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Importance of seep primary production to *Lophelia pertusa* and associated fauna in the Gulf of Mexico

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ABSTRACT

To investigate the importance of seep primary production to the nutrition of *Lophelia pertusa* and associated communities and examine local trophic interactions, we analyzed stable carbon, nitrogen, and sulfur compositions in seven quantitative *L. pertusa* community collections. A significant seep signature was only detected in one of the 35 species tested (*Provanna sculpta*, a common seep gastropod) despite the presence of seep fauna at the three sample sites. A potential predator of *L. pertusa* was identified (*Coralliophila* sp.), and a variety of other trophic interactions among the fauna occupying the coral framework were suggested by the data, including the galatheid crab *Munidopsis* sp. 2 feeding upon hydroids and the polychaete *Eunice* sp. feeding upon the sabellid polychaete *Euratella* sp. Stable carbon abundances were also determined for different sections of *L. pertusa* skeleton representing different stages in the growth and life of the aggregation. There was no temporal trend detected in the skeleton isotope values, suggesting that *L. pertusa* settles in these areas only after seepage has largely subsided. Isotope values of individual taxa that were collected from both *L. pertusa* and vestimentiferan habitats showed decreasing reliance upon seep primary production with average age of the vestimentiferan aggregation, and finally, no seep signature was detected in the coral collections. Together our data suggest that it is the presence of authigenic carbonate substrata, a product of past seep microbial activity, as well as hydrodynamic processes that drive *L. pertusa* occurrence at seep sites in the Gulf of Mexico, not nutritional dependence upon primary production by seep microbes.

1. Introduction

Lophelia pertusa, the most well-known species of cold-water reef-forming coral, has a cosmopolitan distribution. It is found in all the world's oceans except in the polar regions (Cairns, 1994; Zibrowius, 1980). *L. pertusa* reefs enrich local biodiversity (Fosså and Mortensen, 1998; Rogers, 1999) and have long been recognized as prime fishing locations for commercially important deep-water species (Fosså et al., 2002).

L. pertusa was first described by Linnaeus in 1758, but the factors determining the coral's distribution have only been well-studied since the late 1970s (e.g. Rogers, 1999; Wilson, 1979b). Although *L. pertusa* is found worldwide, its distribution is patchy even within a localized region. Understanding the factors that determine *L. pertusa* distribution and its relationship with other species will be instrumental in focusing future conservation efforts for these fragile and important deep-sea ecosystems that are, in some places, already threatened by deep-water fisheries (Fosså et al., 2002) and energy company activities.

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The basic factors that have been proposed to control the distribution patterns of *L. pertusa* include (i) a hard substrate on which to settle and grow, (ii) oceanic water between 4 and 12 °C (Dons, 1944; Teichert, 1958; Frederiksen et al., 1992; Freiwald, 1998), (iii) sufficient current to deliver food and prevent sedimentation without excessive shear force, and (iv) possible reliance upon local production associated with seepage of light hydrocarbons (Hovland and Thomsen, 1997) or other seep products including porewater charged with CO, Ca, or other chemical species derived from oxidation of hydrocarbons (Hovland, 2008). The first two factors have been well-documented, whereas the latter two have not.

Previous studies have documented an increase in density of soft cold water corals (Genin et al., 1986) and *L. pertusa* (Masson et al., 2003) on top of or at the edges of seamounts where current is accelerated relative to the surrounding seafloor. Presumably, an elevated flow rate would increase the encounter rate of the polyps with food particles. Frederiksen et al. (1992) observed that *L. pertusa* occurrence is correlated with a critical slope and proposed that breaking internal waves increase the food supply to the corals by encouraging bottom mixing and concentrating nutrients.

Hovland and Thomsen (1997) proposed a relationship between the occurrence of *L. pertusa* and the seepage of light hydrocarbons from the seabed. *L. pertusa* has been reported in association with hydrocarbon seeps in Norwegian fjords (Hovland and Risk, 2003; Hovland and Thomsen, 1997), on the inside rims of pockmarks at the Kristen hydrocarbon field (Hovland, 2005, 2008), near 70°N on the Norwegian Margin (Lindberg et al., 2007), in the Gulf of Cádiz (eastern central Atlantic) (León et al., 2007), and in the Gulf of Mexico (Schroeder, 2002). More recently, Hovland and Mortensen (1999) proposed a "hydraulic theory" that incorporates both local current flow and hydrocarbon seepage to explain the occurrence and persistence of the Norwegian deep coral reefs. This theory suggests that the turbulent fluid flow over uneven bottom topography acts to concentrate nutrients, but the critical factor that allows for the long-term establishment of a coral reef is the sub-seafloor migration of hydrocarbons. According to this theory, the migrating hydrocarbons fuel carbon fixation by chemosynthetic microbes, which form the basis of portions of the *L. pertusa* community food web.

Circumstantial evidence for the hydraulic theory has accumulated over the past decade. Enhanced seismic reflectors (Hovland and Risk, 2003), adjacent pockmarks (Hovland and Risk, 2003; Lindberg et al., 2007; Sumida et al., 2004), coral rubble (*L. pertusa*, *Madrepora oculata*, *Desmophyllum* sp.) and isolated live corals in areas of active mud volcanoes (León et al., 2007; Sumida et al., 2004), corals colonizing hydrocarbon-derived authigenic carbonates (León et al., 2007; Schroeder, 2002), elevated levels of light hydrocarbons in sediment adjacent to coral, and locally elevated seawater methane and sulfide in sediments at the base of the reef (Hovland and Risk, 2003) are all indications that seeping fluids are present near the corals. A few studies have questioned the nutritional reliance of *L. pertusa* communities upon seep primary production (Duineveld et al., 2004; Kiriakoulakis et al., 2005; Masson et al., 2003) and found no evidence for this linkage.

In this study, we used stable isotopes of carbon, nitrogen, and sulfur to determine whether seep primary production is an important nutritional source for *L. pertusa* and fauna directly associated with the coral. If methanotrophy is a significant source of carbon for *L. pertusa* communities, the tissue of the fauna should have values depleted in ^{13}C reflecting that of the methane in the environment (approx. −55‰ to −40‰ at seeps on the Upper Louisiana Slope (Brooks et al., 1987; Roberts and Aharon, 1994) to −83.7‰ to −80‰ on the Florida Escarpment (Paull et al., 1985)). Determining whether chemoautotrophy is an important nutritional source, however, can be ambiguous using carbon stable isotopes alone. Dissolved carbon dioxide in seawater has a δ^{13}C composition close to 0‰ and carbon fixation by chemoautotrophic microbes via sulfide oxidation can produce organic carbon depleted by up to −25‰ (Ruby et al., 1987). In the Gulf of Mexico, even vestimentiferans and clams, which are known to rely upon their sulfur-oxidizing chemoautotrophic bacterial symbionts for nutrition, have δ^{13}C ranges of −43‰ to −18‰ and −39.8‰ to −30.9‰, respectively (Brooks et al., 1987; Kennicutt et al., 1992). There is a particularly large range of δ^{13}C values in vestimentiferans, which obtain all of their nutrition from their bacterial endosymbionts. At the more negative end of this range, the δ^{13}C values can be explained by seeping hydrocarbons creating an isotopically light dissolved inorganic carbon pool via chemical equilibrium processes or uptake of light porewater dissolved inorganic carbon by vestimentiferans across their plumes and through their roots (Aharon et al., 1992; Freytag et al., 2001). The more positive δ^{13}C value can be explained by lower levels of discrimination as is typical of hydrothermal vent vestimentiferans (Childress and Fisher, 1992). The story is further complicated for heterotrophic fauna which can feed on a mixture of sources, including methanotrophic (δ^{13}C; −40‰) and chemoautotrophic (ca. −27‰; Sassen et al., 1993) free-living bacteria and photosynthetic primary production by surface phytoplankton (−22‰ to −15‰; Gearing et al., 1984). Sulfur isotopes, however, produce a distinctly depleted δ^{34}S signature in animals that rely upon sulfur-oxidizing chemoautotrophic bacteria. Whereas seawater sulfate is the ultimate sulfur source for most marine organisms, the primary sulfur source for chemoautotrophs is pore water sulfide produced by microbial sulfate reduction and methane oxidation. The tissue δ^{34}S values reported for vestimentiferans in the Gulf of Mexico range from −37‰ to −24‰ (MacAvoy et al., 2002, 2005), which is highly depleted in ^{34}S when compared with Gulf of Mexico bottom water sulfate, which averages 20.3‰ (Aharon and Fu, 2003). Thus, if chemoautotrophy is a significant source of nutrition for coral associated animals, we would expect to see notably depleted tissue δ^{34}S values. Although this study focuses mainly on *L. pertusa* communities from the Upper Louisiana Slope (310–634 m), we also analyzed tissue and skeleton from hard and soft corals from deeper sites in the Gulf between 960 and 1400 m to assess whether there is an increased reliance upon seep primary production at depth,