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Influence of seep emission on the non-symbiont-bearing fauna and vagrant species at an active giant pockmark in the Gulf of Guinea (Congo–Angola margin)

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ABSTRACT

Detailed surveying with an ROV found that a dense and diverse cold-seep community colonises a giant pockmark located at 3200 m depth, 8 km north from the deep Congo channel. Several types of assemblages, either dominated by Mytilidae and Vesicomyidae bivalves or Siboglinidae polychaetes, are distributed on the 800-m diameter active area. The site is characterised by a most active central zone in a depression with abundant carbonate concretions and high methane fluxes where high-density clusters of mussels and siboglinids dominate. In contrast, the peripheral zones display large fields of dead and live vesicomyids on soft sediment, with a lower mean density and lower methane concentration in seawater. The associated megafauna includes Alvinocarididae shrimps, echinoids, holothurians of the family Synaptidae, several species of gastropods, two species of galatheids, and Zoarcidae and Ophidiidae fishes. Multivariate analyses of video transect data show that the distribution of these major megafauna species at the pockmark scale is influenced by the habitat heterogeneity due to fluid or gas emission, occurrence of hydrates, substratum variability and by the presence of large symbiont-bearing species. Several assemblages dominated either by mytilids, vesicomyids, or siboglinids have been sampled for megafauna densities and biomass estimations and stable isotope measurements ($\delta^{13}C$ and $\delta^{15}N$) of dominant species and food sources. The highest estimates of megafauna densities have been obtained in mytilid beds. According to their stable isotopes values, non-symbiont-bearing species mainly rely on chemosynthesis-originated carbon, either as primary consumers of chemoautotrophic microorganisms, or at higher trophic level recycling organic matter, or relying on bivalve and tubeworm production. Most of them likely feed on different sources like shrimps, but differences according to habitat have been evidenced. Carbon and nitrogen isotope ratios of galatheids and benthic or benthopelagic fishes captured by trawls at increasing distances from the pockmark provide evidence of the high variability in the proportion of chemosynthesis-originated carbon in their diet, from 15% to 38%, according to the species captured as far as 4 km to the site.

1. Introduction

In deep chemosynthetic environments driven by fluids enriched in methane and sulphide, i.e. hydrothermal vents and cold seeps, extreme habitat heterogeneity and variability suggest that communities are mainly structured by abiotic forces (e.g. Barry et al., 1997; Bergquist et al., 2005; Henry et al., 1992; Levin et al., 2003; MacDonald et al., 2003; Olu et al., 1997; Sahling et al., 2002; Sarrazin et al., 1999; Van Dover, 1995). Nevertheless, the high biomass which characterizes these environments suggests that biotic interactions should also be important community structuring factors at seeps like at vents (Levesque et al., 2003; Micheli et al., 2002; Sarrazin and Juniper, 1999; Tunnicliffe, 1991).

Megafauna, or large-size epifauna at cold seeps, which are associated with biomass-dominant symbiont-bearing species, include high diversity of taxa and almost all the marine phyla (Levin, 2005; Sibuet and Olu, 1998). Diverse communities are probably favoured by substratum heterogeneity that includes both soft bottoms and carbonate concretions, and as well as environmental conditions that are moderate compared to

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hydrothermal vents. Symbiont-bearing megafauna is also considered as a source of habitat heterogeneity, because it generates extensive habitat complexity (Levin, 2005). Megafaunal community structure and diversity are highly variable among seep sites, and is thought to be influenced by factors such as depth, substratum, pelagic or terrestrial inputs (Levin et al., 2000; Levin and Michener, 2002; Sahling et al., 2003; Sibuet and Olu-Le Roy, 2002; Sibuet and Olu, 1998), patch size or age of symbiont-bearing species (Cordes et al., 2005; MacAvoy et al., 2005).

Dense chemosynthetic communities were discovered on a large part of a 800-m diameter pockmark discovered along the Congo–Angola margin a few kilometres from the Congo deep channel (Olu-Le Roy et al., 2007a; Ondréas et al., 2005). These first studies described assemblages visually dominated by symbiont-bearing taxa, Vesicomyidae and Mytilidae bivalves and Siboglinidae polychaetes whose distributions seemed to be controlled by methane fluxes and substratum variability. This giant pockmark is, in fact, a complex (a pockmark 'cluster') of several individual pockmarks of about 100 m in diameter whose variable activities may contribute to the spatial heterogeneity observed on the seafloor (Ondréas et al. 2005). The distribution of other megafaunal species is probably controlled by habitat heterogeneity occurring at the pockmark scale, which is created both by fluid emission-related patterns and by the symbiont-bearing species, serving as 'ecosystem engineers' according to Levin (2005).

Following Carney (1994), associated fauna may be classified as endemic, colonist and vagrant, depending on their abundance at seeps compared to background areas. Stable isotopes, which were first used to demonstrate chemosynthesis processes in seep community, and were mainly applied to symbiont-bearing species (Kennicutt II et al., 1992; Paull et al., 1984, 1985; Rau and Hedges, 1979), can be used to estimate trophic dependence of these 'associate' or 'heterotrophic' species on chemosynthetic production (Levin et al., 2000; Levin and Michener, 2002; MacAvoy et al., 2002). Carbon- and nitrogen-stable isotopes have also been used to decipher nutritional associations among fauna at vents (Colaço et al., 2002; Fisher et al., 1994; Levesque et al., 2006; Polz et al., 1998; Van Dover, 2002; Van Dover and Fry, 1989; Vereshchaka et al., 2000) and, more recently, at seeps (MacAvoy et al., 2005; Van Dover et al., 2003). The fauna closely associated with tubeworm aggregations at cold seeps in the Gulf of Mexico obtains the bulk of its nutrition from local sources of primary production (MacAvoy et al. 2005), but the relative importance of chemosynthetic pathways have been suggested to vary regionally with depth and among microhabitats defined by dominant symbiont-bearing species (Levin and Michener, 2002).

The objective of the present study is to assess the influence of seep emissions on the non-symbiont-bearing megafauna at a giant pockmark recently discovered, and therefore the dependence of these species on the seep energy, by analysing the following: (i) species distribution relative to the distribution of active seeps at the pockmark scale, (ii) densities and biomass at more or less active local seeps and (iii) isotopic signature of their tissues relative to chemoautotrophic or external sources of carbon and nitrogen. Export of local chemosynthetic biomass by large mobile predators captured in the background of the deep seep site is also estimated from stable isotope measurements.

2. Materials and methods

2.1. Video survey and image analysis for megafauna distribution

The giant pockmark named 'REGAB' (Ondréas et al., 2005) was explored by the ROV Victor 6000 in 2001 during the Ifremer-TOTAL collaborative programmes ZAIANGO and BIOZAIRE (Sibuet and Vangriesheim, 2009). This active cold-seep site is located at 3170 m depth on the Gabon continental margin close to the deep Congo channel (5°47,50′S; 9°42′40″E) (Fig. 1). In this paper we will use the term 'pockmark' for the whole pockmark area, not to describe individual pockmarks. Regularly spaced video transects were first performed on the whole structure (Fig. 2). Different types of faunal assemblages forming clusters were subsequently defined and mapped (Olu-le Roy et al., 2007a; Fig. 2) within the pockmark; they were defined as 'chemosynthetic assemblages' and either dominated by large bushes of the siboglinid polychaete *Escarpia southwardae* Andersen et al., 2004, or by two species of vesicomyid bivalves undistinguishable on images but identified from samples as *Laubiericoncha chuni* Thiele and Jaeckel, 1931; see Cosel and Olu (2008) and *Caplytogena regab* Cosel and Olu (2009), or by the Mytilidae *Bathymodiolus* sp. aff. *boomerang* (Olu-Le Roy et al., 2007b). The results of a second phase of video analysis, subsequent to the symbiont-bearing species cluster mapping, are presented in this paper. Video surveys of seven dives were

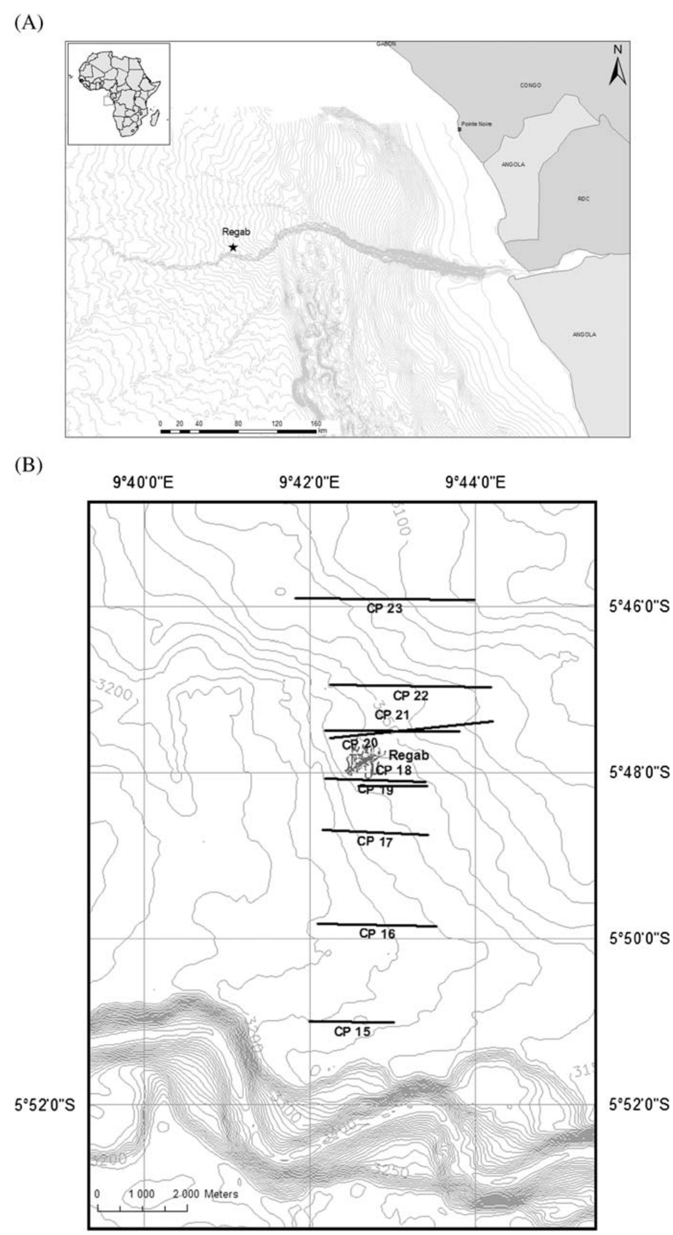

Fig. 1. Location of the REGAB pockmark along the Congo–Angola margin and of the benthic trawls.