



Diversity and distribution of methane-oxidizing microbial communities associated with different faunal assemblages in a giant pockmark of the Gabon continental margin

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ABSTRACT

A giant 800-m-diameter pockmark named REGAB was discovered on the Gabon continental margin actively emitting methane at a water depth of 3200 m. The microbial diversity in sediments from four different assemblages of chemosynthetic organisms, Mytilidae, Vesicomidae, Siboglinidae and a bacterial mat, was investigated using comparative 16S rRNA gene sequence analysis. Aggregates of anaerobic methanotrophic archaea (ANME-2) and bacteria of the *Desulfosarcina/Desulfococcus* cluster were found in all four chemosynthetic habitats. Fluorescence in situ hybridization targeting the ANME-2/*Desulfosarcina/Desulfococcus* aggregates showed their presence few centimeters (3–5 cm) below the surface of sediment. 16S rRNA gene sequences from all known marine ANME groups were detected in the pockmark sediments, as well as from both known bacterial partners. The archaeal diversity was limited to the ANME cluster for all investigated samples. The bacterial diversity included members of the *Proteobacteria*, *Bacilliales*, *Cytophaga/Flavobacteria*, *Verrucomicrobia*, JS1 and *Actinobacteria* clusters. Bacterial 16S rRNA gene sequences related to those of known sulphide-oxidizing symbionts were recovered from tissues of several invertebrates including vesicomid clams and siboglinid tubeworms of REGAB.

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1. Introduction

Deep-sea cold-seep ecosystems are characterized by high fluxes of hydrocarbons and sulphide originating from the subsurface seabed by thermogenic or microbial production. Chemotrophic microorganisms, either free-living or in symbiosis with invertebrates, are abundant at these sites where they derive energy from the oxidation of sulphide or methane (Paull et al., 1984; Sibuet and Olu, 1998; Pancost et al., 2000; Valentine and Reeburgh, 2000; Orphan et al., 2001; Tunnicliffe et al., 2003). Deep-water cold seeps often show substantial accumulations of methane in the seafloor in gaseous, liquid and solid form, the latter also known as gas hydrates (Kvenvolden, 1998; Milkov

and Sassen, 2002). A major fraction of the methane rising from deeper sediments to the seafloor is consumed by microorganisms within the seabed, mainly through the anaerobic oxidation of methane (AOM) (Reeburgh, 1976). The anaerobic oxidation of methane by sulphate reduction leads to the formation of sulphide and carbonate (Barnes and Goldberg, 1976; Reeburgh, 1976). This process is mediated by yet uncultivated methanotrophic archaea related to the methanogens, and sulphate reducers of the Deltaproteobacteria clade (Hinrichs and Boetius, 2002). The sulphate-reducing bacteria (SRB) and anaerobic methanotrophic archaea (ANME) often form aggregates and occur at very high abundances in cold-seep sediments (Boetius et al., 2000; Orphan et al., 2001). Several distinct phylogenetic clusters of *Archaea* are involved in AOM as shown in various observations including proteomic and metagenomic data (Knittel et al., 2005; Kruger et al., 2003; Hallam et al., 2004; Meyerdierks et al., 2005). The ANME-1 group is related to the *Methanosarcinales* and *Methanomicrobiales* orders (Hinrichs et al., 1999), the ANME-2 and ANME-3 groups are related to the *Methanosarcinales* (Boetius et al., 2000; Niemann et al., 2006). The ANME occur in sediments in consortium with sulphate-reducing bacteria (Michaelis et al.,

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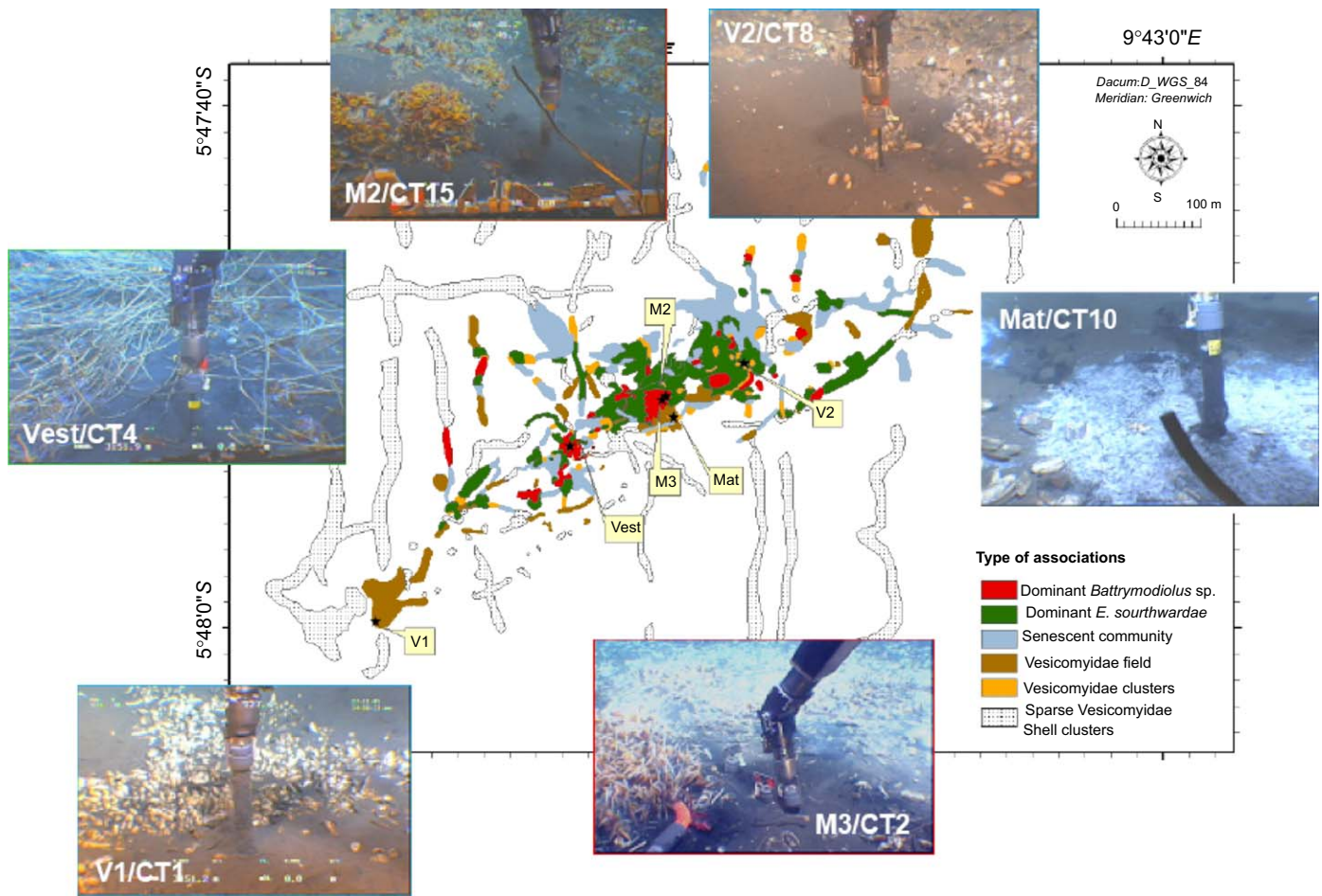


Fig. 1. Map of the REGAB site (adapted from the Olu-Le Roy et al., 2007a) and sediment sampling sites.

2002; Knittel et al., 2005) or as single cells or small assemblages (Orphan et al., 2001; Knittel et al., 2005). ANME-1 and ANME-2 are generally associated with sulphate-reducing bacteria of the *Desulfosarcina/Desulfococcus* cluster, and ANME-3 with the *Desulfobulbus* genus (Lösekann et al., 2007). The AOM process provides high fluxes of sulphide, which nourishes several types of microbe-invertebrate symbioses such as bivalves from the Lucinidae, Thyasiridae, Solemyidae and Vesicomidae families, as well as annelid polychaetes of the family Siboglinidae (Goffredi et al., 2004; Duperron et al., 2007a; Bright and Giere, 2005). Mussels from cold seeps (family Mytilidae) host methanotrophic bacteria (Cavanaugh et al., 1987; Barry et al., 2002) or live in dual symbiosis with both methanotrophic and thiotrophic bacteria (Won et al., 2003; Duperron et al., 2005, 2007b). In most cold-seep environments, such chemosynthetic organisms dominate the community biomass and form specific habitats generally associated with high AOM rates.

Pockmarks are a special type of cold-seep characterized by negative seafloor features caused by the seepage of fluids through the seabed (Hovland and Judd, 1988). They generally occur in unconsolidated fine-grained sediments as cone-shaped circular or elliptical depressions ranging from a few metres to 300 or more in diameter and from 1 to 80 m in depth. The giant 800-m-diameter pockmark REGAB was discovered along the Gabon continental margin at a water depth of 3200 m during the Zaiango cruise by geophysical surveys with the research vessel Suroit (April 2000, Ifremer). REGAB is characterized by high methane emissions and by the presence of methane hydrates in subsurface and surface sediments (Charlou et al., 2004). First dives on REGAB using the remotely operated vehicle (ROV) Victor 6000 (cruises Zaiango and

Biozaire I-2001) showed the occurrence of dense communities of typical seep-associated invertebrates, some of which represent chemosynthetic symbioses (Ondréas et al., 2005; Olu-Le Roy et al., 2007a). Among these were Mytilidae (*Bathymodiolus* aff. *boomerang*, Olu-Le Roy et al., 2007b), Vesicomidae bivalves (von Cosel and Olu, 2009), and Siboglinidae polychaetes (*Vestimentifera*, *Escarpia southwardae* n. sp., Andersen et al., 2005). A few mats of giant sulphide-oxidizing bacteria have also been observed in the pockmark. Three main faunal assemblages were observed (Fig. 1): Mytilidae and Siboglinidae occur in the centre area of the pockmark associated with carbonate crusts, and Vesicomidae mostly in the periphery on soft sediments. The bacterial mats patches were observed close to Vesicomidae. Olu-Le Roy et al. (2007a) found that methane concentrations in the bottom water were the main factor explaining the distribution and high spatial variability of the faunal assemblages. Methane measurements in these habitats suggested that the *Bathymodiolus* species are exposed to highest methane concentrations while Vesicomidae and Siboglinidae occur at the periphery of methane-emitting patches, experiencing lower methane concentrations. The occurrence of *Bathymodiolus* mussels in very large and dense aggregates in the most methane-rich areas is probably linked to their dual symbiosis with methane and sulphide-oxidizing Gammaproteobacteria (Duperron et al., 2005). Vesicomidae and Siboglinidae were assumed to harbour only sulphide oxidizers (Olu-Le Roy et al., 2007a).

In this study, we present a molecular survey of microbial communities associated with different types of habitats in the REGAB giant pockmark. The two main goals were to assess

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