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MINI-REVIEW

Distribution and environmental significance of nitrite-dependent anaerobic methane-oxidising bacteria in natural ecosystems

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Abstract Nitrite-dependent anaerobic methane oxidation (N-DAMO) is a recently discovered process that is performed by "*Candidatus Methylomirabilis oxyfera*" (*M. oxyfera*). This process constitutes a unique association between the two major global elements essential to life, carbon and nitrogen, and may act as an important and overlooked sink of the greenhouse gas methane. In recent years, more and more studies have reported the distribution of *M. oxyfera*-like bacteria and the occurrence of N-DAMO process in different natural ecosystems, including freshwater lakes, rivers, wetlands and marine ecosystems. Previous studies have estimated that a total of 2 %–6 % of current worldwide methane flux in wetlands could be consumed via the N-DAMO process. These findings indicate that N-DAMO is indeed a previously overlooked methane sink in natural ecosystems. Given the worldwide increase in anthropogenic nitrogen pollution, the N-DAMO process as a methane sink in reducing global warming could become more important in the future. The present mini-review summarises the current knowledge of the ecological distribution of *M. oxyfera*-like bacteria and the potential importance of the N-DAMO process in reducing methane emissions in various natural ecosystems. The potential influence of environmental factors on the N-DAMO process is also discussed.

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Introduction

Methane (CH_4) is the simplest hydrocarbon and the main component of natural gas, which plays an important role in human life. In the meantime, the global-warming potential of methane is about 20-fold greater than carbon dioxide (CO_2) on a per mole basis (IPCC 2014). The methane has so far contributed an estimated 20 % of postindustrial global warming (Knittel and Boetius 2009). The current global budget of atmospheric methane is about 500–600 Tg $year^{-1}$ (Conrad 2009), which is increasing by approximately 1 % annually (Cicerone and Oremland 1998; Simpson et al. 2002). Microbial processes are the major source of methane, and they contribute to 69 % of atmospheric methane concentrations (Borrel et al. 2011). The oxidation of methane also mainly depends on microbial processes, which are estimated to consume 60 % of the methane produced in the environment (Borrel et al. 2011; Reeburgh 2007). Different biological pathways are involved in methane oxidation, like the aerobic methane oxidation using oxygen as the electron acceptor, and anaerobic methane oxidation (AMO) using sulphate (Boetius et al. 2000), iron (Beal et al. 2009) or manganese (Beal et al. 2009) as the electron acceptor. Before the discovery of AMO coupled to sulphate reduction in anoxic marine sediments and water columns (Martens and Berner 1974; Reeburgh 1976; Valentine and Reeburgh 2000), microbially mediated methane oxidation was believed to be restricted to oxic environments. The process of AMO coupled to sulphate reduction has been identified as a very important pathway for reducing methane emissions from the ocean into the atmosphere. It is estimated that 90 % of methane produced in the deep ocean can be

consumed by AMO coupled to sulphate reduction (Hinrichs and Boetius 2002; Knittel and Boetius 2009; Reeburgh 2007).

Raghoebarsing et al. (2006) discovered a new AMO process in an enrichment culture, in which AMO coupled to nitrite reduction. The nitrite-dependent anaerobic methane oxidation (N-DAMO) process constitutes a unique association between the carbon and nitrogen cycles, and could serve as an important overlooked methane sink in natural ecosystems (Raghoebarsing et al. 2006; Shen et al. 2012). The N-DAMO process is mediated by the bacterium "*Candidatus Methylomirabilis oxyfera*" (*M. oxyfera*), which is affiliated with the NC10 phylum (Ettwig et al. 2010). Until now, several *M. oxyfera* enrichment cultures have been retrieved from different natural habitats, like the canal sediments, ditch sediments, peatlands and paddy soils (Ettwig et al. 2009; He et al. 2014; Hu et al. 2009; Kampman et al. 2012, 2014; Luesken et al. 2011a; Raghoebarsing et al. 2006; Zhu et al. 2012). Recently, another new AMO process, in which AMO coupled to nitrate reduction, was discovered in an enrichment culture (Haroon et al. 2013). This AMO process is catalysed by the archaeon "*Candidatus Methanoperedens nitroreducens*" (*M. nitroreducens*) (Haroon et al. 2013). Based on the known metabolism of *M. oxyfera* and *M. nitroreducens*, it was hypothesised that *M. oxyfera* and *M. nitroreducens* with co-operation of anammox bacteria could simultaneously remove the methane, ammonium and nitrate/nitrite from wastewater (Shi et al. 2013). *M. nitroreducens* can convert nitrate, both externally fed and produced by anammox, to nitrite, with methane as the electron donor, and anammox bacteria and *M. oxyfera* can jointly remove the nitrite produced, with ammonium and methane as the electron donor, respectively (Shi et al. 2013). Therefore, the coculture of *M. oxyfera*, *M. nitroreducens* and anammox bacteria can be potentially used for anaerobic nitrogen removal from wastewater streams containing ammonium and nitrate/nitrite (Ding et al. 2014; Shi et al. 2013).

Based on the isotopic labeling experiments, Ettwig et al. (2010) hypothesised that *M. oxyfera* can produce oxygen (O_2) via a new intra-aerobic pathway that involves the dismutation of nitric oxide (NO) into dinitrogen gas (N_2) and O_2. Under anoxic conditions, *M. oxyfera* can transcribe and express the entire biochemical pathway of aerobic methane oxidation catalysed by particulate methane monooxygenase (pMMO) (Ettwig et al. 2010; Wu et al. 2011). The *pmo*A gene, which encodes one of the subunits of the pMMO complex, has been proven to be a suitable marker to monitor and identify *M. oxyfera*-like bacteria in natural habitats on a functional level (Luesken et al. 2011b). According to Ettwig et al. (2009), *M. oxyfera*-like bacteria can be mainly divided into two groups, namely group A and group B. Previous studies have reported that only group A of *M. oxyfera*-like bacteria were successfully enriched from various habitats (Ding et al. 2014; Ettwig et al. 2009; He et al. 2014; Hu et al. 2009; Kampman et al. 2012; Luesken et al. 2011a; Zhu et al. 2012), indicating that the group A members are the dominant bacteria responsible for N-DAMO. So far, no study has reported the 16S rRNA gene identity threshold to *M oxyfera* for the distinction between group A and group B members. Based on the reported studies, the 16S rRNA genes of group A members commonly showed >94.0 % identity to the 16S rRNA gene of *M. oxyfera*, while the 16S rRNA genes of group B members showed <94.0 % identity to the 16S rRNA gene of *M. oxyfera* (Ding et al. 2014; Ettwig et al. 2009; He et al. 2014; Hu et al. 2009, 2014; Kampman et al. 2012; Shen et al. 2014a, b, c, d; Zhu et al. 2012, 2014).

In recent years, considering the potential ecological importance of the N-DAMO process, the role of this process in natural ecosystems caused a great deal of attention (Shen et al. 2012). The prerequisite of the occurrence of N-DAMO process is the coexistence of methane and nitrite/nitrate in anoxic environments (Thauer and Shima 2006). Thus, the reduction zone of the sediments (like the lake sediments, river sediments and estuarine sediments) or soils (like the flooded wetland soils) could provide suitable habitats for the N-DAMO process (Fig. 1). With the development of molecular biomarkers (the primers targeting the 16S rRNA and *pmo*A genes of *M. oxyfera*; Table 1), more and more studies have reported the distribution of *M. oxyfera*-like bacteria in different natural ecosystems (Table 2). In addition, isotope labeling experiments indicated the occurrence of N-DAMO process in several natural habitats (Table 2), suggesting that this process has the great potential to reduce methane emissions from natural habitats. The objective of this mini-review is to summarise the recent findings concerning the distribution and diversity of *M. oxyfera*-like bacteria, and the potential importance of the N-DAMO process as a methane sink in reducing methane emissions in various natural ecosystems. In addition, the potential factors influencing the N-DAMO process in natural ecosystems are also discussed in the present mini-review.

N-DAMO in different natural ecosystems

Freshwater ecosystems

Freshwater sediments, which often receive increased fluxes of NO_2^-/NO_3^- from agricultural runoff or wastewater discharge, can theoretically provide a very suitable niche for *M. oxyfera*-like bacteria (Raghoebarsing et al. 2006; Thauer and Shima 2006).

Deutzmann and Schink (2011) provided the direct evidence of the presence of *M. oxyfera*-like bacteria and the occurrence of N-DAMO process in the freshwater sediments of Lake Constance, an oligotrophic freshwater lake in Germany. Radiotracer experiments with the sediments from Lake Constance were performed to follow $^{14}CO_2$ formation

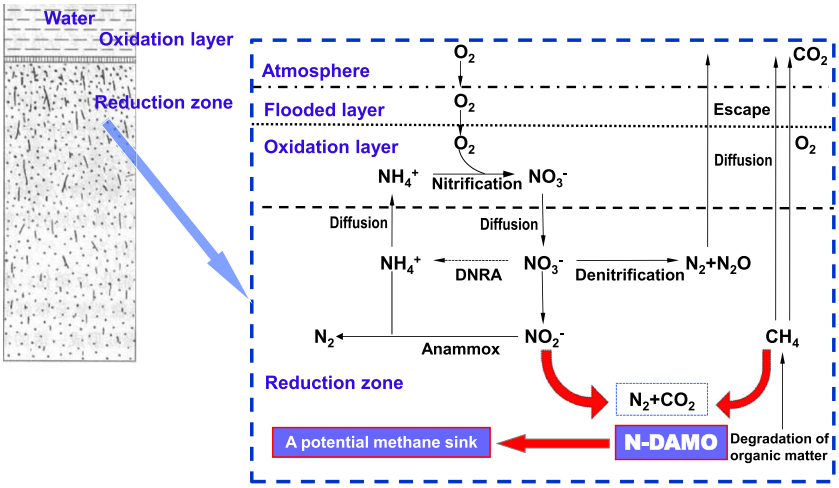

Fig. 1 The occurrence of N-DAMO process in anoxic sediments/soils

from $^{14}CH_4$ in incubations in the presence of different electron acceptors, including NO_3^-, NO_2^-, SO_4^{2-} and O_2. The results showed that $^{14}CO_2$ formation with SO_4^{2-} addition was negligible, while addition of NO_2^-/NO_3^- increased $^{14}CO_2$ formation significantly, suggesting the occurrence of N-DAMO process in this lake. The potential N-DAMO rates measured in the lake sediments was 1.8–3.6 nmol $CO_2 mL^{-1}$ day^{-1} (Deutzmann and Schink 2011). According to the measured rates of aerobic methane oxidation (two orders of magnitude higher than the potential N-DAMO rates), the N-DAMO could contribute less than 5 % to total methane oxidation in the examined lake sediments, suggesting the potential importance of N-DAMO in mitigating methane emissions from lake ecosystems. It was found that the 16S rRNA genes of the group A members and *pmo*A genes of *M. oxyfera*-like bacteria were mainly recovered from profundal (deep water sediments) and not from littoral sediments (shallow water sediments) of the Lake Constance. Furthermore, the potential N-DAMO rates obtained from profundal sediments were higher than those obtained from littoral sediments, suggesting that the

Table 1 PCR primers usually used for molecular detection of *M. oxyfera*-like bacteria in natural ecosystems

Primers	Sequence (5′-3′)	Speciality	References
8F	GACCAAAGGGGGCGAGCG	Bacteria 16S rRNA	Juretschko et al. 1998
1043R	TCTCCACGCTCCCTTGCG	*M. oxyfera* 16S rRNA	Ettwig et al. 2009
202F	GACCAAAGGGGGCGAGCG	*M. oxyfera* 16S rRNA	Ettwig et al. 2009
1545R	CAKAAAGGAGGTGATCC	Bacteria 16S rRNA	Juretschko et al. 1998
NC10-202Fdeg	RACCAAAGGRGGCGAGCG	*M. oxyfera* 16S rRNA	Deutzmann and Schink 2011
NC10-1043Rdeg	TCTCCRCGYTCCCTTGCG	*M. oxyfera* 16S rRNA	Deutzmann and Schink 2011
qP1F	GGGCTTGACATCCCACGAACCTG	*M. oxyfera* 16S rRNA	Ettwig et al. 2009
qP1R	CGCCTTCCTCCAGCTTGACGC	*M. oxyfera* 16S rRNA	Ettwig et al. 2009
qP2F	GGGGAACTGCCAGCGTCAAG	*M. oxyfera* 16S rRNA	Ettwig et al. 2009
qP2R	CGCCTTCCTCCAGCTTGACGC	*M. oxyfera* 16S rRNA	Ettwig et al. 2009
A189_b	GGNGACTGGGACTTYTGG	*M. oxyfera pmo*A	Luesken et al. 2011b
cmo682	AAAYCCGGCRAAGAACGA	*M. oxyfera pmo*A	Luesken et al. 2011b
cmo182	TCACGTTGACGCCGATCC	*M. oxyfera pmo*A	Luesken et al. 2011b
cmo568	GCACATACCCATCCCCATC	*M. oxyfera pmo*A	Luesken et al. 2011b
A189	GGNGACTGGGACTTCTGG	*pmo*A	Holmes et al. 1996
682_NC10	AAATCCGGCGAAGAACGA	*M. oxyfera pmo*A	Kojima et al. 2012
NA638Rdeg	RAATGTTCGRAGCGTVCCBC	*M. oxyfera pmo*A	Deutzmann and Schink 2011
NA720R	TCCCCATCCACACCCACCAG	*M. oxyfera pmo*A	Deutzmann and Schink 2011
HP3F1	CCCAGTACTTCATGTGGGARAARAT	*M. oxyfera pmo*A	Han and Gu 2013
HP3R1	GGGGGCCAGCCANRYCCARTT	*M. oxyfera pmo*A	Han and Gu 2013

Table 2 Diversity, abundance and potential activity of *M. oxyfera*-like bacteria in different natural ecosystems

Ecosystems	No. of OTUs (16S rRNA)	No. of OTUs (*pmo*A)	Abundance (copies g^{-1})	Activity (nmol CO_2 g^{-1} day^{-1})	References
Freshwater habitats					
Lake Constance	5c	1d	ND	1.8–3.6 nmol CO_2 mL^{-1} day^{-1}	Deutzmann and Schink 2011
Lake Biwa	6a	1d	10^5–10^6	ND	Kojima et al. 2012
Qiantang River	15c	13e	10^6–10^7	ND	Shen et al. 2014a
Wetland systems					
Freshwater wetlands	1–8b	1–9b	10^3–10^7	0.2–14.5	Han and Gu 2013; Hu et al. 2014; Shen et al. 2014b; Zhu et al. 2014
Coastal wetlands	2–12c	2–7d	10^5	ND	Chen et al. 2014a; Zhu et al. 2014
Artificial wetlands	7–11c	1–13b	10^3–10^8	0.2–2.1	Han and Gu 2013; Hu et al. 2014; Shen et al. 2014c; Wang et al. 2012; Zhu et al. 2014
Marine habitats					
Jiaojiang Estuary	3c	16e	10^5–10^7	ND	Shen et al. 2014d
South China Sea	8–30c	1–2d	ND	ND	Chen et al. 2014b

ND no data, *a* 1 % sequence cut-off, *b* 2 % sequence cut-off; *c* 3 % sequence cut-off, *d* 5 % sequence cut-off, *e* 7 % sequence cut-off

profundal sediments are the preferred habitats than littoral sediments for *M. oxyfera*-like bacteria (Deutzmann and Schink 2011). Subsequently, Kojima et al. (2012) provided the molecular evidence of the presence of *M. oxyfera*-like bacteria in another lake ecosystem, Lake Biwa, in Japan. It was also found that the group A members and *pmo*A genes of *M. oxyfera*-like bacteria were primarily present in profundal sediments (Kojima et al. 2012). In addition, Kojima et al. (2012) observed that the abundance of *M. oxyfera*-like bacteria decreased with increasing sediment depth. This suggested that the upper layer of the profundal sediments, in which the oxygen was depleted within the top 3 mm of sediment, is the main habitat for *M. oxyfera*-like bacteria in this lake. The stable environmental conditions in profundal sediments seem to be necessary for the slow-growing *M. oxyfera*-like bacteria, as observed for the slow-growing anaerobic ammonium-oxidising bacteria (Dalsgaard et al. 2005). The overall diversity of *M. oxyfera*-like bacteria reported in these two lakes were relatively low, with 5–6 OTUs (operational taxonomic units) of the 16S rRNA genes and only 1 OTU of the *pmo*A genes being reported, respectively (Table 2).

Besides the lake ecosystems, the presence of *M. oxyfera*-like bacteria was recently confirmed in the sediments of a freshwater river, Qiantang River, in China (Shen et al. 2014a). The group A members were found to be the dominant *M. oxyfera*-like bacteria in the examined shallow river sediments (the average water depth is 6–7 m), and the abundance of *M. oxyfera*-like bacteria in this river system is one order of magnitude higher than that in the reported lake sediments (Table 2). This indicates that *M. oxyfera*-like bacteria can adapt to more disturbed environments, thus expanding the knowledge of the biogeography of these bacteria. But no activity data are available to support the occurrence of N-DAMO process in this river and other river systems. Unlike the lake ecosystems, a relatively higher diversity of *M. oxyfera*-like bacteria was observed in the sediments of Qiantang River (Table 2), with a total of 15 OTUs of the 16S rRNA genes and 13 OTUs of the *pmo*A genes being detected, respectively. It was hypothesised that the more dynamic environmental conditions of the river systems could provide diverse micro-environments for different species of *M. oxyfera*-like bacteria (Shen et al. 2014a).

To investigate the potential role of N-DAMO process in freshwater ecosystems, Norði and Thamdrup (2014) recently established nitrate-enriched microcosms of sediment from a freshwater pond. It was reported that the microcosms were allowed to acclimate to nitrate levels of 1–2 mM in the overlying water, and nitrate enrichment significantly stimulated AMO relative to controls. Although the AMO rates in the microcosms were two orders of magnitude lower than aerobic methane oxidation rates reported in freshwater sediments, the AMO process could be of significance in the regulation of methane emission from oxygen-depleted freshwater systems (Norði and Thamdrup 2014). However, the relative significance of N-DAMO is not clear in this study because the AMO coupled to nitrate reduction possibly occurred in the nitrate-enriched microcosms.

Wetland systems

Wetlands are the most productive ecosystems in the world (Mitch and Gosselink 2000). One of the most important

features of wetlands is the wetland soils, which are formed under saturated or flooded conditions to allow anoxic conditions to develop. Such anoxic conditions make wetlands the largest single source of methane, with estimated emissions of 103 Tg $year^{-1}$, accounting for 20 %–40 % of the global annual methane emissions (Bastviken et al. 2011). In addition, the anoxic conditions of the wetland soils can also provide suitable habitats for the N-DAMO process because the wetland soils usually have high levels of methane and inorganic nitrogen but low levels of sulphate (Zhu et al. 2010).

Wang et al. (2012) and Zhou et al. (2014) provided the molecular evidence for the presence of *M. oxyfera*-like bacteria in paddy fields. A heterogeneous distribution of *M. oxyfera*-like bacteria was observed in different layers of the paddy fields. The group A members and *pmo*A genes were primarily detected at the deep layer (40–120 cm) of the paddy fields (Wang et al. 2012; Zhou et al. 2014). Zhou et al. (2014) indicated that the soil/groundwater ecotone of the paddy fields is a favourable environment for the growth of *M. oxyfera*-like bacteria because the abundance of these bacteria peaked at the ecotone. The anoxic environment created in the groundwater and the promoted substrate supply by the water in soil/groundwater ecotone were believed to help the growth of *M. oxyfera*-like bacteria (Zhou et al. 2014). Subsequently, Chen et al. (2014a) investigated the distribution of *M. oxyfera*-like bacteria in the surface and lower layer sediments of the coastal Mai Po wetland. The presence of complex community structures of *M. oxyfera*-like bacteria was reported in this coastal wetland. It was found that the community structures of *M. oxyfera*-like bacteria in the Mai Po wetland were different from those of the freshwater habitats, indicating the unique niche specificity of *M. oxyfera*-like bacteria in this wetland system (Chen et al. 2014a). Recently, Zhu et al. (2014) reported a wide geographical distribution of *M. oxyfera*-like bacteria at oxic/anoxic interfaces of 13 different types of wetlands over the Chinese territory, including paddy field, peatland, river, lake, riparian zone, lake littoral, swamp, tidal land, reservoir, canal, estuary, constructed wetland and groundwater. Furthermore, *M. oxyfera*-like bacteria were detected in some extreme environments, including high temperature (over 80 °C), low temperature (below −25 °C), high pH (over 9), low pH (below 5), oligotrophic and eutrophic environments (Zhu et al. 2014). This indicates that *M. oxyfera*-like bacteria may occupy a wide range of habitats and have strong adaptability to extreme conditions in wetland systems (Zhu et al. 2014).

The widespread distribution of *M. oxyfera*-like bacteria has been confirmed in various types of wetlands, but the evidence of N-DAMO activity in wetland systems is scarce. Zhu et al. (2012) reported the distribution of *M. oxyfera*-like bacteria and the occurrence of N-DAMO process in peatland fed by nitrate-polluted groundwater. After $^{13}CH_4$ and NO_2^- were supplied to soil incubations for 3 months, obvious N-DAMO activity (9.0 nmol $CO_2 g^{-1}$ soil day^{-1}) was observed in the deep layer (80–100 cm) of peatland. The potential N-DAMO rate is at the lower end of aerobic methane oxidation rates reported in wetlands (Segers 1998) but apparently is high enough to balance the methane diffusing upwards from deeper methanogenic layers (Zhu et al. 2012), suggesting the great potential of the N-DAMO process in reducing methane emissions from peatland. Hu et al. (2014) recently reported the occurrence of N-DAMO process in three wetland systems by using ^{13}C stable isotope labeling experiments, including the freshwater wetlands (Xiazhuhu wetland), urban wetlands (Xixi wetland) and paddy fields. The N-DAMO process has been confirmed at different layers (20–30, 50–60 and 90–100 cm) of the wetland soils, with the potential N-DAMO rates of 0.3–5.4 nmol CO_2 g^{-1} soil day^{-1}. In this study, the applied NO_x^- concentration in incubation experiments for determination of N-DAMO rates was similar to the in situ NO_x^- concentration at the layer of 20–30 cm but higher than the NO_x^- concentrations at the layers of 50–60 and 90–100 cm (Hu et al. 2014). Thus, Hu et al. (2014) estimated that a total of 0.5 g CH_4 m^{-2} $year^{-1}$ could be linked to the N-DAMO process in the examined wetlands by only using the potential rates obtained form the layer of 20–30 cm. According to this rate, Hu et al. (2014) further estimated that the N-DAMO process has the potential to consume 4.1–6.1 Tg CH_4 on average each year, assuming that the total area of wetlands in the world is 8–12 million km^2 (Lehner and Döll 2004), which is approximately 2 %–6 % of the current CH_4 flux in wetlands (100–200 Tg $year^{-1}$; Dlugokencky et al. 2011). Overall, the N-DAMO process represents a previously overlooked methane sink in wetlands based on the results of Hu et al. (2014). This finding alters the understanding of the mechanisms for reducing methane emissions from wetlands which aerobic methane oxidation was previously identified as the only important microbial methane sink (Bridgham et al. 2013). It was observed that the group A members, *pmo*A genes and higher potential N-DAMO rates were mainly detected in the deep layers (50–60 and 90–100 cm) of the three wetlands (Hu et al. 2014). The constant environmental conditions and higher concentration of methane were thought to be the main reasons for the N-DAMO process that occurs primarily in deep wetland soils (Shen et al. 2014b). In addition, the presence of a certain concentration of NO_2^-/NO_3^- in deep wetland soils can stimulate the occurrence of N-DAMO process (Shen et al. 2014b, c). The presence of NO_2^-/NO_3^- in the deep wetland soils may be because of NO_2^-/NO_3^- leaching from the upper layer (Shen et al. 2014b, c). Shen et al. (2014b) indicated that the oxygen could be released from the rhizosphere of plants in the upper layer of the wetland soils, which can have an adverse impact on the distribution of *M. oxyfera*-like bacteria. Different levels of *M. oxyfera*-like bacterial diversity were reported in different types of wetlands, with 1–12 and 1–13 OTUs of the 16S rRNA genes and *pmo*A genes being detected, respectively (Table 2).

Marine ecosystems

Coastal marine environments (like the estuaries) are rich in organic carbon, thus they offer ideal conditions for methane production and were reported to be significant source of methane (Liikanen et al. 2009; Middelburg et al. 2002; Upstill-Goddard et al. 2000). Given the worldwide increase in anthropogenic nitrogen pollution in coastal environments (such as agricultural run-off and wastewater discharge), NO_2^-/NO_3^- is very likely to increase to become an important electron acceptor for AMO under anoxic conditions. The methane produced in the organic-rich lower parts of the coastal marine sediments diffuses upwards where it meets NO_2^-/NO_3^- from agricultural runoff or wastewater discharge, making the surface coastal marine sediments as suitable habitats for the N-DAMO process (Shen et al. 2014d).

Shen et al. (2014d) provided the molecular evidence of the distribution of *M. oxyfera*-like bacteria in the surface sediments of Jiaojiang Estuary in China. It was found that the group A members were the dominant *M. oxyfera*-like bacteria in the sediments of Jiaojiang Estuary, and the *pmo*A genes of *M. oxyfera*-like bacteria were detected at all sampling sites examined (Shen et al. 2014d), suggesting that *M. oxyfera*-like bacteria in this estuary may be active and have the potential to reduce methane emissions from the estuary. But the N-DAMO activity should be measured in this estuary and other more estuaries by isotope labeling experiments in the following studies to assess the role of N-DAMO process in reducing methane emissions from estuaries. Besides the coastal environments, Valentine (2011) predicted that the deep-sea sediments might also be suitable habitats for the N-DAMO process. Orcutt et al. (2011) reported that the high rate of AMO coupled to sulphate reduction in deep ocean do not completely prevent the escape of methane to the water column, suggesting the availability of methane for N-DAMO in deep-sea surface sediments. Furthermore, the affinity constant for methane of N-DAMO process was reported to be less than 5 μM (Ettwig et al. 2008) or even less than 0.6 μM (Raghoebarsing et al. 2006), which is significantly lower than the affinity constant for methane of AMO coupled to sulphate reduction (in the order of millimolars; Nauhaus et al. 2002). On the other hand, a certain concentration of NO_2^-/NO_3^- is present in deep-sea surface sediments (up to several tens of μM; Gruber 2008), providing the electron acceptor for N-DAMO. Recently, Chen et al. (2014b) reported the widespread distribution of *M. oxyfera*-like bacteria in the sediments of South China Sea. In this study, phylogenetic analyses of the recovered 16S rRNA and *pmo*A gene sequences from the marine sediments together with the reported freshwater sequences were conducted. It was found that the 16S rRNA gene sequences recovered from marine sediments mainly fall into groups D and E, in contrast to the sequences recovered from freshwater habitats that mainly fall into groups A and B. Furthermore, three new subclusters of *M. oxyfera*-like bacteria were discovered in the sediments of South China Sea based on the recovered *pmo*A genes, which was distantly related to the *pmo*A genes that recovered from freshwater habitats (Chen et al. 2014b). In addition, principal coordinate analysis was performed in this study. Compared with the *M. oxyfera*-like bacterial communities in freshwater habitats, the ones in the sediments of South China Sea seemed more isolated (Chen et al. 2014b). Thus, the community structures of marine *M. oxyfera*-like bacteria are very different from the freshwater ones, indicating that certain clusters (species) of *M. oxyfera*-like bacteria are associated with certain conditions. Compared with the freshwater sediments/soils, the unique environmental conditions in deep-sea sediments, which usually have high levels of salinity but low levels of nutrient, may result in the unique niche specificity for marine *M. oxyfera*-like bacteria. The freshwater sediments/soils may provide more favourable niches for the groups A and B members, while the deep-sea sediments may provide more favourable niches for groups D and E members. A very high diversity of *M. oxyfera*-like bacterial 16S rRNA genes was observed in the examined sampling sites of South China Sea, with 8–30 OTUs being detected (Table 2). The deep-sea water circulation was considered to be a potential factor contribution to the observed high diversity of *M. oxyfera*-like bacteria (Chen et al. 2014b). In contrast, a low level of *pmo*A genes (1–2 OTUs) was observed in the sediments of South China Sea (Chen et al. 2014b).

Although the presence of *M. oxyfera*-like bacteria has been confirmed in the marine ecosystems (Chen et al. 2014b; Shen et al. 2014d), no direct evidence of the occurrence of N-DAMO process has been reported. Actually, we recently proved the occurrence of N-DAMO process by using ^{13}C labeling experiments in marine sediments of Hangzhou Bay of the East China Sea (unpublished data). The potential N-DAMO rates (0.2–1.3 nmol CO_2 g^{-1} day^{-1}) were slightly lower than those measured in freshwater environments. In addition, the potential rates of aerobic methane oxidation and AMO coupled to sulphate reduction were also determined in the studied area. Based on the incubation results, it was estimated that N-DAMO contributed 2.0 %–9.5 % to total methane oxidation in the sediments of Hangzhou Bay, suggesting that N-DAMO is also a previously overlooked methane sink in marine environments.

Potential impacts of environmental factors on N-DAMO

Currently, the potential impact of environmental factors on the N-DAMO process in natural ecosystems is not well known. Based on the reported enrichment conditions of *M. oxyfera*-like bacteria and the environmental conditions of the occurrence of N-DAMO process in natural ecosystems, the main

environmental factors that may have important impact on the N-DAMO process primarily include the following aspects.

Temperature

The temperature range of the current *M. oxyfera* enrichment cultures is 20–35 °C (Ding et al. 2014; Ettwig et al. 2009; He et al. 2013, 2014; Hu et al. 2009; Kampman et al. 2012, 2014; Luesken et al. 2011a; Raghoebarsing et al. 2006), and thus *M. oxyfera*-like bacteria belong to mesophilic bacteria. Hu et al. (2009) obtained two *M. oxyfera* enrichment cultures that were enriched from mixed inoculum, including sediment from a freshwater lake, anaerobic digester sludge and return activated sludge from a sewage treatment plant, under different temperatures. It was found that the N-DAMO activity of the 35 °C enrichment culture was higher than that of the 22 °C enrichment culture. The culture enriched at 22 °C only contained *M. oxyfera*-like bacteria, while the culture enriched at 35 °C contained both *M. oxyfera*-like bacteria and *M. nitroreducens*-like archaea. Ettwig et al. (2009) also found that the N-DAMO activity of *M. oxyfera* enrichment culture increased when the temperature increased from 25 °C to 30 °C. But inconsistent with the results reported by Hu et al. (2009), Ettwig et al. (2009) observed that the archaea disappeared as the temperature increased. Based on the above two studies, it is believed that the temperature could have important impacts on the activity and community structures of *M. oxyfera* enrichment culture. The optimal temperature for *M. oxyfera* enrichment is 30–35 °C, while the selection mechanisms of temperature on the microbial community structures are unclear. The optimum temperature for *M. oxyfera*-like bacteria in most natural habitats (like the marine and freshwater sediments) may be below this range because the in situ temperature is usually less than 30–35 °C. For instance, Deutzmann and Schink (2011) reported N-DAMO activity in the sediments of Lake Constance under the in situ temperature of 4 °C. In addition, Chen et al. (2014b) recently reported that the temperature had an important impact on the diversity of the 16S rRNA genes of *M. oxyfera*-like bacteria in the sediments of South China Sea. But the actual impact of the temperature on the activity and community structures of *M. oxyfera*-like bacteria in natural habitats is still poorly known due to the limited data available. To better understand how global climate change and global warming may alter the biogeochemical cycling of methane and nitrogen, the investigation of temperature response of N-DAMO activity and community structures in different natural habitats should be performed in future studies.

Oxygen

Since *M. oxyfera*-like bacteria can use the intracellularly produced O_2 (Ettwig et al. 2010; Wu et al. 2011), Luesken et al. (2012) investigated the influence of external oxygen (concentrations of 2 % and 8 %) on the activity and gene expression of key enzymes of *M. oxyfera* enrichment culture. The results showed that the applied O_2 concentrations resulted in an instant decrease of methane and nitrite conversion rates of the enrichment culture. Furthermore, the inhibition of central energy metabolism of *M. oxyfera*-like bacteria and the deviation in the stoichiometry of N-DAMO reaction were observed, suggesting that *M. oxyfera*-like bacteria cannot use external O_2 to oxidise methane. Overall, the applied O_2 conditions by Luesken et al. (2012) had a damaging effect on *M. oxyfera*-like bacteria. But it should be noted that the applied O_2 concentration was possibly too high, and the effect of trace oxygen or alternating oxic/anoxic conditions on *M. oxyfera*-like bacteria needs to be further investigated. So far, no study has reported the influence of O_2 on *M. oxyfera*-like bacteria in natural ecosystems. It can be inferred that the distribution of *M. oxyfera*-like bacteria is restricted by O_2 in natural ecosystems because these bacteria were reported to be primarily distributed in the deep water sediments (Deutzmann and Schink 2011; Kojima et al. 2012) and deep wetland soils (Hu et al. 2014; Shen et al. 2014b, c; Wang et al. 2012; Zhou et al. 2014; Zhu et al. 2012).

Nitrite/nitrate

The current *M. oxyfera* enrichment cultures were primarily enriched from freshwater sediments that polluted by inorganic nitrogen or from nitrogen-rich wastewater sludges (Ding et al. 2014; Ettwig et al. 2009; He et al. 2014; Hu et al. 2009; Kampman et al. 2012, 2014; Luesken et al. 2011a; Raghoebarsing et al. 2006), suggesting that the availability of inorganic nitrogen (NO_2^-/NO_3^-) can have an important impact on the N-DAMO process. The concentration of NO_2^- is usually very low in environments because it is very unstable in nature and quickly reacts with other compounds, and the major source of NO_2^- is derived from NO_3^- reduction (like denitrification) under anoxic conditions. Thus, the NO_3^- concentration often determines the NO_2^- concentration in anoxic soils/sediments. Wang et al. (2012) reported that the soil NO_3^- concentration had a significant impact on the distribution of *M. oxyfera*-like bacteria in paddy fields, which the abundance of these bacteria was positively correlated with the soil NO_3^- concentration. Norði and Thamdrup (2014) found that the AMO rates in the nitrate-enriched microcosms significantly correlated with the NO_3^- concentration in the overlying water, suggesting that the availability of NO_2^-/NO_3^- can have an important impact on the potential N-DAMO rates. Chen et al. (2014a, b) reported that the NO_x^- concentration had important impacts on the community structures and distribution of *M. oxyfera*-like bacteria in the sediments of coastal Mai Po wetland and the sediments of South China Sea. In addition, our unpublished results showed that the distribution

and activity of *M. oxyfera*-like bacteria in the sediments Hangzhou Bay were significantly influenced by the NO_3^- concentration in the overlying water.

Methane/organic carbon

Methane (CH_4) is the electron donor of *M. oxyfera*-like bacteria, which use the methane as their sole energy source (Ettwig et al. 2010; Rasigraf et al. 2014). Thus, the concentration of methane could have a great impact on the distribution of *M. oxyfera*-like bacteria and the occurrence of N-DAMO process in environments. Hu et al. (2014) and Shen et al. (2014b, c) found that higher abundance of *M. oxyfera*-like bacteria and higher potential N-DAMO rates were observed in the deep wetland soils where higher concentrations of methane were also observed, indicating that the methane concentration is an important factor influencing the N-DAMO process. The methane is primarily produced by methanogens using organic carbon as the electron donor under anoxic conditions, and many studies have reported that the organic carbon is the controlling factor for the methane emissions (Borrel et al. 2011; Chan et al. 2005; Schwarz et al. 2008). Therefore, the methane concentration is largely determined by the concentration and lability of organic carbon in environments. Furthermore, denitrification can release NO_2^- from NO_3^- for *M. oxyfera*-like bacteria using organic carbon as the electron donor. Thus, the organic carbon concentration can also be an important factor influencing the NO_2^- level. Wang et al. (2012) and Zhou et al. (2014) reported that the concentration of soil organic carbon significantly influenced the distribution of *M. oxyfera*-like bacteria in paddy fields, with the abundance of these bacteria positively correlating with the concentration of organic carbon. Shen et al. (2014a, d) reported that the abundance of *M. oxyfera*-like bacteria significantly correlated with the concentration of sediment organic carbon in Qiantang River and Jiaojiang Estuary, respectively.

Salinity

Up to now, two studies have reported the distribution of *M. oxyfera*-like bacteria in marine environments (Chen et al. 2014b; Shen et al. 2014d). Chen et al. (2014b) found that the salinity is an important factor shaping the community structures of *M. oxyfera*-like bacteria in the sediments of South China Sea, and the salinity showed a significant correlation with the diversity of *M. oxyfera*-like bacterial 16S rRNA genes. A heterogeneous distribution of *M. oxyfera*-like bacteria was observed in the sediments of Hangzhou Bay in our recent study. It was found that the group A members were the dominant *M. oxyfera*-like bacteria in the inner part of Hangzhou Bay, while the group B members were the dominant *M. oxyfera*-like bacteria in the outer edge of the bay. Moreover, both the abundance and activity of *M. oxyfera*-like bacteria showed decreasing trends from the inner part to the outer edge of the bay. Correlation analyses showed negative relationships between the abundance, activity of *M. oxyfera*-like bacteria and the salinity. These results together indicate that the salinity may have an important impact on the distribution and activity of *M. oxyfera*-like bacteria in marine environments.

Conclusions and outlook

Globally, anthropogenic nitrogen inputs are increasing rapidly, suggesting that the NO_2^-/NO_3^- can become the major electron acceptor for AMO under anoxic conditions. Therefore, the N-DAMO process will be globally important and has the great potential to be an important methane sink in natural ecosystems in future because of the increasing nitrogen pollution. However, estimate of the environmental significance of the N-DAMO process as a methane sink in natural ecosystems still appears to be associated with a very large uncertainty. In addition, the ecological distribution of *M. oxyfera*-like bacteria and the relative contribution of N-DAMO to the methane oxidation in natural ecosystems can be significantly influenced by environmental factors. However, the potential interactions between the environmental factors and the N-DAMO process are still poorly understood. Thus, more ecological studies of the N-DAMO process that mimic the in situ conditions as closely as possible are required to determine the quantitative importance of this process as a methane sink in reducing methane emissions in various natural ecosystems and the main factors influencing it.

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