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

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TEMPORAL FLUCTUATIONS IN THE TROPHIC ROLE OF LARGE BENTHIC SULFUR BACTERIA IN MANGROVE SEDIMENT

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Running Head: Fluctuations in trophic role of sulfur bacteria

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 conducing 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 ^{13}C analysis of phospholipid-derived fatty acids (PLFA). 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.

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 meiofauna 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 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).

Abyssal 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 Gaever 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 O_2 and H_2S 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 swept 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 times 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 were evaluated. It was not possible to pick up individually bacterial and diatom communities. We therefore evaluated their $\delta^{13}C$ through their phospholipid-derived fatty acids (PLFA) (Boschker and Middelburg, 2002). Due to the small size of the meiofauna and the low N content of these organisms, $\delta^{15}N$ was not always measurable. We therefore focused principally on $\delta^{13}C$ measurements. We evaluated trophic links by evaluating correlations between changes in the $\delta^{13}C$ content of food sources and consumers.

Material and method

Study area

"Manche à eau" is a small tropical lagoon connected to the marine channel "Rivière Salée" separating the two mains island 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. *Beggiatoacea* 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).

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 m^2 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 (1cm) 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.

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 evaluated *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 hours 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.

Sediment was freeze-dried and phospholipid-derived fatty acids (PLFA) were extracted and their isotopic composition was determined using a gas-chromatograph combustion-interface isotope-ratio mass spectrometer (GC-c-IRMS) following protocol in Boschker *et al.* (1999). Concentrations and $\delta^{13}C$ PLFA specific to all bacteria (i14:0, i15:0, ai15:0, i16:0, C18:1ω7c and cy19:0) and diatoms (C20:4ω6, C20:5ω3, C22:5ω3 and C22:6ω3) were used to estimate the relative contribution of these groups to the total PLFA pool and their weighted-average $\delta^{13}C$ composition. The carbon content of all bacteria and diatoms was evaluated using carbon PLFA/carbon biomass ratios of 0.056 and 0.035, respectively (Boschker and Middelburg, 2002). The C/N ratio and isotopic composition of bulk sediment containing bacteria and diatom communities was determined for each sample from untreated sub-sample for ^{15}N content and from acid (1 M HCl)-treated sub-samples for ^{13}C content. Using mass-balance equations, isotopic compositions and abundances of bacteria and diatom communities evaluated with PLFA were used to calculate isotopic composition of detritus free of bacteria and diatoms.

For fauna abundance evaluations, samples were fixed with formalin 2% and stained with rose Bengal whereas samples for stable isotope analysis were untreated. Rotifers, nematodes and polychaetes were extracted from sediment using Ludox HS40 (de Jonge and Bouwman, 1977). Rotifers and polychaetes were previously identified using morphological traits as *Rotaria* spp. and *Ceratocephale* sp. (Pascal et al., 2014). For each stable isotope sample, 1500 *Rotaria* spp. and 100 *Ceratocephale* sp. were pooled whereas 600 specimens from the nematode community were randomly collected and gathered. Sediment sampled from bacterial mats was allowed to settle few minutes in the lab until until *Macrostomum* sp. migrated above the *Beggiatoa* biofilm created and for each sample 100 specimens were individually picked alive.

Isotope samples were analyzed at the Isotope Facility at the University of California, Davis, using an elemental-analyzer isotope ratio mass spectrometer. Samples were reported relative to the standards atmospheric N_2 and Vienna PeeDee Belemnite carbon. Stable isotope values are reported in δ notation (in ‰):

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 10^3$$

where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. Using standards, analytical precision was estimated to 0.2‰ for both ^{13}C and ^{15}N.

Data analyses

One-way analysis of variance (ANOVA) was used to test for differences in *Beggiatoa* abundances. Normality of residuals was tested using Shapiro-Wilk tests before performing ANOVA. When overall ANOVA tests were significant, Tuckey test were used for post hoc comparisons. To analyse the variability of food items that potentially influence grazers, principal component analysis (PCA) was performed using the R package FactoMineR (Lê et

al., 2008) on abundances of *Beggiatoa,* all bacteria and diatom, C:N of sediment and $\delta^{13}C$ of *Beggiatoa*, all bacteria, diatoms and sediment (n =27).

Spearman rank (r_s) correlations were performed to investigate the relationships between abundances and isotopic compositions of preys and grazers.

Results

Prey

During the survey, filaments of *Beggiatoa* presented an average width of 45.3 ± 5.0 µm (n = 390) and a carbon content of 24.4 ± 9.4% (n = 27). Filtration of *Beggiatoa* solution revealed a carbon content per volume of 2.6 fg C μm^{-3}. Along the year, evaluation of *Beggiatoa* biomass through picture analyses revealed an average biomass of 118.2 ± 19.9 mg C m^{-2} (n = 27). Biomass was similar between sampling locations or sampling seasons (ANOVA, not significant) whereas they were significantly different between weeks (ANOVA, $p<0.01$). *Beggiatoa* biomass was considerably lower than the average biomass of all bacteria and diatoms, as evaluated through PLFA analyses, reaching respectively 11.5 ± 6.4 g C m^{-2} and 5.4 ± 4.1 g C m^{-2}, respectively (n = 27) (Tab. 1). Biomass of *Beggiatoa* was not related to all bacteria and algal biomass as p-values of Spearman correlation analysis were not significant.

Among potential food items of mangrove sediment, *Beggiatoa* were always more depleted in ^{13}C (Fig. 2). Along the year, they presented a mean $\delta^{13}C$ of -28.9 ± 3.2‰ whereas all bacteria, diatoms and bulk detritus had a higher $\delta^{13}C$ with respectively: -25.4 ± 1.5‰, -25.8 ± 4.3‰ and -25.2 ± 0.5‰ (n = 27). *Beggiatoa* $\delta^{13}C$ was not significantly correlated with $\delta^{13}C$ of all bacteria, diatoms and detritus (Tab. 2). Also $\delta^{13}C$ of all bacteria and diatom were not linked (r_s = 0.558, n.s.), whereas $\delta^{13}C$ of detritus and all bacteria were slightly correlated (r_s = 0.405, $p<0.05$). Detritus presented lower variability in their ^{13}C composition than other

food source (Fig. 3). As PLFA analyses do not allow measurements of $\delta^{15}N$, *Beggioata* were the only prey analyzed and they present a mean $\delta^{15}N$ of 2.9 ± 1.8‰ (n = 27) (Fig. 4).

The PCA performed on characteristics of food items that potentially influence grazers (Fig. 4), showed that spatial and week variations appeared to be lower than seasonal variations. The F1 and the F2 axes together explained 62% of observed variability and data points clustered according to seasons (Fig. 5). The cyclonic period was characterized by high $\delta^{13}C$ of all food items (*Beggiatoa*, all bacteria, diatom and detritus) and wet season was characterized by high abundance of all bacteria and diatoms whereas dry season samples showed high C:N ratio and higher abundance of *Beggiatoa* (Fig. 5).

Grazers

Individual weights of grazers were derived from stable isotope samples (n = specimen per sample × replicates). The weight per specimen (means ± SD) was 115.7 ± 96.3 ng for rotifers (n = 1500 × 18), 449.3 ± 334.3 ng for nematodes (n = 600 × 27), 2.8 ± 2.1 µg per *Ceratocephale* sp (n = 100 × 27) and 10.6 ± 10.4 µg for *Macrostomum* sp. (n = 100 × 24).

Along the survey (n = 27), in the surficial centimeter of sediment, most abundant grazers were rotifers (269 ± 230 10^3 ind/m^2) followed by nematodes (242 ± 181 10^3 ind/m^2), polychaete (46 ± 34 10^3 ind/m^2) and copepods (11 ± 12 10^3 ind/m^2). Fluctuations of grazer biomass are presented in Table 1. Among grazers, polychaete represented the highest biomass (56 ± 42 10^3 mg C/m^2) followed by nematodes (51 ± 38 10^3 mg C/m^2), rotifers (13 ± 11 mg C/m^2) and copepods (4 ± 4 mg C/m^2).

None of the grazer biomass data were correlated with all bacteria and diatom biomass (Tab. 3). However, biomass of rotifers (r_s = -0.535, p<0.01) and polychaetes (r_s = -0.477, p<0.05) were negatively correlated with *Beggiatoa* biomass (Tab. 3).

Among grazers, rotifers presented the $\delta^{13}C$ value with the lowest variability ($\delta^{13}C$ = -24.6 ± 0.3‰, n = 16). ^{13}C compositions of other grazers presented higher standard deviation

253among samples: nematode ($\delta^{13}C$ = -24.5 ± 2.5‰, n = 27), *Macrostomum* sp. ($\delta^{13}C$ = -22.3 ±
2542.5‰, n = 23) and polychaete ($\delta^{13}C$ = -22.0 ± 2.4‰, n = 27) (Fig. 2). Measurement of $\delta^{15}N$
255was not possible for rotifer and *Macrostomum* sp. due to low sample amount. Mean $\delta^{15}N$ (n =
25627) was 6.6 ± 0.7‰ for nematode community and 5.1 ± 1.4‰ for polychaete (Fig. 4).

257 None of the grazers $\delta^{13}C$ data correlated with $\delta^{13}C$ of *Beggiatoa* (Tab. 2). The $\delta^{13}C$ of
258nematode community was strongly linked with $\delta^{13}C$ of diatoms (r_s = 0.666, p<0.001) (Tab. 2).
259$\delta^{13}C$ of polychaetes were strongly correlated with $\delta^{13}C$ of all bacteria (r_s = 0.643, p<0.001)
260and detritus (r_s = 0.645, p<0.001). $\delta^{15}N$ of *Beggiatoa* was not correlated either with $\delta^{15}N$ of
261*Ceratocephale* sp. (r_s = -0.239, n.s.) and nematode community (r_s = -0.022, n.s.). $\delta^{15}N$ of other
262grazers were not available due to low samples biomass.

263

Discussion

A) Methodological considerations

The abundance of *Beggiatoa* varies over different time scales (Bernard and Fenchel, 1995). Biomass displays seasonal variation (Bernard and Fenchel, 1995; Jørgensen, 1977) but can also change rapidly due to the migration behavior of this bacteria (Fenchel and Bernard, 1995; Garcia-Pichel et al., 1994; Nelson and Castenholz, 1982) and to unusual weather conditions (Elliott et al., 2006; Grant and Bathmann, 1987; Jørgensen, 1977). This survey suggests that the abundance of *Beggiatoa* varies more at the weekly than at the seasonal scale although multivariate analyses revealed a greater fluctuation of general environmental conditions over the seasonal time scale. Sampling strategy designed to explore variations at both the weekly and seasonal time scales should, therefore, cover a large range of environmental conditions.

We used several approaches simultaneously to investigate the trophic role of *Beggiatoa* mats in a Guadeloupean mangrove. Each of these approaches presents potential bias that should be borne in mind when interpreting the results obtained.

Trophic relationships between grazers and their prey were evaluated by assessing changes in the respective abundances of these organisms. Such surveys are easy to perform but can be difficult to interpret, because grazers may affect their prey through processes other than grazing: (*i*) many meiofauna organisms secrete mucus which has been shown to increase microbial growth (Moens et al., 2005; Riemann and Schrage, 1978) and (*ii*) bioturbation by the meiofauna increases the fluxes of oxygen and nutrient through the sediment (Alkemade et al., 1992; Bonaglia et al., 2014). Both these activities influence the production and diversity of microbial compartments, including *Beggiatoa* mats (Salvadó et al., 2004).

The role of *Beggiatoa* as a food item has also been evaluated through stable isotope. This method has been widely used over the last few decades, to provide information about

289food webs in estuaries and oceans (Boecklen et al., 2011; Layman et al., 2012). The stable
290isotope compositions of consumers differ from those of their food source in a predictable
291manner and can therefore be used to evaluate dietary composition (Fry, 2006). However,
292stable isotopes are more useful in studies of systems with food sources presenting different
293isotope values (Moncreiff and Sullivan, 2001). In the mangrove environment studied,
294*Beggiatoa* present a $\delta^{13}C$ lower than that of other food sources due to its chemoautotrophic
295growth (Güde et al., 1981). Enrichment experiments artificially enhance difference in isotopic
296compositions of food items and were previously used to confirm that stable isotopes are
297reliable for evaluation of the contribution of *Beggiatoa* to the diet of grazers from the studied
298mangrove (Pascal et al., 2014). We determined the isotopic composition of bacterial and
299diatom communities by measuring the $\delta^{13}C$ of specific phospholipid-derived fatty acids
300(PLFA) (Boschker and Middelburg, 2002). Strong trophic links between a prey and a grazer
301result in parallel fluctuations in their isotopic compositions. In this survey, we evaluated the
302correlation between the $\delta^{13}C$ of prey and grazers. A lack of covariation between $\delta^{13}C$ of the
303different food sources is required for this approach and was previously verified (Tab. 2).

304 During each sampling session, samples were collected from three different sites
305separated by 10 m. $\delta^{13}C$ of food sources and grazers appeared to be highly variable, with
306considerable differences between sites (Fig. 2). Nevertheless, this approach was found to be
307suitable for the evaluation of trophic links as it highlighted the role of particular food sources
308in the diet of consumers, revealing the importance of diatoms in the diet of nematodes, for
309example.

310 In this study, we used a combination of approaches to decrease the uncertainty
311associated with potential biases and to strengthen our conclusions. The time scales over which
312changes in meiofaunal abundance and isotopic composition occur are different, so the results

obtained may differ between approaches. However, both approaches yielded similar results in our study: *Beggiatoa* mats made only a minor contribution to the diet of grazers.

2) Diet of grazers

Rotifers were the most abundant members of the meiofauna in this survey. Rotifers are common members of the benthic and pelagic communities in fresh and brackish waters, whereas they are thought to be rare in marine environments (Fontaneto et al., 2006; Schmid-Araya, 1998). Nevertheless, rotifers can occasionally dominate the marine benthos in terms of both abundance (Sommer et al., 2007; Sommer et al., 2003) and biomass (Johansson, 1983). They have been found in sulfide-rich sediments containing *Beggiatoa* in coastal (Bernard and Fenchel, 1995; Fenchel and Riedl, 1970) and deep sea areas (Sommer et al., 2007; Sommer et al., 2003). Bdelloid rotifers have different modalities of food collection: suspension feeding, scraping or browsing (Melone et al., 1998). They can consume diverse type of prey (bacteria, algae and yeasts) and are able to ingest their prey in a selective manner (Mialet et al., 2013). The possible uptake of sulfur-oxidizing bacteria by rotifers has already been suggested (Fenchel and Riedl, 1970) and isotope enrichment experiments confirmed that *Beggiatoa* was ingested by rotifers in the mangrove studied *(Pascal et al., 2014)*. However, rotifers were unlikely to be very dependent on this food resource as they were also present in sediments adjacent to mats in the mangrove (Pascal et al., 2014) and in deep-sea habitats without *Beggiatoa* (Sommer et al., 2003). The weak links observed between *Beggiatoa* and rotifers in the present survey also suggest that these bacteria are not the principal component of the rotifer diet.

Macrostomum spp were shown to ingest sulfur-oxidizing bacteria in a ^{13}C labeling study (Pascal et al., 2014). *Macrostomum lignano* is a turbellarian species that is cultured with diatoms in experimental conditions (Ladurner et al., 2005). Our results suggest that, in natural

environments, *Macrostomum* spp. have a mixed diet not dominated by a single item such as diatoms or *Beggiatoa*.

The ingestion of sulfur-oxidizing bacteria by nematodes has been observed (Bernard and Fenchel, 1995) and detected on the basis of isotopic composition (Pascal et al., 2014; Spies and DesMarais, 1983; Van Gaever et al., 2006). Some deep-sea nematode species feed exclusively on *Beggiatoa* (Spies and DesMarais, 1983), whereas the nematodes in this study appeared to be less dependent on these bacteria as a food source. The correlation between $\delta^{13}C$ of diatoms and nematodes revealed a strong trophic role of algae. Benthic diatoms can develop in environments with high sulfide concentrations (Admiraal and Peletier, 1979; Round, 1979). Compared to adjacent sediments, *Beggiatoa* mats can host diatoms with similar (Montagna and Spies, 1985) and even higher abundances (Powell et al., 1986) as already reported for the mangrove studied (Pascal et al., 2014). Stable isotope composition studies have revealed that the microphytobenthos is the principal food source of the nematode community in temperate intertidal mudflats (Moens et al., 2002; Montagna et al., 1995b; Riera et al., 1996; Rzeznik-Orignac et al., 2008). However, the contribution of these algae may be smaller in other environments such as salt marshes (Riera et al., 1999), in which other where other food sources are available such as detritus from marine phanerogams (Couch, 1989) or allochtonous stranded macroalgae (Riera and Hubas, 2003). Mangrove and saltmarsh ecosystems have similar profiles of organic carbon sources in their surface sediments (Middelburg et al., 1997). In mangroves, microalgae are generally considered to have only a small input, due to light limitation and inhibition by tannins (Alongi, 1994). However, despite this minor contribution to the total productivity of the ecosystem, the microphytobenthos can represent a major source of carbon for the benthic macrofauna (Bouillon et al., 2004; Bouillon et al., 2002) and play a key role in supporting higher trophic levels (Robertson and Blaber,

3611992). The results presented here also suggest that the microalgae play an important role as 362the principal source of food for the nematode community.

363 *Ceratocephale* sp. belong to the Nereididae family and their isotopic compositions 364indicate that, among food source studied, bacterial community and detritus present higher 365importance in their diet. $\delta^{13}C$ of detritus and bacteria are linked, as the particulate organic 366carbon of detritus is the main source of carbon for bacteria (Boschker et al., 2005). The 367members of the Nereididae are remarkably diverse in their potential diets as the different 368species may be carnivorous, deposit feeder, selective or non-selective suspension feeder or 369microbial "gardener" based on the laying and the ingestion of mucus trap lines (Jumars et al., 3702015). Moreover, some species are omnivorous, displaying dietary plasticity (Grippo et al., 3712011; Scaps, 2002). Observations of the gut contents of *Ceratocephale* from the Middle 372Atlantic Bight suggested that the diet of this organisms consisted largely of detritus (Gaston, 3731987). Stable isotope labeling experiments in the Carolina margin identified *Ceratocephale* as 374one of the most active consumers of phytodetritus among polychaetes (Levin and Blair, 3751999). Our findings also suggest a strong role of detritus in the diet of *Ceratocephale*. During 376*in situ* experiments with dual-labeled preys, polychaetes appeared to ingest bacteria 377selectively whereas nematodes preferentially ingested microphytobenthos (Montagna, 1984). 378The results of the present survey revealed similar trends in the dietary compositions of each of 379the grazers analyzed in this tropical marine sulfide-rich environment.

380 3) Trophic role of *Beggiatoa*

381 The lack of correlation of abundance and isotopic composition between potential grazers 382and *Beggiatoa* suggests that none of the grazers has a diet dominated by these large sulfur-383oxidizing bacteria. Moreover, the trophic role of *Beggiatoa* does not seem to be influenced by 384the abundances of other trophic resources. Despite the potential biases inherent to these 385correlation approaches, they are appropriate because they clearly demonstrated the dominance

386of diatoms in the nematode diet and the important role of detritus and all bacteria in the diet of 387*Ceratocephale* sp. This limited trophic role of *Beggiatoa* is consistent with the findings of 388previous studies in this mangrove, which suggested that *Beggiatoa* are ingested but that the 389presence of this bacteria does not modify the overall contribution of all bacteria to the diet of 390grazers (Pascal et al., 2014).

391 In food-limited deep sea habitats, sulfur bacteria increase the food supply and are 392ingested in large numbers by grazers, leading to an increase in grazer abundance (Levin, 3932005). Sulfur bacteria may have a similar structuring role in the food webs of shallower 394environments in conditions in which food resources are limiting (Powell et al., 1986). The 395contribution of chemosynthetic carbon to the diet of grazers increases with increasing depth 396and decreasing levels of photosynthetic primary production (Levin, 2005; Levin and 397Michener, 2002). Mangrove sediments are rich in organic carbon sources, some of which are 398locally produced (mangrove leaves, diatoms and cyanobacteria), whereas others originate 399from adjacent systems (Kristensen et al., 2008; Victor et al., 2004). In the mangrove 400environment, the addition of a food source such as *Beggiatoa* is therefore likely to have a 401much smaller effect than that in environments with fewer food sources. This survey suggests 402that these bacteria played a limited role that remained constant throughout the year.

403 The limited trophic contribution of *Beggiatoa* may be due to its low organic matter 404content. *Beggiatoa* of the present study had a carbon content of only 2.6 fg C μm^{-3}, which is 405more than an order of magnitude lower than the lowest volume reported for bacteria 406(Fagerbakke et al., 1996) and bacteria with volumes below 0.05 μm^3 can even reach values of 407500 fg C μm^{-3} (Troussellier et al., 1997). As this ratio decreases with increasing bacterial cell 408size (Lee and Fuhrman, 1987; Simon and Azam, 1989) and as *Beggiatoa* are among the 409largest known prokaryotes (Schulz and Jørgensen, 2001), this bacteria would be expected to 410have a particularly low carbon content. Moreover, this ratio is directly related to the water

content of the bacteria (Fagerbakke et al., 1996). *Beggiatoa* has a large central vacuole and its confined cytoplasm accounts for less than 16% (Jannasch et al., 1989) or 2% of the total biovolume (Schulz and Jørgensen, 2001), depending on the study considered. This "hollowness" of *Beggiatoa* (Larkin and Henk, 1990) decreases its dry-matter content. Consistently, an analysis of PLFA content along a transect in the mangrove studied revealed that total bacterial abundance in the uppermost centimeter of sediment was not significantly higher in *Beggiatoa* mat sediments than in adjacent sediment without mats (Pascal et al., 2014). *Beggiatoa* thus accounted for a much smaller amount of dry matter than suggested by its volume (Bernard and Fenchel, 1995) and the biomass of *Beggiatoa* would therefore have been smaller than that of other bacteria and other food sources. This lower organic matter content may have reduced its nutritive value and attractiveness for grazers.

In the mangrove studied, a spatial approach revealed that the presence of mats of sulfur bacteria had no effect on the general structure of the benthic food web and the role of bacteria in the diet of grazers (Pascal et al., 2014). This survey revealed that this conclusion was valid throughout the year, as the trophic role of *Beggiatoa* was limited at all sampling times, regardless of the fluctuations in available food sources. Thus, in habitat in which food resources are not limiting, the spatial concentration of bacteria in mats does not make them more attractive than other food resources.

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Tables

Season	Cyclonic			Wet			Dry		
Week	1	2	3	1	2	3	1	2	3
Carbon / Nitrogen of sediment	10.1 ± 1.4	10.7 ± 0.9	13.1 ± 1.4	10.9 ± 0.8	10.4 ± 0.9	11.8 ± 0.8	13.3 ± 0.5	13.7 ± 1.0	14.0 ± 1.0
Beggiatoa mat biomass (mg C m^{-2})	79.5 ± 4.6	102.1 ± 14.8	139.6 ± 25.4	136.5 ± 14.6	107.4 ± 23.9	116.0 ± 4.4	127.1 ± 23.7	116.7 ± 23.1	138.9 ± 4.7
Total bacterial biomass (g C m^{-2})	7.0 ± 2.8	8.3 ± 3.2	8.1 ± 2.5	18.9 ± 7.2	16.8 ± 4.0	15.7 ± 3.2	10.9 ± 4.2	11.4 ± 9.2	4.0 ± 3.8
Diatom biomass (g C m^{-2})	1.7 ± 0.4	3.6 ± 1.1	3.9 ± 0.7	8.0 ± 1.7	12.3 ± 4.9	9.1 ± 1.2	3.3 ± 3.2	1.5 ± 1.1	3.4 ± 0.5
Rotifer community biomass (mg C m^{-2})	19.2 ± 4.1	31.9 ± 0.6	6.7 ± 2.5	11.3 ± 8.9	9.8 ± 2.5	27.6 ± 6.1	0.6 ± 0.4	4.0 ± 1.4	5.2 ± 1.8
Nematode community biomass (mg C m^{-2})	42 ± 17	35 ± 5	26 ± 13	22 ± 7	54 ± 12	56 ± 26	27 ± 9	63 ± 26	134 ± 50
Ceratocephale sp. biomass (mg C m^{-2})	81 ± 32	131 ± 14	101 ± 32	37 ± 14	36 ± 17	57 ± 20	16 ± 10	31 ± 19	17 ± 4
Copepod community biomass (mg C m^{-2})	3.9 ± 1.1	4.6 ± 1.6	10.2 ± 8.2	3.0 ± 0.4	1.2 ± 0.3	6.1 ± 1.4	0.7 ± 0.4	1.6 ± 1.0	0.6 ± 0.3

Table 1. C/N ratio of sediment and abundances of prey and grazers in surficial centimetre of sediment through the year (means ± SD, n = 3)

3

	Beggiatoa ^{13}C	Bacterial ^{13}C	Diatom ^{13}C	Detritus ^{13}C
All bacteria ^{13}C	0.135			
Diatom ^{13}C	0.002	0.244		
Detritus ^{13}C	-0.056	0.405*	-0.061	
Rotifer community ^{13}C	0.278	0.421	0.492	0.216
Nematode community ^{13}C	-0.056	0.292	0.663***	0.027
Ceratocephale sp. ^{13}C	0.355	0.643***	0.094	0.645***
Macrostomum ^{13}C	0.283	0.513*	0.533*	0.259

4Table 2. Correlation coefficients (r_s, Spearman rank) of isotopic compositions of food

5sources and grazers (n = 27 ; * p<0.05, ** p<0.01, *** p<0.001)

6

	Beggiatoa biomass g C m^{-2}	Total bacterial biomass g C m^{-2}	Diatom biomass g C m^{-2}
Rotifer community g C m^{-2}	-0.535**	0.121	0.389
Nematode community g C m^{-2}	0.109	-0.276	-0.036
Ceratocephale sp. g C m^{-2}	-0.477*	0.068	0.156
Copepod community g C m^{-2}	0.149	0.226	0.301

7Table 3. Correlation coefficients (r_s, Spearman rank) on abundances of food sources

8and grazers (n = 27 ; * p<0.05, ** p<0.01, *** p<0.001)

9

Figure

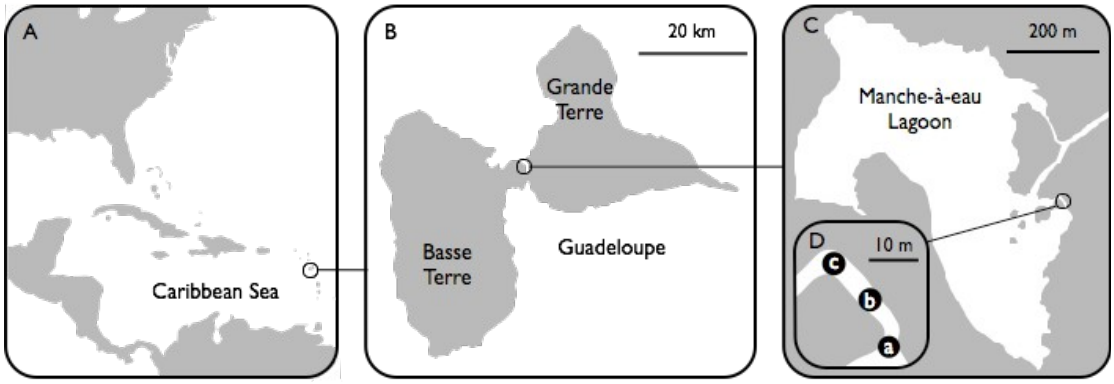

Figure 1. A: location of Guadeloupe archipelago in the Caribbean Sea, B: location of Manche-à-Eau lagoon in Guadeloupe, C: location of sampling area, D: location of sampling stations (a, b, c)

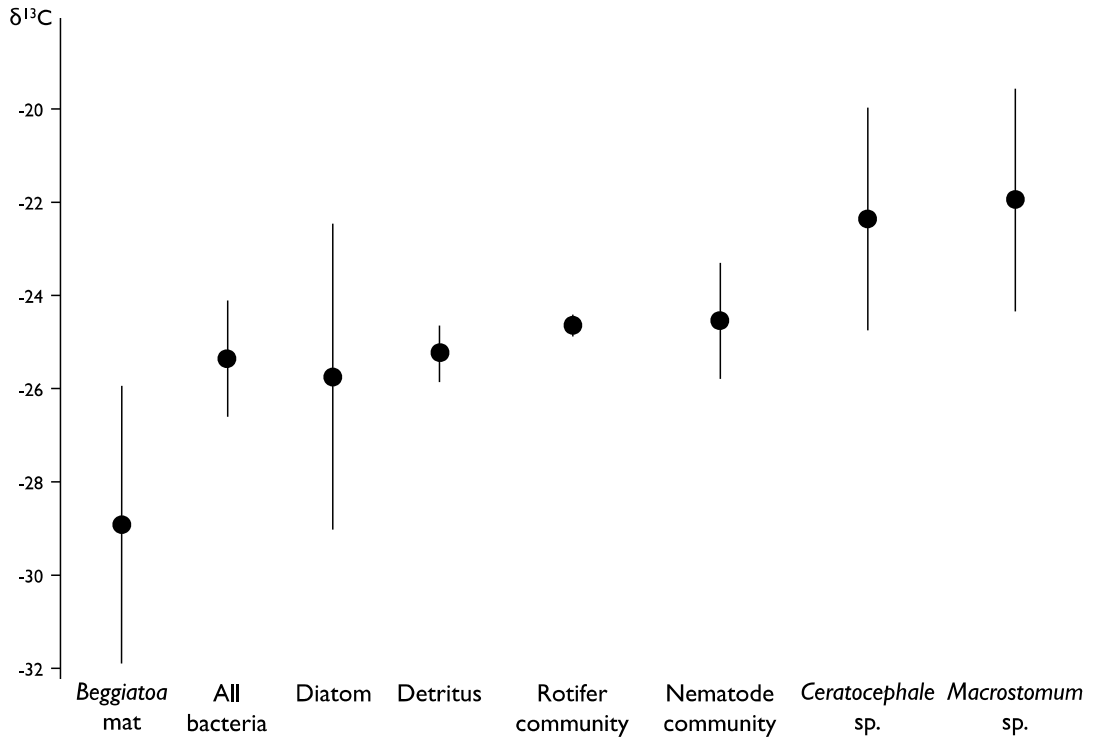

Figure 2. Mean carbon isotopic composition (‰) of food sources (*Beggiatoa* mat, all bacteria, diatom and detritus) and grazers (rotifer community, nematode community, *Ceratocephale* sp. and *Macrostomum* sp.) along the year (means ± SD, n = 27 except for rotifer community n = 18)

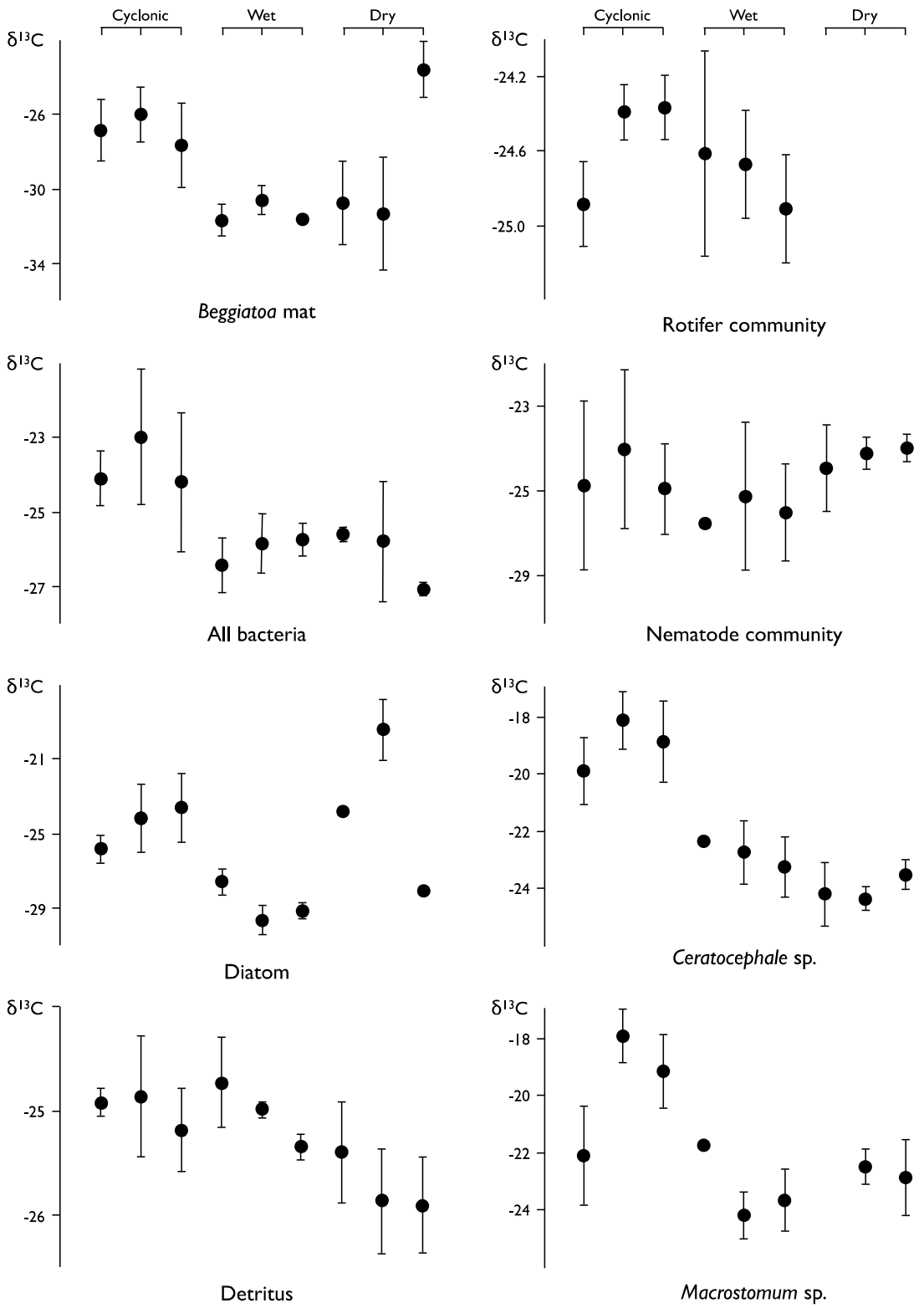

Figure 3. Carbon isotopic composition (‰) of food sources (*Beggiatoa* mat, all bacteria, diatom and detritus) and grazers (rotifer community, nematode community, *Ceratocephale* sp. and *Macrostomum* sp.) during each sampling session (means ± SD, $n = 3$)

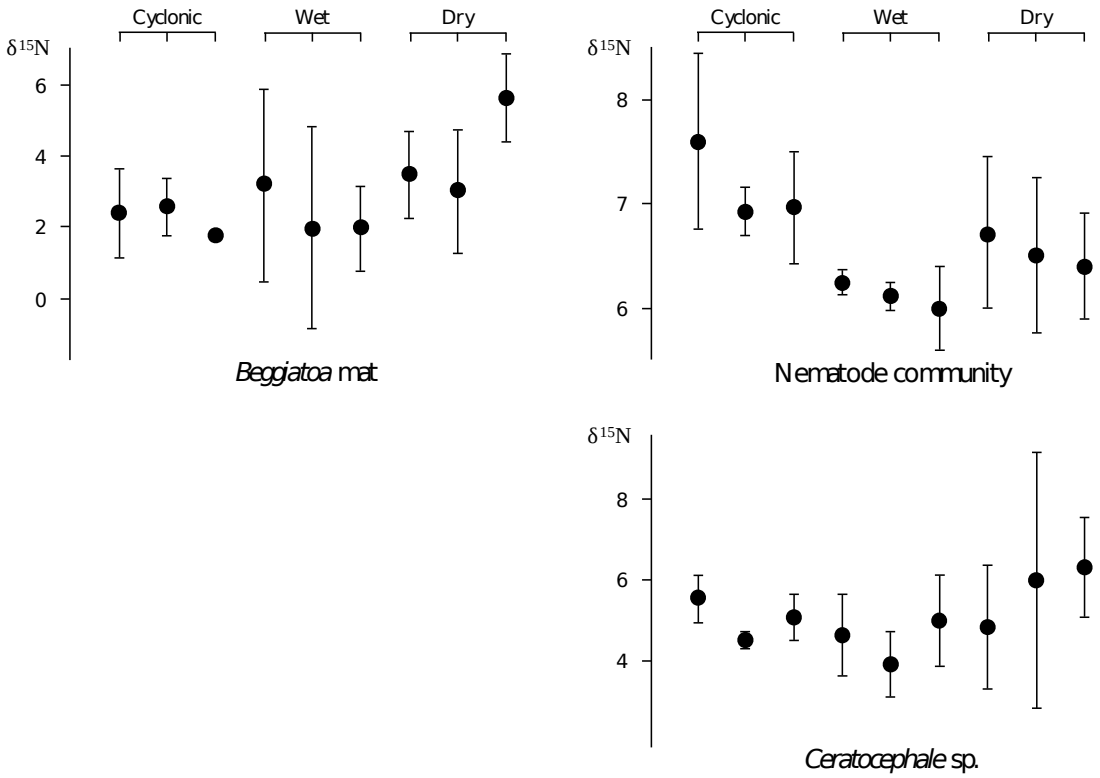

Figure 4: Nitrogen isotopic composition (‰) of *Beggiatoa* mat, nematode community and *Ceratocephale* sp.during each sampling session (means ± SD, *n* = 3)

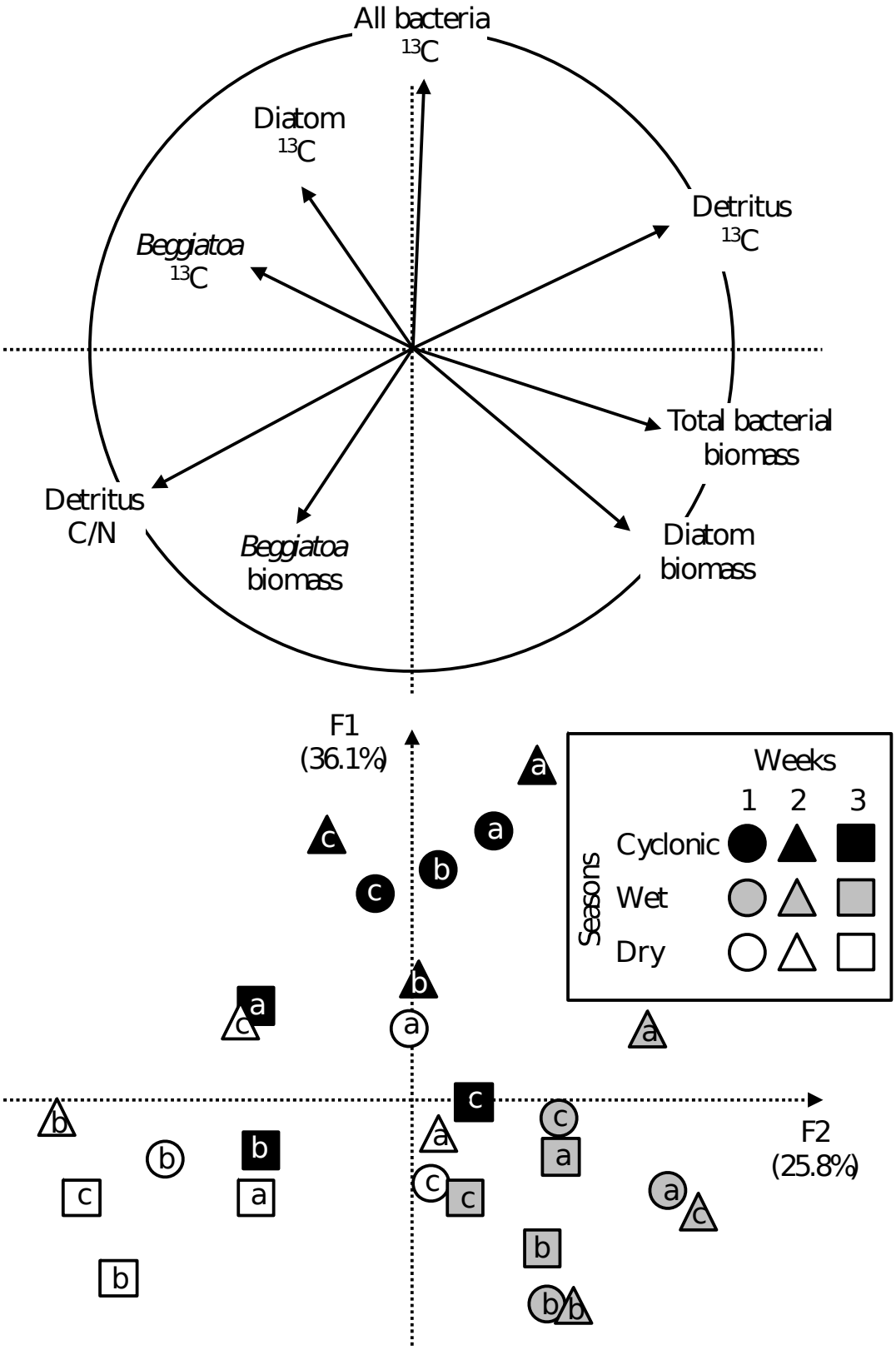

Fig 5. PCA calculated using 27 observations (replicates a, b and c during 3 weeks during 3 seasons) and 8 variables. For each variable, the circle of correlation is reported