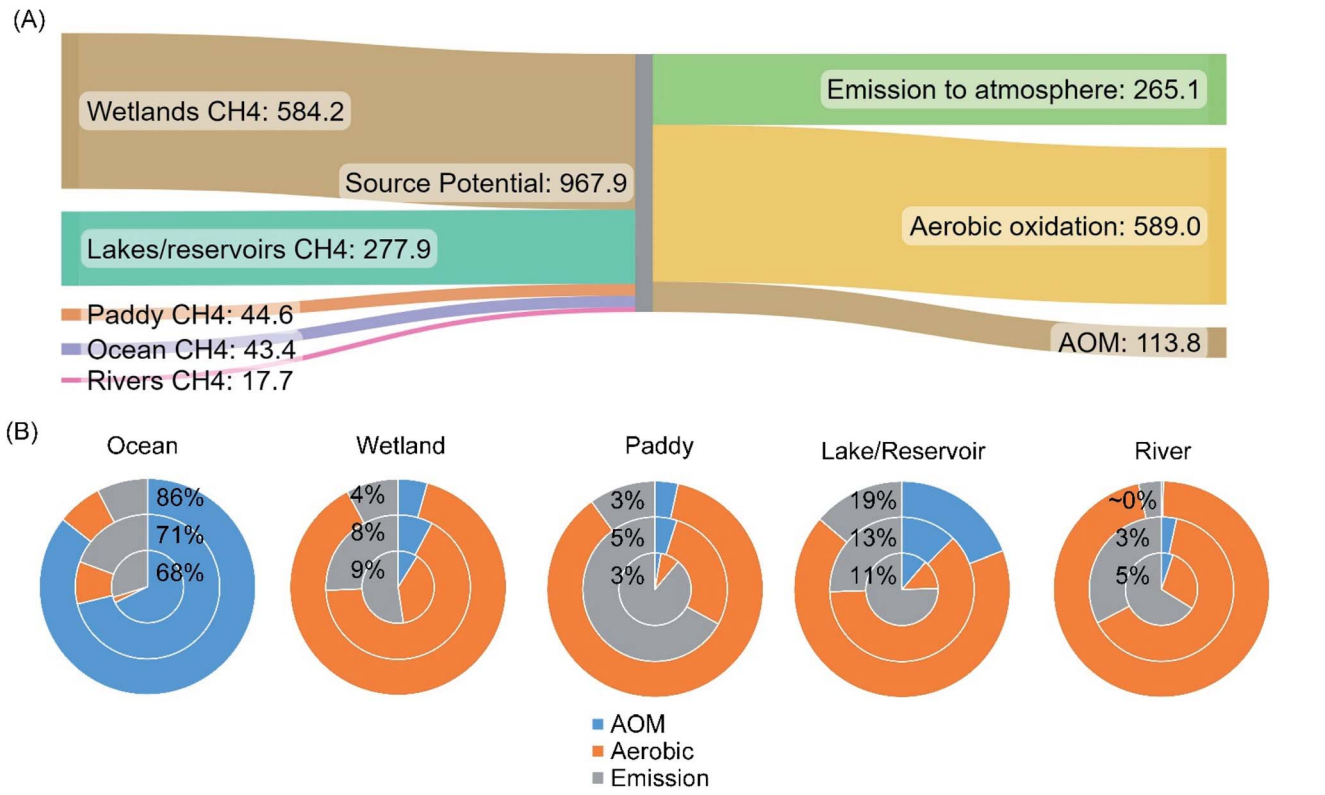

Fig. 8 Estimated methane emission potentials (aerobically and anoxically oxidized + efflux to the atmosphere) from the studied methane sources and the approximate methane budgets in Tg_{CH_4} per year (A). Estimated medians as shown in Table 1 were plotted. Panel (B) shows the relative proportions of methane consumed by anoxic (labeled with percentages) and aerobic oxidation in estimated methane release potential from individual natural ecosystems. The inner circles, middle circles, and outer circles sequentially show the results calculated with 25% percentile, median, and 75% percentile aerobic/anoxic methane oxidation rates, respectively. Each level was paired with the corresponding level of methane efflux to the atmosphere.

extrapolation based on the compiled reaction rates, this estimated median AOM capacity is close to the estimated average AOM capacity (45 Tg_{CH_4} per year) with a regression model using diffusive fluxes of methane to the SMTZ.[15] Besides, the higher end of the current estimation is of the same order of magnitude as the most frequently cited global AOM estimate, which is 382 Tg_{CH_4} per year.[15,34] As mentioned in the previous sections, since the AOM rates are mostly obtained in incubation studies under ideal laboratory conditions, the AOM capacity here should be treated as a reference value or more as an approximate number for the ability of methanotrophs in anaerobic and anoxic zones in the marine environment. The further validation of these estimations is currently difficult or even impossible because it is not clear whether the methanogenesis in marine sediment[15,178] (approximately 92–101 Tg_{CH_4} per year) and the still unknown amount of methane released from seep systems[179] can support such high sulfate-driven methanotrophic activity (*i.e.*, a few hundred Tg_{CH_4} per year). Therefore, the estimated median value is used in the discussion in the following sections to reduce the uncertainties associated with the data extrapolation.

It is noteworthy that some of the seemingly low AOM rates may be subjected to modification in the future because some earlier AOM rates were obtained at ambient pressure, which is much lower than the *in situ* pressure. For instance, a substantial difference between measured AOM rates at ambient pressure and estimated/measured values from deep water sites or ocean bottoms has been reported.[8,158,180] Specifically, the incubation of the Eckernförde Bay sediment at 10.1 MPa of methane atmosphere enriched ANME-2a/b/c and SRB, yielding an AOM rate of 0.046 $\mu mol_{CO_2}\ cm^{-3}\ d^{-1}$, a few times higher than that at ambient pressure.[181] Similarly, incubations simulating the *in situ* pressure in the deep sea with sediments collected from a cold seep in the Gulf of Mexico and a hydrothermal site in the Guaymas Basin yielded 50 mM of dissolved methane, which supported AOM at 3.6–4.8 $\mu mol_{CH_4}\ cm^{-3}\ d^{-1}$.[8] These results suggest that sulfate-AOM in the marine environment may be limited by methane.

Regarding marine aerobic methanotrophs, most of the rates are from the continental margins as well, ranging from 3.4×10^{-8} to 1.1 $nmol_{CH_4}\ cm^{-3}\ d^{-1}$ with a median of 9.1×10^{-5} $nmol_{CH_4}\ cm^{-3}\ d^{-1}$ (Q1–Q3: 4×10^{-6} to 2.5×10^{-4} $nmol_{CH_4}\ cm^{-3}\ d^{-1}$).[83,153,171,182–194] Based on the rates of aerobic methane oxidation, the median depths of oxic surface seawater, 530 [Q1–Q3: 153–975] m, and the area of the coastal ocean and continental shelf (9% of total ocean area), aerobic methanotrophs solely in the water column of this region are capable of oxidizing 4 [Q1–Q3: 0.4–25] Tg_{CH_4} per year (Table 1). Alternatively, considering the pertinent estimates that (a) methane efflux from coastal and open sea ranges from 9 to 22 Tg_{CH_4} per year (mean: 13 Tg_{CH_4} per year),[1] (b) coastal ocean accounts for approximately 75% of the global marine methane efflux to the atmosphere,[195] and (c) aerobic methanotrophs in the coastal ocean water column can consume 1.2–19 times (median = 2.5) of methane as compared to methane efflux to the atmosphere,[195] the aerobic methanotrophs in the coastal ocean water column oxidize 17 to 41 Tg per year (mean: 28 Tg per year) of methane. The results from both approaches suggest that aerobic methanotrophy is a significant methane sink. Besides, it is also speculated that aerobic methane oxidation also exists under the vast open sea because aerobic methanotrophic activity was detected in the oxygen minimum zone and the water column beneath (approximately 1000–2500 m under the sea surface).[83,196,197] However, data from such areas are limited, as compared to the relatively well-studied continental margins. Therefore, more methane may be oxidized by aerobic methanotrophs.

Overall, the methane oxidation rate seems to be weakly correlated with the initial methane partial pressure during the incubation for rate quantification (R^2 = 0.52–0.54, linear regression lines not shown, Fig. 7). This trend for AOM rates, albeit weak, is consonant with the observed increased methane oxidation rates at higher methane partial pressures.[8,158,180] Regarding the fractional turnover per unit time, K (per day), those of aerobic (median = 0.0025 per day, Q1–Q3: 0.00035–0.022 per day) and anoxic methanotrophs (median = 0.00091 per day, Q1–Q3: 0.0003–0.011 per day) are not significantly different (Mann–Whitney U-test, $p = 0.07$, Fig. 7B). Comparable K values of aerobic and anaerobic methane oxidation in the marine environment have been observed previously,[82] indicating that aerobic and anaerobic methanotrophs in the marine environment are similarly active if both methane oxidation rates follow first-order kinetics. If the estimated median capacity of AOM was realized, the AOM accounts for approximately 71% of the methane emission potential in the marine sediment, close to previously reported values, approximately 75–90%.[198,199]

2.2.2 AOM driven mainly by metal oxides. Despite the prevalence of sulfate-AOM in marine sediment, other electron acceptors can also support AOM in marine environments. The concentrations of electron acceptors and the energy yields of the redox reactions eventually determine the distinct dominant oxidant profiles along the depth of marine sediment.[200] Studies that report the presence of non-sulfate-based electron acceptors in marine AOM often show the decoupling of sulfate reduction and AOM.[10,75,166,170,175,201] For example, the incubation of sediments from cold seeps and hydrothermal sites showed that the AOM rate is constantly higher than the sulfate-reduction rate when the methane concentration was 5–50 mmol L^{-1}, suggesting that other electron acceptors participated in AOM.[8] In another study, AOM by ANME-1d from deep Black seawater was enhanced when sodium molybdate was added, implying that sulfate reduction was not coupled to AOM.[202]

Among various non-sulfate electron acceptors, iron oxide is a frequently reported one. The AOM driven by metal oxides is generally faster than sulfate-AOM (Fig. 3). Recent studies demonstrated that iron oxides can induce AOM below the SMTZ where sulfate is less available or in places where iron does not precipitate as iron sulfide.[165,203] For example, in the Helgoland Mud Area of the North Sea, incubation studies of sediments below the SMTZ indicate that iron oxide-driven AOM occurred at a rate of 0.095 ± 0.03 nmol $cm^{-3}\ d^{-1}$.[165] Additionally, in estuaries and coastal regions with a high inflow of iron, iron oxides can also serve as an electron acceptor.[154,204] For instance, ferrihydrite-driven AOM has been reported in an incubation

study of brackish coastal sediments from the Bothnian Sea, and the AOM reached 3.6 ± 0.2 nmol cm^{-3} d^{-1}.[205] In some other cases, non-sulfate-based electron acceptors become important due to the inactivation of SRB. For example, in metalliferous hydrothermal sediments where the temperature is high (*e.g.*, 90 °C) and the activity of SRB was found to be greatly inhibited, ANME-1a may couple the reduction of ferric iron to AOM, reaching 0.152 μmol_{CH_4} cm^{-3} d^{-1}.[166] Furthermore, ferric iron-driven AOM has also been proposed to explain the high dissolved ferrous iron concentrations in the pore water in some marine sediments, such as that in the Bothnian sea, an oligotrophic and low salinity coastal basin[206] and the oligotrophic sediment from the southeastern Mediterranean continental shelf.[207] Although some non-sulfate-based electron acceptors, such as metal oxides, are thermodynamically more favorable electron acceptors than sulfate and tend to compete with sulfate for methane, they do sometimes facilitate sulfate-AOM, such as in the case of the cryptic sulfur cycle.[208,209]

2.2.3 DAMO in estuaries and intertidal zones. Coastal seas account for approximately 15% of the global ocean surface area but are responsible for approximately 75% of the marine methane efflux to the atmosphere.[195] Research in the past decade indicates that non-sulfate-AOM exists in estuaries and intertidal zones.[210,211] For instance, the incubation of sediments collected from various sites along the riverbank in the Yangtze Estuary in China showed active nitrite-DAMO at 0.2–84.3 $nmol_{CO_2}$ g^{-1} d^{-1} and nitrate-DAMO at 0.4–32.6 $nmol_{CO_2}$ g^{-1} d^{-1}.[74] The incubation and analysis of sediments from marine coastal ecosystems found that DAMO bacteria are active.[22,163] These observations corroborated the previous results from the analysis of the 16S rRNA gene and *pmoA* sequences of DAMO bacteria, which indicate that their richest community is from marine and coastal environments.[155] Seawater enriched subgroup A cells of the NC10 phylum showed an affinity coefficient of 9.8 ± 2.2 μmol_{CH_4} L^{-1} and this value is in the range of measured affinity coefficients in freshwater systems,[212] suggesting that the DAMO rates may be similar to those observed in terrestrial ecosystems. The DAMO activities by *M. oxyfera*-like and *M. sinica*-like bacteria detected in the Zhoushan islands intertidal zone yielded a similar AOM rate (nitrite-DAMO: 0.6–5.7 $nmol_{CO_2}$ g^{-1} d^{-1}) to sulfate-AOM by the same sediment.[213] Similarly, DAMO archaea detected in the intertidal zone also support a similar AOM rate (nitrate-DAMO: 0.16–1.49 $nmol_{CO_2}$ g^{-1} d^{-1}) to sulfate-AOM.[214] Temperature and nitrogen compound concentration were found to be the two most influential factors that affect the DAMO bacteria abundance.[213] Comparable AOM rates were detected in another intertidal zone in the Chongming eastern intertidal flat in China, where DAMO bacteria and archaea showed methane oxidation rates of 0.1–39.9 $nmol_{CO_2}$ g^{-1} d^{-1} and 0.1–46.7 $nmol_{CO_2}$ g^{-1} d^{-1}, respectively.[162,215] Similar to sulfate-AOM, the rate of DAMO tends to increase after a long term of cultivation,[212] but AOM rates from such systems were excluded from this review.

2.2.4 Sulfate-AOM in marine mud volcanoes and hydrothermal vents. Several recent publications also reported AOM, $nmol_{CH_4}$ cm^{-3} d^{-1} to a few μmol_{CH_4} cm^{-3} d^{-1}, at marine mud volcanoes and hydrothermal vents,[167,171,216,217] which have been recognized as the major geological formations that release methane to the hydrosphere and atmosphere.[218] ANME-1, ANME-2, and/or ANME-3 have been reported to be responsible for the observed AOM in these environments.[167,217] For example, ANME-1 and ANME-2 were detected in mud volcano deposits in Ginsburg MV,[167] while ANME-2c and ANME-3 were found to participate in sulfate-AOM in mud volcanoes in the Canadian Beaufort Sea.[219] Besides, the cultivation of the sediments (854 m below the water level) from the mud volcano Peschanka enriched ANME-2 and bacteria belonging to the NC10 phylum,[220] implying that AOM may be active in this sediment. Incubation studies showed that the AOM in hydrothermal vents is usually temperature-dependent, and AOM activity persists in a wide range of temperatures up to 90 °C.[166,217] However, with limited information on geographical coverage and reaction rates, these AOM rates at elevated temperatures are not considered during the AOM capacity estimation.

3. Some of the possibly highest AOM rates

The publications on nitrite/nitrate-DAMO raised the interest in engineering this AOM pathway for denitrification, which is currently a main nutrient removal step in the biological wastewater treatment process.[47,48,221] Besides, DAMO may also be applied for methane emission reduction from ruminant livestock,[222] which accounts for almost one-third of total anthropogenic methane emissions.[1] DAMO (nitrogen mainly as NO_2^-/NO_3^-) and DAMO coupled with anaerobic ammonium oxidation (DAMO-Anammox, NO_2^-/NO_3^- together with a significant concentration of NH_4^+) are two of the commonly studied AOM pathways for denitrification. The sources of inoculum for these studies include paddy soils, freshwater sediments, wastewater, and marine sediments.[21,53,223,224] Overall, with an enriched microbial consortium in a pure or close-to-pure methane atmosphere (usually balanced with 5% CO_2), lab-scale reactors generally demonstrated much higher unit-volume-based AOM rates than those measured with the original inocula. Hence, the AOM rates obtained with bioreactors are compiled here as references for the maximum possible AOM rates (Fig. 3), with the caveat that these high rates may not exist in nature.

Specifically, nitrite-based DAMO in bioreactors usually shows methane oxidation at 0.00004–22.31 μmol_{CH_4} cm^{-3} d^{-1},[22,49,53,62,63,98,110,224–229] often higher than nitrite-DAMO observed in terrestrial and marine environments. Besides, unlike sulfate-AOM, it seems that the nitrite-DAMO is not limited by methane.[230] For systems with both nitrate-DAMO and nitrite-DAMO, similar AOM rates of 3×10^{-6} to 11.5 μmol_{CH_4} cm^{-3} d^{-1} (ref. 28, 50, 53, 92, 122 and 231–234) were reported. Currently, the highest AOM rate observed in bioreactors with nitrogen removal as the objective was from coculturing of DAMO archaea and Anammox bacteria.[28,45,46,235] Overall, the methane consumption rate of DAMO-Anammox ranges from 0.078 to 138 μmol cm^{-3} d^{-1},[23,24,33,45,46,50,235–239] and it seems that dissolved methane is not a limiting factor during DAMO-Anammox as well because elevated methane partial pressure had little effect on the activity of DAMO microorganisms.[51]

4. Factors that influence the AOM rates and issues in rate measurement

4.1 Factors that influence the AOM rates

The AOM rate in a studied environment can be reasonably estimated according to the measured biogeochemical parameters and the concentration-depth profiles of major reactants.[4,31,83] The AOM rate reflects the activities of local microbiota, which are under the control of multiple environmental factors. In addition to the availability of methane and a suitable electron acceptor, other environmental factors, such as temperature,[97,216] pressure,[171,181,216,240] accessibility of essential metal ions,[241] the turnover rate of electron acceptors,[200] organic content,[172,175] *etc.*, have all been documented to affect the AOM rate. It seems that no straightforward model can explain all the observations across different environments due to the different concentrations/levels of these above factors. In a natural ecosystem, the effect of one factor can often be compounded with the effects of other factors. For example, the incubation of slurries of the sediments from rivers with sandy riverbeds suggests that the AOM microbes were limited by electron acceptors because only the addition of both methane and the electron acceptors, nitrite for DAMO bacteria and nitrate for DAMO archaea, significantly stimulated the growth of the respective microorganisms.[31] While in a study of the AOM rate of coastal freshwater and brackish wetland sediments with dissolved methane close to saturation, the added electron acceptors mostly inhibited AOM, as opposed to boosting the activity,[242] and the results, together with the increased utilization of added electron acceptors, suggest that organic matter contained in the sediments was oxidized instead of methane. Thus, unknown heterotrophic microorganisms competed with methanotrophs for the electron acceptors, and methanogenesis might have also been inhibited in the presence of excessive electron acceptors, leading to limited methane supply for AOM and the eventually decreased methane oxidation.

A potential limiting factor reported in many of the cited references is the commonly encountered slow growth of the methanotrophs. Specifically, the doubling time for ANME, including ANME-1 and ANME-2a/c, from marine sediment ranges from 33–225 days according to ^{15}N and $^{13}CO_2$ assimilation tests.[10,201,243] The doubling time of the freshwater bacterium *M. oxyfera* from the NC10 phylum was estimated to be around 7 to 14 days,[2] while the marine NC10 bacteria showed a longer doubling time of 38.7 to 48.9 days.[244] Compared to the NC10 phylum bacteria, the DAMO archaea grow faster.[92] The doubling times for DAMO microorganisms are close to the reported values of Anammox bacteria, 18–46 days (29 °C) and 24–79 days (down to 12.5 °C),[245] although some highly active Anammox bacteria showed a much shorter doubling time (around 2 days).[246] The generally long doubling times explain why AOM microorganisms require months or years to be enriched[247] and the low biomass can limit the overall rate of AOM.

Carbon assimilation, one aspect of cell growth, seems to be a reason behind the slow growth of anaerobic methanotrophs. One previously observed methanotrophic consortium for sulfate-AOM showed over 20% of ^{13}C (from $^{13}CH_4$) incorporation by solely archaea,[248] while another showed less than 10% incorporation by the whole methanotrophic consortium:[8] the AOM rate of the former (286 μmol cm^{-3} d^{-1}) is over 500 times that of the latter (approximately 0.5 μmol cm^{-3} d^{-1}), indicating that a higher rate of organic carbon assimilation is a key determinant of the AOM rate. Nevertheless, many studies reported that ANME prefers the energy-consuming pathways involving inorganic carbon reduction and incorporation. For ANME, the assimilated carbon (*e.g.*, 96% (ref. 10)) can be from bicarbonate as opposed to carbon from methane. In a study of AOM communities enriched from the Guaymas Basin and the Elba seep, methane-derived carbon only accounted for 3–15% of the total biomass, in which ANME-1 or ANME-2 was the dominant methanotroph.[249] It is conceivable that the preferred assimilation of bicarbonate over reduced carbon from methane limited the growth of these methanotrophs.

From the perspective of methane utilization, the low solubility of methane at ambient pressure and the high activation energy (439 kJ mol^{-1} CH_4) required to break the first C–H bond in the methane molecule by methyl coenzyme M reductase have been thought to partly explain the generally slow AOM rate.[250,251] However, as shown in the previous sections, higher dissolved methane concentrations at higher partial methane pressure do not always lead to increased methane oxidation. Besides, the dissociation of the C–O bond in acetate by coenzyme A is in a similar range, 452 kJ mol^{-1} acetate,[252] but acetate can be utilized by microorganisms at a much faster rate than methane. Thus, these factors alone cannot explain the low AOM rates. The list of references in this review is not exhaustive; however, the compiled AOM rates indicate that the median AOM rates (less influenced by the extreme values) in wetlands, paddy fields, and freshwater systems are comparable (Fig. 3A, Mood's median test, $p = 0.395$). The median AOM rates from these environments are statistically higher than that of the marine environment (Fig. 3A, Mood's median test, $p < 0.005$) in which sulfate-AOM is the main AOM pathway. Since the dominant methanotrophs in the studied freshwater, wetlands, and paddy fields are often DAMO microorganisms, this contrast in AOM rates may be partly attributed to the complicated syntrophic interactions between the methanotrophic archaea and SRB in the marine environment.[35,253] Hence, it is likely that other environmental factors are secondary to the microorganisms and the AOM pathway in determining the overall rate.

4.2 Some issues in the rate measurement

In contrast to the more standardized methods for methane efflux measurement (*e.g.*, static chamber, floating chamber, and core incubation) and modeling[55] or even direct methane emission monitoring *via* a satellite-based survey,[254] microbiological methane oxidation rates usually are obtained from incubation studies and multiple rate quantification methods are available. Therefore, caution must be taken that the spatiotemporal variance of the methane oxidation rates collected from both natural and anthropogenic environments, the overestimated, and sometimes underestimated oxidation rates may introduce uncertainties to the AOM capacity estimations in Section 2.

The techniques applied and the quality control of measurement are two of the crucial factors for accurate rate measurement. In addition to the lack of carbon assimilation information as mentioned in Section 2, some common issues are listed here as potential sources of uncertainties as well as opportunities for future research. First, likely, some of the methane oxidation rates measured in laboratory conditions may not represent the *in situ* methane oxidation rate. The common use of well-mixed slurries or microcosms with excessive liquid medium might disturb the original physical structures of the soil/sediments and influence the microbiological community. In these cases, the differences in terms of the availability of methane and the transport of the other nutrient and ions to and from the microbial cells may cause discrepancies between these estimated rates and the *in situ* rates. For example, during batch cultivation, it was demonstrated that shaking of bottles during incubation can lead to inaccurate estimation of either AOM or aerobic methane oxidation rates.[86,255] Besides, as shown in Section 2, AOM rates in some environments may be methane-limited due to the low methane partial pressure, while the often higher methane partial pressure in lab-scale microcosms often tends to yield a higher AOM rate during incubation. Therefore, the determination of *in situ* methane concentration or partial pressure is necessary to adjust the measured rate. On the other hand, some studies of AOM in marine sediment suggest that the AOM rates measured at ambient pressure may have greatly underestimated the *in situ* AOM rates. As mentioned in Section 2.2.1, there are a few of studies in which increased methane partial pressure induced higher AOM rates. Another obvious issue is the reporting of AOM rates. Most studies normalized the rates by the mass of dried sediment/soil or the volume of either the enrichment slurry or the cell suspension, although the normalization of rates by biomass is better for the evaluation of the actual AOM activity.

5. Conclusions and potential directions for future research

Methane is the most abundant hydrocarbon in the atmosphere and important greenhouse gas. Current biogeochemical models and analyses of methane sources and sinks often consider only aerobic methane oxidation.[256–258] Here, the estimated significance of AOM in various methane sources indicates that it is necessary to incorporate AOM in future methane budget analysis. Based on the estimated median methane oxidation capacities, AOM can reduce approximately 3–71% of the methane entering the anoxic and anaerobic zones in the studied environments (Fig. 8). For example, approximately 68–86% of the generated methane in oceans can be oxidized anoxically. In contrast, AOM is generally secondary to aerobic methane oxidation in the other studied environments, including wetlands, paddy systems, lakes/reservoirs, and rivers. The back-calculated median methane emission potentials (*i.e.*, total oxidized plus efflux to the atmosphere) suggest that approximately 72.6% of the methane from the studied sources is oxidized by methanotrophs before entering the atmosphere, and AOM accounts for 11.7% in the total source potential. Meanwhile, it has to be acknowledged that the insufficient information on the geographic coverage of each ecosystem as well as the spatiotemporal variation in methanotrophic activities[1,15,55,135] all contribute to the wide range of estimated AOM capacities. Therefore, to assist in adjusting the total strength of methane sources and in improving the accuracy of the output from various biogeochemical models, which eventually would lead to a better forecast of methane emission potentials in various environments, more systematic research of the AOM in anaerobic and anoxic zones is warranted.

Moreover, during the 2008–2017 decade, approximately 60% of atmospheric methane is attributed to anthropogenic sources.[1] According to the assessment published by the United Nations Environment Programme, reducing methane emissions from human activities is one of the most cost-effective strategies to reduce the rate of global warming.[259] The study of various AOM pathways in nature not only reforms our understanding of this methane sink, but the knowledge gained also expands our repertoire of methane control strategies. With the discovery of AOM activities in more natural environments and a better understanding of the control factors in regulating the rates of AOM, AOM may be engineered shortly as a tool for mitigating methane emission from both human activities and natural environments.

Abbreviations

AOM	Anaerobic oxidation of methane
ANME	Anaerobic methanotrophs
Anammox	Anaerobic ammonium oxidation
DAMO	Denitrifying anaerobic methane oxidation
SMTZ	Sulfate–methane transition zone
SRB	Sulfate-reducing bacteria

Author contributions

Yaohuan Gao: conceptualization, methodology, data curation, visualization, writing, and editing; Yong Wang: data curation; Hyung-Sool Lee: reviewing; Pengkang Jin: reviewing and editing.

Conflicts of interest

There are no conflicts to declare.

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