



Factors controlling the types of microbial consortia in cold-seep environments: A molecular and isotopic investigation of authigenic carbonates from the South China Sea

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ABSTRACT

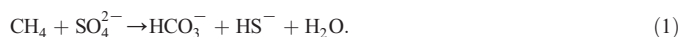
Authigenic carbonates were recovered from several locations of the South China Sea continental slope at a 470 m to 770 m water depth. The sources of seeping fluids, the time involved in carbonate formation and the potential driving forces are increasingly understood, but little is known about the biogeochemical processes that occur during this type of carbonate precipitation. Here, a molecular and isotopic investigation of authigenic carbonates was conducted to determine the factors controlling the types of microbial consortia in cold-seep environments. The studied carbonates were one aragonitic crust and three high-Mg calcitic tubular concretions from specific sites. A significant input of biogenic methane to the carbon pool during the precipitation of the carbonates was suggested by the presence of ¹³C-depleted molecular fossils of methanotrophic archaea (with $\delta^{13}\text{C}$ values as negative as -141.5‰) and sulfate-reducing bacteria (with $\delta^{13}\text{C}$ values as negative as -128.5‰). The methane was primarily oxidized in an anaerobic process. The predominant consortia were ANME-2 assemblages in the aragonitic carbonate (sample TVG3-C2), whereas high-Mg calcitic carbonates (samples TVG14-C2 and TVG8-C5) were dominated by ANME-1 assemblages according to the specific biomarkers observed. Taking the favored environments for specific AOM consortia and crystallization conditions for aragonite and calcite together, the factors selecting for specific AOM communities appear to be constrained by their biogeochemical settings. Accordingly, higher alkalinity, abundant sulfate concentration and being closer to the water–sediment interface conditions favor the precipitation of aragonite over high-Mg calcite.

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1. Introduction

The anaerobic oxidization of methane (AOM), which is conjointly conducted by consortia of anaerobic methane-oxidizing archaea (ANME) and sulfate-reducing bacteria (SRB), is the most important sink for methane in marine environments (Reeburgh, 1976, 1996; Boetius et al., 2000). Up to 90% of the methane produced in anoxic marine settings is oxidized anaerobically (Reeburgh, 1976; Reeburgh et al., 1993) and can affect the atmospheric methane concentration, the local oceanic redox conditions and the carbon cycle (Hinrichs and Boetius, 2002; Pape et al., 2005; Bouloubassi et al., 2006; Feng et al., 2009a,b; Birgel et al., 2011; Schrag

et al., 2013). During AOM, alkalinity increases because of the production of bicarbonate [HCO_3^-] in the following reaction:



The reaction promotes the precipitation of carbonate minerals close to the seafloor (Berner, 1980).

To date, three distinct archaeal lineages (ANME-1, ANME-2, and ANME-3) have been discovered. The sulfate-reducing partners of ANME-1 and ANME-2 are two different eco-types of SRB related to the *Desulfosarcina/Desulfococcus* (DSS) cluster (Boetius et al., 2000; Orphan et al., 2001; Knittel et al., 2003), whereas ANME-3 is associated with *Desulfobulbus* spp. (DBB) (Knittel et al., 2005; Niemann et al., 2006; Losekann et al., 2007). According to microscopy, fluorescent in situ hybridization (FISH), and secondary ion mass spectrometry (SMIS) studies, ANME-2 archaea are closely associated with their SRB partners (Hinrichs and Boetius, 2002), whereas the ANME-1 archaeal group more frequently exists in monospecific aggregates and single cells (Orphan et al., 2002).

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Furthermore, ANME-1/DSS clusters are able to deal with lower methane concentrations and are more sensitive to oxygen than those of ANME-2 (Elvert et al., 2005; Knittel et al., 2005; Nauhaus et al., 2005), whereas ANME-2/DSS are better adapted to lower temperatures than those of ANME-1/DSS (Nauhaus et al., 2005). Recently, studies have suggested that aragonite is often deposited at sites dominated by ANME-2 consortia, whereas ANME-1 consortia are dominant during the precipitation of high-Mg calcites (Stadnitskaia et al., 2008a; Haas et al., 2010; Birgel et al., 2011). It appears that high alkalinity, high sulfate concentration and conditions closer to the water–sediment interface favor the precipitation of aragonite over high-Mg calcite (Burton, 1993; Savard et al., 1996; Aloisi et al., 2000; Greinert et al., 2001). This assumption is consistent with the observation that the dominant environments for ANME-2/DSS occur in surface sediments, and the dominant ANME-1/DSS environments occur in relatively deeper sediments. The modern AOM communities appear to be ubiquitous in marine seep sites (Blumenberg et al., 2004; Rossel et al., 2011). However, the factors selecting for a particular AOM community are relatively poorly constrained.

Lipid biomarkers combined with compound-specific stable carbon isotopes allow the identification of dominant microbes, formation environments and their carbon fixation pathways at methane-seeps (Alberts et al., 2002; Peckmann et al., 2004; Brocks and Pearson, 2005; Birgel et al., 2011). There are several organic and inorganic-related studies about the authigenic carbonates of Dongsha and Shenhu in the South China Sea. For example, studies have examined the lipid biomarkers, mineralogy, petrography, and stable carbon and oxygen isotope compositions (Birgel et al., 2008; Han et al., 2008; Yu et al., 2008; Ge et al., 2010, 2011; Tong et al., 2013), but the relationship between the predominant consortia and mineral compositions, as well as factors favoring specific AOM communities remain unclear.

In this study, we present detailed molecular and isotopic data obtained from lipid biomarkers in one aragonitic crust and three high-Mg calcitic tubular concretions. The obtained data, together with mineral composition and $\delta^{13}\text{C}$ values (Han et al., 2008; Tong et al., 2013), were used to determine the relationship between the predominant consortia and mineral compositions and provide new insights on the factors selecting for a particular AOM community at seeps in the South China Sea.

2. Geological setting and materials

The South China Sea is located in the convergent hinge of the Eurasian plate, the Philippine Sea and the Indo-Australian plate. It is bordered to the north and west by passive continental margins and to the east by the eastward-dipping subduction zone of the Manila Trench (Taylor and Hayes, 1980; Pautot et al., 1986). The Dongsha area of the South China Sea is located at the transition between the passive northern margin and the accretionary eastern margin off SW Taiwan Island, which is characteristic of the passive continental margin in the Cenozoic, and rich in oil- and gas-bearing basins (Shyu et al., 1998).

The joint Chinese–German RV Sonne Cruise 177 discovered cold seep carbonates in the NE part of the Dongsha area in 2004 (Fig. 1). Seep carbonates were sampled at three sites on two adjacent ridges: Site 1 is the shallowest site, with water depths between 473 m and 498 m. Samples from Site 1 mainly consist of tubes, blocks, cemented burrows, and doughnut/irregular-shaped concretions. Carbonate chimneys and chimney fragments are common at Site 2. At Site 3, a carbonate edifice called the Jiulong Methane Reef stands above the surrounding seafloor (Fig. 2, Table 1) (Suess, 2005; Han et al., 2008). Samples collected at this site are mainly green-gray irregular concretions and crusts, and this site is still weakly active, whereas the other sites are extinct. Sample TVG3-C2 is mainly composed of aragonite, whereas the other three samples (TVG12-C3, TVE14-C2, and TVG8-C5) are dominated by high-Mg calcite. The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of these authigenic carbonates vary from -56.3‰ to -35.7‰ and from 2.3‰ to 5.3‰ , respectively (Table 2) (Han et al., 2008; Tong et al., 2013).

3. Methods

3.1. Lipid extraction

The carbonate samples were crushed into small pieces, ground into powders and dried. The samples were subsequently Soxhlet-extracted for 72 h with a mixture of dichloromethane and methanol (9:1; v:v). The total lipid extracts were dried with sodium sulfate and saponified with 6% KOH (w/v) in methanol. The neutral fractions were extracted 3–5 times with hexane until the extracts turned colorless. Next, to

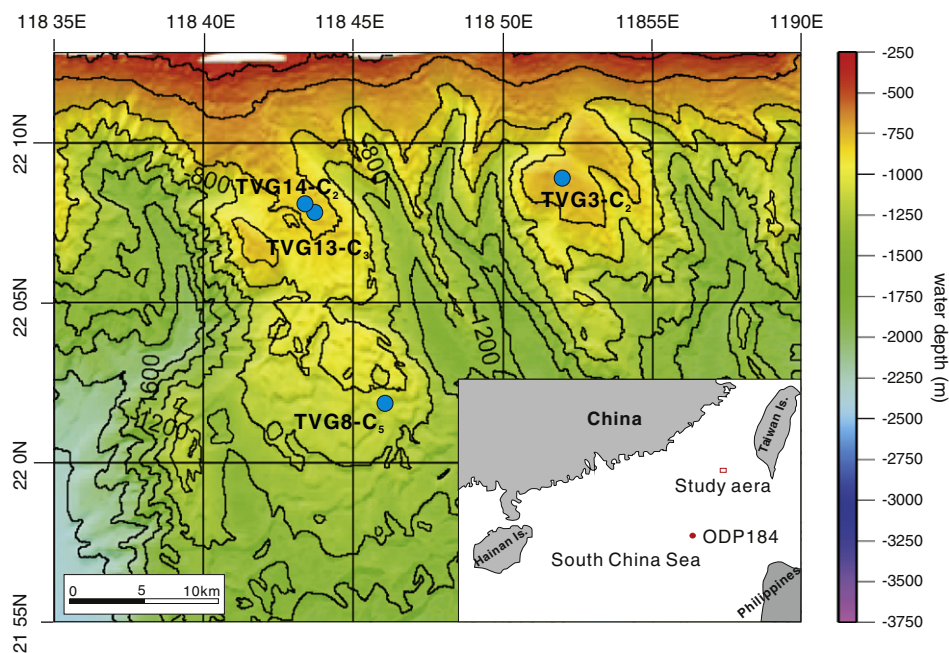


Fig. 1. Bathymetry map showing the location of samples analyzed in this study (see Table 1 for detail).

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