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Macrofaunal communities associated with chemosynthetic habitats from the U.S. Atlantic margin: A comparison among depth and habitat types

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ABSTRACT

Hydrocarbon seeps support distinct benthic communities capable of tolerating extreme environmental conditions and utilizing reduced chemical compounds for nutrition. In recent years, several locations of methane seepage have been mapped along the U.S. Atlantic continental slope. In 2012 and 2013, two newly discovered seeps were investigated in this region: a shallow site near Baltimore Canyon (BCS, 366–412 m) and a deep site near Norfolk Canyon (NCS, 1467–1602 m), with both sites containing extensive chemosynthetic mussel bed and microbial mat habitats. Sediment push cores, suction samples, and Ekman box cores were collected to quantify the abundance, diversity, and community structure of benthic macrofauna (>300 µm) in mussel beds, mats, and slope habitats at both sites. Community data from the deep site were also assessed in relation to the associated sediment environment (organic carbon and nitrogen, stable carbon and nitrogen isotopes, grain size, and depth). Infaunal assemblages and densities differed both between depths and among habitat types. Macrofaunal densities in microbial mats were four times greater than those present in mussel beds and slope sediments and were dominated by the annelid families Dorvilleidae, Capitellidae, and Tubificidae, while mussel habitats had higher proportions of crustaceans. Diversity was lower in BCS microbial mat habitats, but higher in mussel and slope sediments compared to NCS habitats. Multivariate statistical analysis revealed specific sediment properties as important for distinguishing the macrofaunal communities, including larger grain sizes present within NCS microbial mat habitats and depleted stable carbon isotopes ($\delta^{13}C$) in sediments present at mussel beds. These results suggest that habitat differences in the quality and source of organic matter are driving the observed patterns in the infaunal assemblages, including high β diversity and high variability in the macrofaunal community composition. This study is the first investigation of seep infauna along the U.S. Atlantic slope north of the Blake Ridge Diapir and provides a baseline for future regional comparisons to other seep habitats along the Atlantic margin.

1. Introduction

Cold seeps occur worldwide, often where methane or sulfide is forced upward through the sediment by pressure gradients (Levin, 2005). Anaerobic oxidation of methane and sulfate reduction results in the formation of carbonates and often high concentrations of hydrogen sulfide in sediments, which is toxic to most fauna (Vetter et al., 1991). The flow of seep products through sediments often results in recognizable biogenic habitats, including mussel and clam beds, microbial mats, and tube worm aggregations (Bernardino et al., 2012), where the dominant megafauna are dependent on chemoautotrophic endosymbiotic bacteria for nutrition (Kochevar et al., 1992). In addition, the physical structure created by chemosynthetic organisms provides heterogeneous habitat for diverse communities (Bergquist et al., 2003; Van Dover and Trask, 2000); thus these organisms serve as ecosystem engineers (e.g., Jones et al., 1996).

Sediment fauna associated with seep communities, including microbial mats and clam beds, have been studied in many locations worldwide (Cordes et al., 2010b; Levin, 2005; Sibuet and Olu, 1998); however, sediments associated with mussel habitats have only been examined at a few locations, including the Blake Ridge Diapir (Robinson et al., 2004) and the Gulf of Guinea (Menot et al., 2010). Densities of macrofauna in seep sediments are often higher

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than in background non-seep sediments, particularly at increasing water depth (Levin, 2005) where food is often a limited resource and seep-derived carbon provides an additional food source (Levin and Michener, 2002). Globally, however, density differences among seep habitat types has been variable (Bernardino et al., 2012), with microbial mat, clam beds, or mussel beds exhibiting similar (Levin et al., 2010) or differing densities in comparison to each another (Levin et al., 2015; Menot et al., 2010; Robinson et al., 2004; Sahling et al., 2002). At the Blake Ridge Diapir, macrofaunal densities in sediments near mussels were higher than in microbial mat sediments, although macrofaunal densities were low for all sampled habitats (0–6400 ind. m^{-2}; Robinson et al., 2004). High densities found in microbial mat habitats have been attributed to the exploitation of the chemosynthetically derived food source by seep tolerant taxa, and has been compared to similar faunal responses from disturbance and sediment organic enrichment events (Bernardino et al., 2012; Sahling et al., 2002).

Macrofaunal diversity patterns among seep and non-seep habitats have also been variable. Microbial mat habitats often exhibit low diversity and high dominance of a few tolerant taxa compared to other seep and non-seep habitats due to high sediment sulfide concentrations (Levin et al., 2003; Sahling et al., 2002). However, low sulfide concentrations in clam beds on the California slope led to increased macrofaunal diversities by supporting populations of both ambient and sulfophilic taxa (Levin et al., 2003). In other locations, macrofaunal diversity in sediments associated with clam beds has been similar (Hydrate Ridge, Sahling et al., 2002) or lower (Gulf of Guinea, Menot et al., 2010) than non-seep habitats. Differences in the diversity of mussel-bed sediment macrofauna have also been mixed, and possibly related to site-specific factors. Higher diversities were found in mussel-associated sediments compared to microbial mats and non-seep sediments at Blake Ridge (Robinson et al., 2004); in contrast, diversity was lower in sediments adjacent to mussels than non-seeps in the Gulf of Guinea (Menot et al., 2010). High β diversity has also been reported for seep habitats, supported by the habitat heterogeneity of foundation species and the varying geochemical environments (Cunha et al., 2013; Cordes et al., 2010b).

Infaunal community assemblages associated with different seep habitats are distinct from one another (Bernardino et al., 2012; Levin, 2005; Menot et al., 2010) and differ from background non-seep sediments. Dorvilleid polychaetes are common in seep habitats (Levin, 2005) and are particularly abundant in microbial mat habitats, which is attributed to their broad environmental tolerance to sulfide concentrations and opportunistic lifestyle (Levin et al., 2013, 2006, 2003; Robinson et al., 2004; Sahling et al., 2002). Other characteristic seep macrofauna include the polychaete families Siboglinidae, Capitellidae, and Ampharetidae, oligochaetes, and thyasirid bivalves (Bernardino et al., 2012; Dando et al., 1991; Levin et al., 2000, 2003), some of which can benefit from reducing habitats (Levin et al., 2000). At Blake Ridge, mussel sediment communities were more similar to non-seep communities (60% similar) than to microbial mat communities (11–54%), suggesting that mussels help maintain low concentrations of methane and sulfide in sediments, facilitating communities more similar to non-seep sediments (Robinson et al., 2004). In addition, the specific mussel species present in the sediments has been found to influence the associated faunal community assemblage (Cordes et al., 2010a). Mussels in the *Bathymodiolus childressi*-complex contain only methanotrophic symbionts, while those of the *Bathymodiolus boomerang*-complex, including *Bathymodiolus heckerae* present at Blake Ridge, contain both methanotrophs and thiotrophs (Olu-Le Roy et al., 2007b). The effect of mussel species composition on epifaunal communities has been suggested to act as a proxy for habitat chemistry (Cordes et al., 2010a), since the resources (i.e., methane or sulfide) required by the endosymbionts of the different mussel types are likely indicative of the chemical environment surrounding the mussels. The extent of endemic infauna in seep habitats globally is still unresolved (Bernardino et al., 2012), but may be a function of depth (Cordes et al., 2010a; Levin, 2005; Sahling et al., 2003), with many species occupying seep sediments comprised of the regionally available taxon pool (e.g., Levin, 2005).

Depth-related patterns have been observed among seep sites worldwide, with communities at upper bathyal depths (200–1500 m) distinct from those at deeper depths (> 1500 m; Bernardino et al., 2012). However, there are few comparisons of seeps with depths ranging > 1000 m within a geographic region (Cunha et al., 2013; Rodrigues et al., 2013; Cordes et al., 2010a; Sahling et al., 2003), where other factors structuring deep-sea communities (e.g., food availability, bottom water oxygen concentrations) are more directly comparable. In the Gulf of Cadiz, shallow (353–732 m) mud volcanoes exhibited higher diversity, lower heterogeneity, and different community assemblages from deep (1318–3860 m) mud volcanoes (Cunha et al., 2013). Cordes et al. (2010a) observed distinct depth-related patterns in both mussel and tube worm communities in the Gulf of Mexico (1005–2746 m), with mussel beds exhibiting a mid-slope (~1000 m) diversity maximum, consistent with similar trends for soft-sediment communities. However, the relationship between depth and the sediment communities found within microbial mats and along the fringe of mussel beds within a particular region is unknown.

The distinct epifaunal and infaunal assemblages present in seep habitats are a function of their proximal sediment geochemical environment (Levin et al., 2003; Sibuet and Olu, 1998), including seepage rates, sulfide concentrations, and biological activity (Cordes et al., 2010a; Olu et al., 2009; Levin, 2005; Sahling et al., 2002). Microbial mats often form in habitats with high methane flux rates, with corresponding high sulfide concentrations and low oxygen penetration into the sediment (Sahling et al., 2002). In contrast, habitats that support clam beds exhibit lower but variable methane flow through sediments, lower sulfide concentrations, and higher oxygen penetration through bioturbation (Levin et al., 2003). Comparable data from mussel beds is limited; however, while these habitats can have similar oxygen penetration profiles, their associated sediment organic carbon concentrations and methane concentrations in the overlying water (Menot et al., 2010; Olu-Le Roy et al., 2007a) are often higher than clam beds. Due to variations in seep activity and fluid flux, the sediment geochemical properties (e.g., organic carbon and nitrogen, stable carbon and nitrogen isotopes, grain size) often differ between seep and non-seep habitats (Levin et al., 2000, 2010; Menot et al., 2010; Valentine et al., 2005). Microbial mats have been documented to contain higher percent carbon content, high carbon to nitrogen (C:N) ratios, and lower percent nitrogen content than clam beds and non-seep sediments (Levin et al., 2010). Clam and mussel beds also contain higher organic carbon content than non-seep sediments at multiple depths (Levin et al., 2000, 2010; Menot et al., 2010; Valentine et al., 2005).

Stable carbon isotopic ($\delta^{13}C$) composition of sediments and fauna from seep habitats often reflects the primary nutritional sources available in the environment, where phytoplankton-derived organic matter typically produce $\delta^{13}C$ values ranging from −25‰ to −15‰ (Fry and Sherr, 1984), very low $\delta^{13}C$ values derived from biogenic methane (≤ −50‰; Van Dover, 2007; Whiticar, 1999), and carbon derived from sulfide oxidation with $\delta^{13}C$ ranging from −37‰ to −27‰ (Brooks et al., 1987; Fisher, 1990; Robinson and Cavanaugh, 1995). In the Gulf of Mexico, sediments near seeps containing bacterial filaments were depleted in both ^{13}C and ^{15}N compared to those with no bacterial filaments present (Demopoulos et al., 2010). Stable isotope values of seep sediments can vary with seep activity, where higher methane fluxes near mytilid beds were associated with lower $\delta^{13}C$ and $\delta^{15}N$ as compared to clam beds, and the sediments may contain different microorganism

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