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Biodiversity and community composition of sediment macrofauna associated with deep-sea *Lophelia pertusa* habitats in the Gulf of Mexico

Amanda W.J. Demopoulos [a,*], Jill R. Bourque [b], Janessy Frometa [b]

[a] U.S. Geological Survey, Southeast Ecological Science Center, 7920 NW 71st St, Gainesville, FL, USA
[b] Cherokee Nation Technology Solutions, Contracted to the U.S. Geological Survey, Southeast Ecological Science Center, 7920 NW 71st St, Gainesville, FL, USA

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ABSTRACT

Scleractinian corals create three-dimensional reefs that provide sheltered refuges, facilitate sediment accumulation, and enhance colonization of encrusting fauna. While heterogeneous coral habitats can harbor high levels of biodiversity, their effect on the community composition within nearby sediments remains unclear, particularly in the deep sea. Sediment macrofauna from deep-sea coral habitats (*Lophelia pertusa*) and non-coral, background sediments were examined at three sites in the northern Gulf of Mexico (VK826, VK906, MC751, 350–500 m depth) to determine whether macrofaunal abundance, diversity, and community composition near corals differed from background soft-sediments. Macrofaunal densities ranged from 26 to 125 individuals 32 cm^{-2} and were significantly greater near coral versus background sediments only at VK826. Of the 86 benthic invertebrate taxa identified, 16 were exclusive to near-coral habitats, while 14 were found only in background sediments. Diversity (Fisher's α) and evenness were significantly higher within near-coral sediments only at MC751 while taxon richness was similar among all habitats. Community composition was significantly different both between near-coral and background sediments and among the three primary sites. Polychaetes numerically dominated all samples, accounting for up to 70% of the total individuals near coral, whereas peracarid crustaceans were proportionally more abundant in background sediments (18%) than in those near coral (10%). The reef effect differed among sites, with community patterns potentially influenced by the size of reef habitat. Taxon turnover occurred with distance from the reef, suggesting that reef extent may represent an important factor in structuring sediment communities near *L. pertusa*. Polychaete communities in both habitats differed from other Gulf of Mexico (GOM) soft sediments based on data from previous studies, and we hypothesize that local environmental conditions found near *L. pertusa* may influence the macrofaunal community structure beyond the edges of the reef. This study represents the first assessment of *L. pertusa*-associated sediment communities in the GOM and provides baseline data that can help define the role of transition zones, from deep reefs to soft sediments, in shaping macrofaunal community structure and maintaining biodiversity; this information can help guide future conservation and management activities.

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1. Introduction

Coral reefs create heterogeneous, three-dimensional structures providing niches for a variety of species, enhancing local diversity (Wenner et al., 1983; Gratwicke and Speight, 2005), and influencing the structure and function of benthic communities found in adjacent soft sediments (Posey et al., 1992; Posey and Ambrose, 1994; Barros et al., 2001; Langlois et al., 2005, 2006). Reefs modify sediment characteristics by altering flow environments, facilitating localized sediment deposition and enhancing available organic material, all of which can affect adjacent benthos (Jumars and Nowell, 1984; Lenihan, 1999). Effects of reef proximity, often termed reef halos (e.g., Posey et al., 1992; Langlois et al., 2005), can include increased benthic diversity and abundance associated with enhanced organic input from reefs (Barros et al., 2001; Danovaro et al., 2002), or decreased abundance of sediment fauna associated with increased foraging by predators utilizing the reef habitat as a refuge (Posey et al., 1992; Posey and Ambrose, 1994; Langlois et al., 2005), although both effects are often considered localized and highly variable at distances less than 10 m from the

* Corresponding author. Tel.: +1 352 264 3490; fax: +1 352 378 4956.
E-mail address: ademopoulos@usgs.gov (A.W.J. Demopoulos).

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reef (Posey et al., 1992; Barros et al., 2001; Danovaro et al., 2002). Habitat fragmentation and varying patch sizes can also influence sediment community structure by altering the proportion of critical edge and transitional habitat (Harwell et al., 2011). In addition, increased three-dimensional habitat complexity has been linked to increased abundance and diversity of fauna found within a reef (Auster et al., 2005; Gratwicke and Speight, 2005; Wilson et al., 2007), which may have a corresponding effect on adjacent benthos. Despite the potential importance of adjacent sediment habitats in maintaining reef biodiversity and ecosystem functioning, the overall spatial extent of the influence of an individual reef on the surrounding substrate is still poorly understood.

In cold-water environments, the globally distributed azooxanthellate scleractinian coral *Lophelia pertusa* is the most common reef-building species, occurring in water temperatures ranging from 4 to 12 °C and at depths ranging from 200 to 1000 m (Freiwald et al., 2004; Thiem et al., 2006). *Lophelia pertusa* reefs occur on topographic high points (Frederiksen et al., 1992; Rogers, 1999) where accelerated currents influence larval transport and enhance organic matter supply (Thiem et al., 2006; van Oevelen et al., 2009) facilitating coral settlement onto hard substrates. Growth of *L. pertusa* is estimated at 1–25 mm per year (Roberts, 2002), with some reefs calculated to be >1000 years old (Rogers, 1999; Costello et al., 2005). Given their slow growth rates and vulnerability to human disturbances such as fishing, trawling (Fosså et al., 2002; Hall-Spencer et al., 2002), and oil excavating activities (Gass and Roberts, 2006), characterizing the relationship between *L. pertusa* and its associated fauna is needed to quantify the diversity associated with reef habitats and understand deep-sea coral ecosystem function (Mortensen and Fosså, 2006) prior to disturbance.

Lophelia pertusa reefs enhance local biodiversity by facilitating the colonization of sessile fauna onto coral skeletons, providing structural refuges within created microhabitats, increasing spawning habitat and nursery grounds, and enhancing available organic material (i.e., food) within the structure through enhanced sediment accumulation (e.g., Jensen and Frederiksen, 1992; Mortensen et al., 1995; Fosså et al., 2002; Raes and Vanreusel, 2005; Reed et al., 2006; Dorschel et al., 2007; Henry and Roberts, 2007; Sulak et al., 2007, 2008; Buhl-Mortensen et al., 2010). High fish and invertebrate diversity and abundance are associated with *L. pertusa* habitats in the eastern North Atlantic and Gulf of Mexico (Jensen and Frederiksen, 1992; Rogers, 1999; Costello et al., 2005; Mortensen and Fosså, 2006; Henry and Roberts, 2007; Sulak et al., 2007; Bongiorni et al., 2010). In particular, invertebrate diversity was estimated to be up to three times higher than the surrounding seabed (Henry and Roberts, 2007) and comparable to tropical coral reefs (Rogers, 1999). Beta diversity of meiofauna and macrofauna (species turnover) varied across coral habitat type, including live and dead coral, and coral rubble (Roberts et al., 2009; Bongiorni et al., 2010; Henry et al., 2010), with the highest alpha diversity found in areas dominated by mixed live and dead coral skeletons (megafauna and macrofauna, Mortensen and Fosså, 2006), dead coral skeletons (Jensen and Frederiksen, 1992) or live coral and coral rubble (meiofauna, Bongiorni et al., 2010). In contrast, low diversity and high density were associated with *L. pertusa* rubble at the base of coral mounds (macrofauna, Mortensen et al., 1995; Mortensen and Fosså, 2006) and significant declines in faunal abundance with distance were observed at Norwegian *L. pertusa* reef habitats (Jonsson et al., 2004). Much like shallow-water reefs, deep-sea coral reef size may also influence the structure of associated fauna (Jonsson et al., 2004), with larger patches supporting increased abundances of omnivores and mobile organisms but decreased abundance of deposit feeders.

In the northern Gulf of Mexico (nGOM), *L. pertusa* is found on authigenic carbonate deposits precipitated from microbial activity associated with hydrocarbon seepage (Schroeder, 2002; Formolo et al., 2004; Roberts et al., 2010a). In contrast to the NE Atlantic communities, where *L. pertusa* often forms large banks (e.g., Sula Ridge, >14 km in length and >30 m high) and mounds (e.g., Porcupine Seabight, 1 km in diameter and up to 100 m high) (Roberts et al., 2003), *L. pertusa* in the nGOM forms both large banks and mounds (up to 600 m in length; Cordes et al., 2008; Lunden et al., 2013) and less dense and scattered colonies (~1 to 2 m long and 1 to 2 m high; Brooke and Schroeder, 2007; Lunden et al., 2013) referred to as macrohabitats (Roberts et al., 2009). *Lophelia pertusa* habitats in the well-studied Viosca Knoll (VK) area of the nGOM have similar temperature, salinity, and current speed regimes, but have lower dissolved oxygen content (Davies et al., 2010) and higher particle loads (Mienis et al., 2012) compared to NE Atlantic habitats. Current direction generally oscillates between eastward and westward flow along isobaths, with current speeds averaging 8 cm s^{-1} (Mienis et al., 2012).

Ecological studies of *L. pertusa* habitats in the nGOM have focused on large macrofaunal (>2 mm) invertebrates and fish communities occupying and utilizing the coral matrix (Sulak et al., 2007; Cordes et al., 2008; Sulak et al., 2008; Lessard-Pilon et al., 2010), whereas no studies have assessed the infaunal communities associated with *L. pertusa* adjacent sediments. Using video analysis, Sulak et al. (2007) recorded diverse fish populations associated with *L. pertusa* habitats at two VK sites, but noted a decrease in density associated with depth. Diversity of megafaunal invertebrates based on rarefaction was significantly lower within live *L. pertusa* compared to soft-sediments, and significant differences in the communities were observed between two sites at VK (Sulak et al., 2008). Lessard-Pilon et al. (2010) characterized megafaunal associations using photomosaics collected from *L. pertusa* habitats, and found communities were more similar within a site (approximately 600 m^2) than among sites separated by 37 km, and identified smaller-scale site differences at distances greater than 316 m. *Lophelia pertusa* habitat (e.g., live, dead, rubble) had higher diversity than other nearby habitats (e.g., bacterial mats, tubeworms, sponges, other corals), and the percentage of standing dead coral was a significant determinant for the community composition at VK. Lessard-Pilon et al. (2010) hypothesized that the association of higher-order consumers with dead coral and rubble suggests the effect of the reef itself extends to the communities in the soft-sediments and rubble surrounding the coral beds. In situ collections of *L. pertusa* communities yielded 68 taxa (>2 mm) living within fifteen discrete *L. pertusa* habitats, including taxa found regionally within the nGOM slope habitats (Cordes et al., 2008). Coral-associated fauna were significantly different from nearby seep communities, although certain taxa were shared between habitats (Cordes et al., 2008). However, neither Cordes et al. (2008) nor Lessard-Pilon et al. (2010) conducted direct comparisons to the adjacent soft-sediment environment, which is almost ubiquitous in the nGOM.

This paper presents new data examining macrofaunal community structure within sediments directly adjacent (within 1 m) to deep-sea coral habitats. The primary objective of this study was to compare soft-sediment benthos adjacent to *L. pertusa* reefs to other soft-sediment habitats in the nGOM. We address the hypothesis that the habitat heterogeneity provided by biogenic structures in the deep sea influences the abundance, diversity, and composition of benthic communities in adjacent soft-sediments. We tested two null hypotheses: (1) macrofaunal abundance, taxa diversity, dominance, and feeding group assemblages in near-coral (*L. pertusa*) sediments are not significantly different from background, non-coral soft-sediments and (2) macrofaunal polychaete family composition near corals is not significantly different from background sediments or from other soft-sediment habitats within the Gulf of Mexico region. Alternatively, because *L. pertusa*