Deep-Sea Research II 137 (2017) 26–41

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Regular article

Methane seepage effects on biodiversity and biological traits of macrofauna inhabiting authigenic carbonates

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ARTICLE INFO

Available online 3 June 2016

Keywords:
Biodiversity
Biological trait analysis
Carbonate
Deep sea
Macrofauna
Methane seep
Oxygen
Hydrate Ridge

ABSTRACT

Authigenic carbonate rocks at methane seeps are recognized as hosting diverse and abundant invertebrate assemblages, with potential forcing from fluid seepage and hydrography. Mensurative studies of carbonate macrofauna (> 0.3 mm) at Hydrate Ridge, OR revealed little effect of water depth and overlying oxygenation (at 600 m and 800 m) but a large influence of seepage activity on density, taxonomic composition, diversity, and biological traits (feeding, lifestyle, motility, size and calcification). Rocks exposed to active seepage had 3–4 × higher total macrofaunal densities than under inactive conditions. Assemblages exhibited higher species richness and reduced evenness (greater dominance) under active seepage than inactive conditions, but no difference in H' or rarefaction diversity. Actively seeping sites were characterized by errant (motile), bacterial grazing, small- and medium-sized, heavily calcified species, whereas inactive sites exhibited a greater diversity of feeding modes and more burrowers, sessile, large and lightly calcified species. Active rocks supported more exogonid (Syllidae), ampharetid, and cirratulid polychaetes, provannid snails, pyropeltid limpets, nemerteans, and sponges; whereas inactive rocks supported higher densities of ophiuroids, isopods, gammarid amphipods, hydroids, *Typosyllis* (Syllidae) and tanaids. Transplant experiments, in which rocks were transferred between active and inactive sites at Hydrate Ridge North (600 m), revealed that assemblages respond within 13 months to increase or cessation of seepage, taking on the feeding, size and calcification characteristics of the background fauna at the new site. Lifestyles and motility patterns shifted more slowly as the sessile, attached species did not track seepage as quickly. Provannid snails and pyropeltid limpets rapidly colonized rocks transplanted to active sites and disappeared when transplanted to inactive sites. Given the known variability of fluid fluxes and rapid community response, a mosaic of communities changing in space and time is hypothesized to generate the relatively high species diversity at methane seeps.

1. Introduction

The ocean's continental margins hold vast repositories of buried methane which escapes upward to the seafloor, fueling methane seep ecosystems reliant on chemosynthetic microbial activity (Levin, 2005). Where this occurs sulfate-coupled anaerobic methane oxidation (AOM) is catalyzed by syntrophic methanotrophic archaea (ANME) and sulfur-metabolizing deltaproteobacteria (SRB) (Boetius et al., 2000). This process can significantly shape the seep landscape, through the authigenic precipitation of carbonate rock. Carbonate features include extensive pavements, mounds, slabs, boulders and nodules (Aloisi et al., 2002) that persist for extended periods at sites with active and past seepage (e.g., Peckmann and Thiel, 2004; Birgel et al., 2008; Birgel and Peckmann, 2008; Scott Shapiro, 2004). Massive AOM-based carbonate formations are well described in the eastern Pacific Ocean from the margins of Alaska (Gieskes et al., 2005), Oregon (Bohrmann et al. 1998), California (Stakes et al., 1999), Costa Rica (Han et al., 2004) and Chile (Sellanes et al., 2004). Carbonates form extensive habitat in the Black Sea (Reitner et al., 2005; Bahr et al., 2009), the eastern Mediterranean Sea (Heijs et al., 2006), off W. Africa (Menot et al., 2010), and at most W. Atlantic seeps Van Dover (2003).

Seep carbonates have recently been shown to serve as a unique habitat and an important methane sink, by hosting active methane-oxidizing ANME-SRB microbial consortia (Marlow et al., 2014a, 2014b). Molecular analyses of the microbial diversity associated with carbonates from active seepage areas at Hydrate Ridge OR reveal archaeal and bacterial 16S rRNA phylotypes that are broadly

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http://dx.doi.org/10.1016/j.dsr2.2016.05.021
0967-0645/

similar to the assemblages recovered from seep sediments (Marlow et al., 2014a). However, there is a distinction in community structure in carbonates from active seepage areas compared to those from quiescent, off-seep locations (Marlow et al., 2014a). The discovery of viable methane-oxidizing ANME-SRB consortia within the interior of seep carbonates (Marlow et al., 2014b), introduces questions about the use of carbonates as a habitat and food source by metazoans.

It is only recently that the eukaryote macrofaunal communities associated with seep carbonates have been described (Gaudron et al., 2010; Ritt et al., 2011; Grupe et al., 2015; Levin et al., 2015). Common faunal associations with carbonates include loosely associated mobile megafauna, attached epifauna, and endolithofauna (those that live in burrows, crevices and mineral lattices within the rock). The rocks may provide substrate for settlement and attachment, reproductive sites, refuge from predators and, in many cases, a food supply. Limited study of carbonate-hosted macrofauna in the Mediterranean (Ritt et al., 2010; Gaudron et al., 2010) and Atlantic (Cunha et al., 2013a) suggests that faunal densities may be low and heterogeneity high compared to seep sediments. Grupe et al. (2015) and Levin et al. (2015) document abundant macrofauna on carbonates from the Del Mar Seep, CA and Costa Rica seeps, respectively. However faunal communities on carbonates appear more likely to resemble seep sediments when the carbonate rocks occur in a sedimented habitat (e.g., clam bed or bacterial mat) than when associated with biotic mussel beds or tubeworm bushes (Levin et al., 2015).

The community structure and ecological roles of carbonate biota within seep ecosystems and their links to AOM are just starting to be addressed. For example, a dorvilleid polychaete species dwelling within carbonates has $\delta^{13}C = -92‰$ and derives most of its carbon from AOM consortia (Thurber et al., 2012). Intensive trophic resource partitioning of chemoautotrophic microbes occurs among multiple species of dorvilled polychaetes in NE Pacific seep sediments (Levin et al., 2013), and among other heterotrophic meiofauna and macrofauna at hydrothermal vents (Levesque et al. 2003; Govenar et al., 2015).

Beyond stable isotope analyses, additional approaches are needed to gain insight into the functional attributes of seep biota. Biological trait analysis (BTA), a method for incorporating information about species' biological characteristics to summarize assemblage composition (Bremner et al., 2006), has been employed to inform about ecosystem function in freshwater and shallow marine benthic communities (e.g., Usseglio-Polatera et al., 2000; Schratzberger et al., 2007; Marchini et al., 2008; Paganelli et al., 2012; Menezes et al., 2010; Van der Linden et al., 2012). To date there has been little application of BTA to the deep sea or to hard-substrate ecosystems. Although macrofaunal communities on authigenic carbonates at methane seeps are now being described taxonomically, information about biological trait structure, with respect to lifestyle, mobility, size, feeding mode and calcification, may provide additional insight into the function of these ecosystems.

At the class and order level the carbonate fauna resembles rocky shore communities (Levin et al., 2015; Grupe et al., 2015) with dominance by grazing gastropods, although microbes rather than algae form the base of the food chain. In shallow marine settings gastropods are notorious for being keystone consumers – i.e. they control the biomass and diversity of algae and often other biota through their intense grazing activity (Dayton, 1971; Lubchenco, 1978; Branch and Moreno, 1994). Gastropods can be extraordinarily abundant on hard substrates at both hydrothermal vents and methane seeps; with multiple genera co-occurring (Warén and Bouchet 1989, 2009; Waren et al., 2006; Génio et al., 2013). The high density and rapid colonization ability of some gastropod taxa at vents (Kelly and Metaxas, 2008) and seeps (Gaudron et al. 2010; Cunha et al., 2013a; Grupe, 2014) suggest potential for gastropod grazing activities to control microbial cover and possibly composition in chemosynthetic ecosystems. Additional common consumers that appear to process significant amounts of methane-derived C at methane seeps include ampharetid polychaetes, which consume aerobic methane-oxidizing bacteria (Thurber et al., 2014), dorvilleid polychaetes which consume the AOM consortia (Thurber et al., 2012), and lepetopsid limpets which can graze carbonate directly (Levin et al., 2015).

Climate change is leading to a range of ocean responses that may impact environmental conditions at methane seeps on continental margins (Levin and Le Bris, 2015). These changing ocean conditions will also have consequences for the structure of communities on authigenic carbonates. Warming of bathyal waters or shifts in warm currents may dissociate gas hydrates, leading to more widespread seepage and/or higher fluxes on continental margins (Phrampus and Hornbach, 2012). Warmer waters also hold less oxygen, raise metabolically driven oxygen consumption, may lead to intensified upwelling of low-oxygen waters (Bakun, 2015; Bakun et al., 2015), and exhibit increased stratification thereby reducing ventilation – all contributing to ocean deoxygenation (Keeling et al., 2010). Because of these effects and intensification of a poleward-moving undercurrent, oxygen levels on the NE Pacific margin and in the California Current system have been declining over the past 25–50 yrs (Bograd et al., 2015). Thus, understanding how methane seep communities respond to variation in methane seepage and oxygenation of overlying waters could help predict the impacts of climate-induced environmental change.

2. Objectives and questions

The primary objective of this study was to identify the influence of methane seepage and location on the structure of macrofaunal assemblages inhabiting authigenic carbonates. We asked: (1) Do macrofaunal abundance, composition, diversity and biological traits vary as a function of (a) high and low seepage activity and (b) location, where the shallower location (HR North – 587–618 m) is associated with higher overlying $[O_2]$ (0.34–0.52 ml/l) and the deeper location (HR South – 775–800 m) is associated with lower $[O_2]$ (0.24 ml/l). To understand the role of methane seepage and depth location (oxygenation) we sampled carbonates from three active and three inactive seepage sites each at HR North at the boundary of the oxygen minimum zone (OMZ) and at HR South within the center of the OMZ. The functional (biological) attributes of the macrofauna were characterized with respect to feeding guild, mobility, lifestyle, body size and calcification and were analyzed as a function of seepage activity and location. The dynamic effects of seepage onset and cessation were studied by transplanting carbonates between active and inactive sites at HR North and recovering rocks after 13 months to examine community structure.

3. Methods

3.1. Field sites and characteristics

Investigations were carried out on the northern and southern mounds of Hydrate Ridge (HR) located on the Cascadia margin off Oregon, USA. We refer to these sites as HR North (44°40′N, 125°6′W) and HR South (44°34′N, 125°9′W) (Fig. 1). HR South sampling was done at and near the base of a carbonate edifice called the pinnacle at depths of 775–800 m. HR North sampling was carried out on mixed substrate of carbonate slabs and shallow sediments at depths of 587–618 m (Table 1). The region has been extremely well studied with respect to geophysics, hydrology and geochemistry (Tryon et al., 1999, 2002), carbonate formation (Greinert et al., 2001; Teichert et al., 2005), seep microbiology