



Temporal fluctuations in the trophic role of large benthic sulfur bacteria in mangrove sediment



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ABSTRACT

Filamentous sulfur bacteria of the genus *Beggiatoa* form large mats covering the sediment in the shallow waters of a Guadeloupean mangrove (French West Indies). The abundance of these bacteria varies over the year and their trophic role may, therefore, also vary. We investigated this variation by conducting a survey examining the stable isotopic compositions of four grazers and four food sources during nine sampling sessions in three different periods of the year. We analyzed bulk isotopic compositions for each component except for the bacterial and diatom communities, for which we carried out a compound-specific ¹³C analysis of phospholipid-derived fatty acids (PLFAs). Correlations between isotopic compositions revealed a predominance of diatoms in the diet of nematodes and the important role of detritus and bacteria in the diet of the polychaete *Ceratocephale* sp. None of the grazers had an isotopic composition correlated with that of *Beggiatoa* suggesting that sulfur bacteria were not a predominant part of the diet of any grazer. *Beggiatoa* has a large central vacuole, resulting in a very low carbon content-to-volume ratio, potentially accounting for its low level of attractiveness to grazers. Mangrove sediments are habitats rich in organic carbon, in which, the addition of a food source, such as *Beggiatoa*, would have a limited effect on the structure of the food web over the course of the year.

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1. Introduction

Bacteria are an important resource in pelagic food webs (Sherr et al., 1987). Despite bacterial abundance 1000 times higher in sediment than in the water column, the trophic role of bacteria has been little studied in benthic systems due to methodological difficulties (Kemp, 1990). Benthic bacteria are generally thought to make a limited contribution to the diet of grazers, satisfying less than 10% of the total carbon demand of the meiofauna from estuarine (van Oevelen et al., 2006a; van Oevelen et al., 2006b) and deep-sea environments (Gontikaki et al., 2011). By contrast, benthic microalgae constitute a major food source for many coastal meiofaunal species (Middelburg et al., 2000; Montagna et al., 1989; Riera et al., 1996). Previous grazing experiments with dual-labeled food items (bacteria and diatoms) have shown that meiofaunal grazers, which are smaller and have a higher selection efficiency than the macrofauna, preferentially ingest benthic microalgae (Pascal et al., 2008; Pascal et al., 2013).

These organisms may preferentially ingest algae rather than bacteria for a number of reasons. The benthic microalgae have a high nutritional value (Kathiresan and Bingham, 2001) and contain essential components,

such as fatty acids, lacking from bacteria (Zhukova and Kharlamenko, 1999). Differences in the spatial distributions of these two types of food source may also have an effect. Benthic algae are usually concentrated in biofilms, whereas benthic bacteria are more evenly distributed over a vertical gradient within the sediment (Joint, 1978; Nugteren et al., 2009) and are attached to sediment particles. The ingestion of algae, rather than bacteria, thus entails energy savings in the search for food and through prevention of the ingestion of indigestible material. This hypothesis could be tested by determining whether the consumption of bacteria by benthic organisms is greater when the bacteria are concentrated in mats.

Beggiatoa are multicellular, filamentous white bacteria and are among the largest prokaryotic organisms (Larkin et al., 1994). Members of this genus are found within and just above highly reduced, organic or hydrocarbon-rich sediments (Jørgensen, 1977). Those chemolithotrophic microorganisms are located at the oxic/anoxic interface, where they oxidize sulfides to generate elemental sulfur (that can be intracellularly stored), which they then oxidize further to generate sulfate (Jørgensen, 1977). They are widespread in fresh and marine waters, from coastal to abyssal depths, and from tropical to polar latitudes. They are found in diverse environments such as mud volcanoes, hydrothermal vents (Jannasch et al., 1989), hydrocarbon and methane cold seeps (Montagna and Spies, 1985; Powell et al., 1986) and below productive upwelling

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areas (Schulz and Jørgensen, 2001). These bacteria form mats that may be up to 3 cm thick and have a patchy distribution (Lloyd et al., 2010).

Abysal communities are dependent principally on photosynthetic material from the surface that is partially mineralized by the time it reaches the deep-sea floor. The limited nature of this energy resource generally results in a steady decrease in the abundance of the benthic fauna from the shelf to the abyss (Rex and Etter, 2010). Organic carbon generated by chemosynthesis constitutes islands of primary production in the otherwise monotonous and food-limited deep-sea environment. Carbon from chemoautotrophs is ingested in the deep sea and contributes to increase standing stocks of macro (Desmopoulos et al., 2010) and meiofauna (Pape et al., 2011; Van Gaeve et al., 2006). The flux of particles from surface waters typically decreases with increasing water depth, and the dependence of the fauna on material generated by chemosynthetic processes therefore increases with depth (Levin and Mendoza, 2007; Levin and Michener, 2002). However, chemosynthetic bacteria are also ingested by the meiofauna in shallower environments in hydrothermal vents (Kamenev et al., 1993), brine (Powell et al., 1986) and hydrocarbon seeps (Kamenev et al., 1993; Spies and DesMarais, 1983). In temperate shallow waters, observations reveal ingestion of filamentous sulfur bacteria by nematode (Bernard and Fenchel, 1995). A trophic role of these bacteria has also been demonstrated in a Caribbean mangrove, in which comparisons of the isotopic composition in natural conditions and after artificial enrichment revealed that sulfur bacteria were ingested by the meiofauna (Pascal et al., 2014).

Beggiatoa mats follow a succession of patterns (Bernard and Fenchel, 1995) over different time scales. In response to changes in O₂ and H₂S concentration gradients, they can move rapidly into the sediment by gliding motility (Dunker et al., 2010). In sediments containing photosynthetic microorganisms, *Beggiatoa* are known to perform diurnal migrations, being more abundant in the superficial sediment at night but moving down below the layer of sediment with photosynthetic activity in the light (Fenchel and Bernard, 1995; Garcia-Pichel et al., 1994; Nelson and Castenholz, 1982). The distribution of filamentous sulfur bacteria is also influenced by unusual weather, as turbulent water flow can sweep these bacteria away or increase the oxygenation of the overlying water inducing the downward migration of *Beggiatoa* deeper into the sediment (Elliott et al., 2006; Grant and Bathmann, 1987; Jørgensen, 1977). The species composition of mats of sulfur bacteria depends on the age of the mat (Bernard and Fenchel, 1995). Total *Beggiatoa* biomass may also vary considerably between seasons (Bernard and Fenchel, 1995; Jørgensen, 1977) and, over longer time scales, variations in the abundance of these bacteria are used to monitor the remediation of contamination due to organic waste from fish farming (Brooks et al., 2004; Hamoutene et al., 2015).

In a mangrove on the Caribbean island of Guadeloupe (French West Indies), a previous study based on a spatial approach revealed that despite the ingestion of sulfur bacteria, the presence of mats did not increase the general contribution of bacteria to the diet of the fauna present (Pascal et al., 2014). As the abundance of sulfur bacteria fluctuates during the course of the year, the conclusions drawn in this spatial study could not necessarily be extended to other periods. The diet of meiofaunal grazers is influenced by food availability (Giere, 2009; Moens and Vincx, 1997) and there are alternative dynamic states of microbial food webs with an inverse correlation between the ingestion of algae and bacteria by grazers (Epstein, 1997; Montagna et al., 1995a). The trophic role of sulfur bacteria may therefore depend on the availability of other food sources.

The goal of this study was to determine the contribution of sulfur bacteria to the meiofaunal diet during a survey in a mangrove on Guadeloupe. This survey was set up so as to cover a large range of environmental conditions. We evaluated the abundances and natural isotopic compositions of potential food sources, including *Beggiatoa* mats and consumers. It was not possible to pick up individually bacterial and diatom communities. We therefore evaluated their $\delta^{13}\text{C}$ through their phospholipid-derived fatty acids (PLFAs) (Boschker and Middelburg,

2002). Due to the small size of the meiofauna and the low N content of these organisms, $\delta^{15}\text{N}$ was not always measurable. We therefore focused principally on $\delta^{13}\text{C}$ measurements. We evaluated trophic links by evaluating correlations between changes in the $\delta^{13}\text{C}$ content of food sources and consumers.

2. Material and method

2.1. Study area

“Manche à eau” is a small tropical lagoon connected to the marine channel “Rivière Salée” separating the two main islands of Guadeloupe (French West Indies) (Fig. 1). In this lagoon, tides are semidiurnal with mean tidal amplitude of 30 cm (Tide gauge of Pointe-à-Pitre, REFMAR®). Temperature and salinity at 0.5 m depth were relatively constant, with average values of 28 °C and 35, respectively.

The lagoon is bordered by a mangrove forest dominated by *Rhizophora mangle*. The sediment (<1 m water depth) between mangrove trees roots is characterized by high sulfide concentrations up to 750 μM (Maurin, 2009). In some places, the sediment is covered by patches of large (20–60 μm diameter) filamentous white sulfur bacteria visible with unaided eyes. *Beggiatoa* bacteria belong to, at least, two genus: *Maribeggiatoa* and *Isobeggiatoa* (Jean et al., 2015). Along the year, the size of those bacterial patches is highly variable covering often several square meters. High numbers of interstitial organisms such as ciliates, nematodes and turbellarians are associated with the mats (Pascal et al., 2014).

2.2. Period of sampling

The sampling strategy was set up to explore highest variations in environmental conditions along the year evaluating small time scale changes during three distinct seasons. Total of 9 sampling sessions were performed with one-week interval during cyclonic season (7, 14 and 20 of September 2011), wet season (28 of November and 5 and 12 of December 2011) and dry season (10, 17 and 24 of March 2012). During each sampling session, samples were collected by snorkeling in three fixed locations spaced of 10 m from each other with a water depth of ~0.5 m (Fig. 1). In each location, 20 tubes (inside diameter = 55 mm) were randomly placed in 2 m² and gently pushed in sediment to avoid sediment suspension. Syringes were used to collect i) 10 samples of the thin layer of surficial mate until white filaments were no longer visible for *Beggiatoa* analyses and ii) 10 samples of the surficial sediment (1 cm) for all other analyses. Two types of sediment samples collected were independently mixed and the suspended sediment samples were split several times with Motoda splitter in order to reach concentration adapted for analyses of abundance of *Beggiatoa* and meiofauna. Motoda splitter is commonly used in plankton ecology to equally fractionate water samples (Motoda, 1959). This sub-sampling step was taken into account in order to report abundances per unit surface area.

2.3. Abundance and isotopic composition

In *Beggiatoa* samples, the imaging software ImageJ (Abràmoff et al., 2004) was used to measure surface covered by *Beggiatoa* after dilution with Motoda splitting box ($n = 30$ per sample) and average diameter of *Beggiatoa* filament ($n = 30$ per sample). Surface and diameter measurements were both used to evaluate *Beggiatoa* biovolume by assuming simple geometric shape of cylinder of bacterial filament. *Beggiatoa* suspension of a known biovolume was filtered on 0.2 μm pre-weighted filters. Filters were weighted again after drying at 60 °C for 24 h in order to determine the ratio between biovolume and dry weight of *Beggiatoa*. Dry weight were converted to carbon content based on elemental-analyzer isotope ratio mass spectrometer data. Dilution steps were taken into account in order to express results in carbon weight per surface unit.

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