



Review

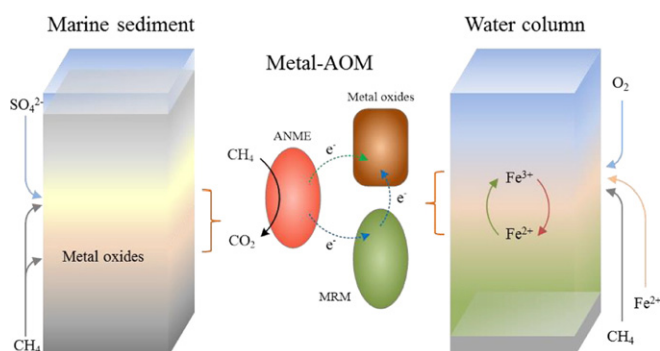
Microbiological and environmental significance of metal-dependent anaerobic oxidation of methane

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HIGHLIGHTS

- The process of prediction and discovery of metal-AOM is reviewed.
- Responsible microorganisms and mechanisms of metal-AOM are identified.
- Environmental significance of methane cycle and geochemistry is presented.
- Effects of environmental factors and metal forms on metal-AOM are discussed.

GRAPHICAL ABSTRACT



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ABSTRACT

Anaerobic oxidation of methane (AOM) can be coupled to the reduction of sulfate, nitrate and nitrite, which effectively reduces methane emission into the atmosphere. Recently, metal-dependent AOM (metal-AOM, AOM coupled to metal reduction) was demonstrated to occur in both environmental samples and enrichment cultures. Anaerobic methanotrophs are capable of respiration using Fe(III) or Mn(IV), whether they are in the form of soluble metal species or insoluble minerals. Given the wide distribution of Fe(III)/Mn(IV)-bearing minerals in aquatic methane-rich environments, metal-AOM is considered to be globally important, although it has generally been overlooked in previous studies. In this article, we discuss the discovery of this process, the microorganisms and mechanisms involved, environmental significance and factors influencing metal-AOM. Since metal-AOM is poorly studied to date, some discussion is included on the present understanding of sulfate- and nitrate-AOM and traditional metal reduction processes using organic substrates or hydrogen as electron donors. Metal-AOM is a relatively new research field, and therefore more studies are needed to fully characterize the process. This review summarizes current studies and discusses the many unanswered questions, which should be useful for future research in this field.

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1. Introduction

Methane is quite rare in the atmosphere but is the second most important greenhouse gas, just following carbon dioxide, and contributes about 20% to current global warming (Su et al., 2015; Cai et al., 2016). In the past three decades, the level of global atmospheric methane has increased from 1.6 to 1.8 ppm (there was a general stabilization from 1999 to 2006), and its effect has attracted great attention in the scientific community (Kirschke et al., 2013; Nisbet et al., 2014). Microbial anaerobic oxidation of methane (AOM) plays a role in methane regulation and reduces methane release from both marine and freshwater ecosystems (Hu et al., 2014b; He et al., 2015a; Segarra et al., 2015). AOM is well known to be coupled with sulfate reduction (sulfate-dependent AOM, sulfate-AOM) in marine ecosystems, and anaerobic methanotrophic archaea (ANME) are generally partnered with sulfate-reducing bacteria (SRB) in microbial consortia (Knittel and Boetius, 2009; Milucka et al., 2012; McGlynn et al., 2015; Wegener et al., 2015). The process of nitrate/nitrite-dependent AOM was discovered by Raghoebarsing et al. (2006), and has been extensively studied in the following decade (Ettwig et al., 2010; Haroon et al., 2013; He et al., 2013; Deutzmann et al., 2014; Hu et al., 2014a; Chen et al., 2015; He et al., 2015d; Zhu et al., 2015; He et al., 2016a; Shen et al., 2016).

Recently, it was demonstrated that AOM can be coupled with the dissimilatory reduction of metals, including Fe(III) and Mn(IV) (metal-dependent AOM, metal-AOM) (Ettwig et al., 2016; Fu et al., 2016; Scheller et al., 2016). Since Fe(III)/Mn(IV)-bearing minerals and methane are widely distributed in the biosphere, metal-AOM may be globally significant in the methane cycle and in the biogeochemistry of Fe, Mn and other related elements. It has been suggested that metal-AOM occurs in some marine and freshwater ecosystems (Beal et al., 2009; Crowe et al., 2011; Amos et al., 2012; Wankel et al., 2012; Norði et al., 2013; Egger et al., 2015). It has also been speculated that metal-AOM might have thrived on the early Earth (anoxic, iron-rich and sulfate-poor environments) and be involved in the geological evolution of the Earth (Beal et al., 2009; Norði et al., 2013; Ettwig et al., 2016). Notably, gas, liquid and solid phases are involved in the reactions of metal-AOM, which can result in low reaction rates (Beal et al., 2009) and complex mechanisms (Ettwig et al., 2016; Fu et al., 2016).

In this article, we review results and findings from studies pertaining to the microbiology, ecology and biogeochemistry of metal-AOM. The discovery, responsible microorganisms, microbial mechanisms,

environmental significance and factors influencing metal-AOM are discussed, according to the present knowledge about metal-AOM, other processes of AOM, and known bacterial metal reduction processes. To conclude, some unanswered questions and directions for future research on metal-AOM are discussed.

2. Prediction and discovery of metal-AOM

2.1. Thermodynamic considerations

As early as 1980, Zehnder and Brock (1980) speculated that iron and manganese might be involved in AOM. In 2008, Caldwell et al. (2008) calculated the Gibbs free energy of methane oxidation with various environmentally relevant oxidants and proposed the possibility that some microorganisms or syntrophic consortia can use Fe(III) as an electron acceptor for methane oxidation. They calculated the Gibbs free energy under conventional standard conditions for chemical reactions (ΔG° ; 1 mol L⁻¹ of H⁺, pH = 0), instead of the standard conditions for biological processes (ΔG° ; pH = 7). Here, we have calculated the biological standard Gibbs free energy (ΔG°) of Fe-dependent AOM (Fe-AOM) to be -81.6 kJ mol⁻¹, which is significantly lower than that at pH 0 (-454.6 kJ mol⁻¹). Notably, limited by the low solubility of ferrous hydroxide at pH 7, the solubility of Fe²⁺ of 4.86 mmol L⁻¹ was introduced in the above calculation instead of the standard condition of 1 mol L⁻¹. Despite this, it is still larger than the energy of sulfate-AOM

Table 1
Standard and *in situ* actual Gibbs free energies of different AOMs.

Reaction	ΔG° (kJ mol ⁻¹ CH ₄)	<i>in situ</i> ΔG (kJ mol ⁻¹ CH ₄)
CH ₄ + SO ₄ ²⁻ → HCO ₃ ⁻ + HS ⁻ + H ₂ O	-16.6	-22 ~ -35 (Caldwell et al., 2008)
CH ₄ + 8Fe(OH) ₃ + 15H ⁺ → HCO ₃ ⁻ + 8Fe ²⁺ + 21H ₂ O	-81.6 ^a	-270.3 (Beal et al., 2009)
CH ₄ + 4MnO ₂ + 7H ⁺ → HCO ₃ ⁻ + 4Mn ²⁺ + 5H ₂ O	-494.0	-556 (Beal et al., 2009)
CH ₄ + 4NO ₃ ⁻ → CO ₂ + 4NO ₃ ⁻ + 2H ₂ O	-519.8	N.A.
CH ₄ + 8/3NO ₂ ⁻ + 8/3H ⁺ → CO ₂ + 4/3N ₂ + 10/3H ₂ O	-928	N.A.

N.A.: not available.

^a The concentration of Fe²⁺ is limited to 4.86 mmol L⁻¹ due to its solubility at pH 7 (the standard pH for biological reactions).

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