

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

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

3

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15 Key Words : *Beggiatoa*, mangrove, benthic food web, seasonality, meiofauna,

16 nematode, Ceratocephale, stable isotope

17 Running Head: Fluctuations in trophic role of sulfur bacteria

18 **Abstract**

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

35 **Introduction**

36 Bacteria are an important resource in pelagic food webs (Sherr et al., 1987). Despite
37 bacterial abundance 1000 times higher in sediment than in the water column, the trophic role
38 of bacteria has been little studied in benthic systems due to methodological difficulties
39 (Kemp, 1990). Benthic bacteria are generally thought to make a limited contribution to the
40 diet of grazers, satisfying less than 10% of the total carbon demand of the meiofauna from
41 estuarine (van Oevelen et al., 2006a; van Oevelen et al., 2006b) and deep-sea environments
42 (Gontikaki et al., 2011). By contrast, benthic microalgae constitute a major food source for
43 many coastal meiofaunal species (Middelburg et al., 2000; Montagna et al., 1989; Riera et al.,
44 1996). Previous grazing experiments with dual-labeled food items (bacteria and diatoms) have
45 shown that meiofauna grazers, which are smaller and have a higher selection efficiency than
46 the macrofauna, preferentially ingest benthic microalgae (Pascal et al., 2008; Pascal et al.,
47 2013).

48 These organisms may preferentially ingest algae rather than bacteria for a number of
49 reasons. The benthic microalgae have a high nutritional value (Kathiresan and Bingham,
50 2001) and contain essential components, such as fatty acids, lacking from bacteria (Zhukova
51 and Kharlamenko, 1999). Differences in the spatial distributions of these two types of food
52 source may also have an effect. Benthic algae are usually concentrated in biofilms, whereas
53 benthic bacteria are more evenly distributed over a vertical gradient within the sediment
54 (Joint, 1978; Nugteren et al., 2009) and are attached to sediment particles. The ingestion of
55 algae, rather than bacteria, thus entails energy savings in the search for food and through
56 prevention of the ingestion of indigestible material. This hypothesis could be tested by
57 determining whether the consumption of bacteria by benthic organisms is greater when the
58 bacteria are concentrated in mats.

59 *Beggiatoa* are multicellular, filamentous white bacteria and are among the largest
60 prokaryotic organisms (Larkin et al., 1994). Members of this genus are found within and just
61 above highly reduced, organic or hydrocarbon-rich sediments (Jørgensen, 1977). Those
62 chemolithotrophic microorganisms are located at the oxic/anoxic interface, where they
63 oxidize sulfides to generate elemental sulfur (that can be intracellularly stored), which they
64 then oxidize further to generate sulfate (Jørgensen, 1977). They are widespread in fresh and
65 marine waters, from coastal to abyssal depths, and from tropical to polar latitudes. They are
66 found in diverse environments such as mud volcanoes, hydrothermal vents (Jannasch et al.,
67 1989), hydrocarbon and methane cold seeps (Montagna and Spies, 1985; Powell et al., 1986)
68 and below productive upwelling areas (Schulz and Jørgensen, 2001). These bacteria form
69 mats that may be up to 3 cm thick and have a patchy distribution (Lloyd et al., 2010).

70 Abyssal communities are dependent principally on photosynthetic material from the
71 surface that is partially mineralized by the time it reaches the deep-sea floor. The limited
72 nature of this energy resource generally results in a steady decrease in the abundance of the
73 benthic fauna from the shelf to the abyss (Rex and Etter, 2010). Organic carbon generated by
74 chemosynthesis constitutes islands of primary production in the otherwise monotonous and
75 food-limited deep-sea environment. Carbon from chemoautotrophs is ingested in the deep sea
76 and contributes to increase standing stocks of macro (Desmopoulos et al., 2010) and
77 meiofauna (Pape et al., 2011; Van Gaever et al., 2006). The flux of particles from surface
78 waters typically decreases with increasing water depth, and the dependence of the fauna on
79 material generated by chemosynthetic processes therefore increases with depth (Levin and
80 Mendoza, 2007; Levin and Michener, 2002). However, chemosynthetic bacteria are also
81 ingested by the meiofauna in shallower environments in hydrothermal vents (Kamenev et al.,
82 1993), brine (Powell et al., 1986) and hydrocarbon seeps (Kamenev et al., 1993; Spies and
83 DesMarais, 1983). In temperate shallow waters, observations reveal ingestion of filamentous

84sulfur bacteria by nematode (Bernard and Fenchel, 1995). A trophic role of these bacteria has
85also been demonstrated in a Caribbean mangrove, in which comparisons of the isotopic
86composition in natural conditions and after artificial enrichment revealed that sulfur bacteria
87were ingested by the meiofauna (Pascal et al., 2014).

88 *Beggiatoa* mats follow a succession of patterns (Bernard and Fenchel, 1995) over
89different time scales. In response to changes in O₂ and H₂S concentration gradients, they can
90move rapidly into the sediment by gliding motility (Dunker et al., 2010). In sediments
91containing photosynthetic microorganisms, *Beggiatoa* are known to perform diurnal
92migrations, being more abundant in the superficial sediment at night but moving down below
93the layer of sediment with photosynthetic activity in the light (Fenchel and Bernard, 1995;
94Garcia-Pichel et al., 1994; Nelson and Castenholz, 1982). The distribution of filamentous
95sulfur bacteria is also influenced by unusual weather, as turbulent water flow can sweep these
96bacteria away or increase the oxygenation of the overlying water inducing the downward
97migration of *Beggiatoa* deeper into the sediment (Elliott et al., 2006; Grant and Bathmann,
981987; Jørgensen, 1977). The species composition of mats of sulfur bacteria depends on the
99age of the mat (Bernard and Fenchel, 1995). Total *Beggiatoa* biomass may also vary
100considerably between seasons (Bernard and Fenchel, 1995; Jørgensen, 1977) and, over longer
101times scales, variations in the abundance of these bacteria are used to monitor the
102remediation of contamination due to organic waste from fish farming (Brooks et al., 2004;
103Hamoutene et al., 2015).

104 In a mangrove on the Caribbean island of Guadeloupe (French West Indies), a
105previous study based on a spatial approach revealed that despite the ingestion of sulfur
106bacteria, the presence of mats did not increase the general contribution of bacteria to the diet
107of the fauna present (Pascal et al., 2014). As the abundance of sulfur bacteria fluctuates during
108the course of the year, the conclusions drawn in this spatial study could not necessarily be

109extended to other periods. The diet of meiofaunal grazers is influenced by food availability
110(Giere, 2009; Moens and Vincx, 1997) and there are alternative dynamic states of microbial
111food webs with an inverse correlation between the ingestion of algae and bacteria by grazers
112(Epstein, 1997; Montagna et al., 1995a). The trophic role of sulfur bacteria may therefore
113depend on the availability of other food sources.

114 The goal of this study was to determine the contribution of sulfur bacteria to the
115meiofaunal diet during a survey in a mangrove on Guadeloupe. This survey was set up so as
116to cover a large range of environmental conditions. We evaluated the abundances and natural
117isotopic compositions of potential food sources, including *Beggiatoa* mats and consumers
118were evaluated. It was not possible to pick up individually bacterial and diatom communities.
119We therefore evaluated their $\delta^{13}\text{C}$ through their phospholipid-derived fatty acids (PLFA)
120(Boschker and Middelburg, 2002). Due to the small size of the meiofauna and the low N
121content of these organisms, $\delta^{15}\text{N}$ was not always measurable. We therefore focused principally
122on $\delta^{13}\text{C}$ measurements. We evaluated trophic links by evaluating correlations between changes
123in the $\delta^{13}\text{C}$ content of food sources and consumers.

124 **Material and method**

125 *Study area*

126 “Manche à eau” is a small tropical lagoon connected to the marine channel “Rivière
127Salée” separating the two mains island of Guadeloupe (French West Indies) (Fig. 1). In this
128lagoon, tides are semidiurnal with mean tidal amplitude of 30 cm (Tide gauge of Pointe-à-
129Pitre, REFMAR®). Temperature and salinity at 0.5 m depth were relatively constant, with
130average values of 28°C and 35, respectively.

131 The lagoon is bordered by a mangrove forest dominated by *Rhizophora mangle*. The

132sediment (< 1 m water depth) between mangrove trees roots is characterized by high sulfide
133concentrations up to 750 μM (Maurin, 2009). In some places, the sediment is covered by
134patches of large (20-60 μm diameter) filamentous white sulfur bacteria visible with unaided
135eyes. *Beggiatoacea* bacteria belong to, at least, two genus: *Maribeggiatoa* and *Isobeggiatoa*
136(Jean et al., 2015). Along the year, the size of those bacterial patches is highly variable
137covering often several square meters. High numbers of interstitial organisms such as ciliates,
138nematodes and turbellarians are associated with the mats (Pascal et al., 2014).

139 *Period of sampling*

140 The sampling strategy was set up to explore highest variations in environmental
141conditions along the year evaluating small time scale changes during three distinct seasons.
142Total of 9 sampling sessions were performed with one-week interval during cyclonic season
143(7, 14 and 20 of September 2011), wet season (28 of November and 5 and 12 of December
1442011) and dry season (10, 17 and 24 of March 2012). During each sampling session, samples
145were collected by snorkeling in three fixed locations spaced of 10 m from each other with a
146water depth of ~ 0.5 m (Fig. 1). In each location, 20 tubes (inside diameter = 55 mm) were
147randomly placed in 2 m^2 and gently pushed in sediment to avoid sediment suspension.
148Syringes were used to collect *i*) 10 samples of the thin layer of surficial mate until white
149filaments were no longer visible for *Beggiatoa* analyses and *ii*) 10 samples of the surficial
150sediment (1cm) for all other analyses. Two types of sediment samples collected were
151independently mixed and the suspended sediment samples were split several times with
152Motoda splitter in order to reach concentration adapted for analyses of abundance of
153*Beggiatoa* and meiofauna. Motoda splitter is commonly used in plankton ecology to equally
154fractionate water samples (Motoda, 1959). This sub-sampling step was taken into account in
155order to report abundances per unit surface area.

156 *Abundance and isotopic composition*

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

167 Sediment was freeze-dried and phospholipid-derived fatty acids (PLFA) were extracted
168 and their isotopic composition was determined using a gas-chromatograph combustion-
169 interface isotope-ratio mass spectrometer (GC-c-IRMS) following protocol in Boschker *et al.*
170 (1999). Concentrations and $\delta^{13}\text{C}$ PLFA specific to all bacteria (i14:0, i15:0, ai15:0, i16:0,
171 C18:1 ω 7c and cy19:0) and diatoms (C20:4 ω 6, C20:5 ω 3, C22:5 ω 3 and C22:6 ω 3) were used to
172 estimate the relative contribution of these groups to the total PLFA pool and their weighted-
173 average $\delta^{13}\text{C}$ composition. The carbon content of all bacteria and diatoms was evaluated using
174 carbon PLFA/carbon biomass ratios of 0.056 and 0.035, respectively (Boschker and
175 Middelburg, 2002). The C/N ratio and isotopic composition of bulk sediment containing
176 bacteria and diatom communities was determined for each sample from untreated sub-sample
177 for ^{15}N content and from acid (1 M HCl)-treated sub-samples for ^{13}C content. Using mass-
178 balance equations, isotopic compositions and abundances of bacteria and diatom communities
179 evaluated with PLFA were used to calculate isotopic composition of detritus free of bacteria
180 and diatoms.

181 For fauna abundance evaluations, samples were fixed with formalin 2% and stained with
182 rose Bengal whereas samples for stable isotope analysis were untreated. Rotifers, nematodes
183 and polychaetes were extracted from sediment using Ludox HS40 (de Jonge and Bouwman,
184 1977). Rotifers and polychaetes were previously identified using morphological traits as
185 *Rotaria* spp. and *Ceratocephale* sp. (Pascal et al., 2014). For each stable isotope sample, 1500
186 *Rotaria* spp. and 100 *Ceratocephale* sp. were pooled whereas 600 specimens from the
187 nematode community were randomly collected and gathered. Sediment sampled from
188 bacterial mats was allowed to settle few minutes in the lab until until *Macrostomum* sp.
189 migrated above the *Beggiatoa* biofilm created and for each sample 100 specimens were
190 individually picked alive.

191 Isotope samples were analyzed at the Isotope Facility at the University of California,
192 Davis, using an elemental-analyzer isotope ratio mass spectrometer. Samples were reported
193 relative to the standards atmospheric N₂ and Vienna PeeDee Belemnite carbon. Stable isotope
194 values are reported in δ notation (in ‰):

$$195 \quad \delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

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

198 *Data analyses*

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

204al., 2008) on abundances of *Beggiatoa*, all bacteria and diatom, C:N of sediment and $\delta^{13}\text{C}$ of
205*Beggiatoa*, all bacteria, diatoms and sediment ($n = 27$).

206 Spearman rank (r_s) correlations were performed to investigate the relationships between
207abundances and isotopic compositions of preys and grazers.

208 **Results**

209 *Prey*

210 During the survey, filaments of *Beggiatoa* presented an average width of $45.3 \pm 5.0 \mu\text{m}$
211($n = 390$) and a carbon content of $24.4 \pm 9.4\%$ ($n = 27$). Filtration of *Beggiatoa* solution
212revealed a carbon content per volume of $2.6 \text{ fg C } \mu\text{m}^{-3}$. Along the year, evaluation of
213*Beggiatoa* biomass through picture analyses revealed an average biomass of $118.2 \pm 19.9 \text{ mg}$
214 C m^{-2} ($n = 27$). Biomass was similar between sampling locations or sampling seasons
215(ANOVA, not significant) whereas they were significantly different between weeks (ANOVA,
216 $p < 0.01$). *Beggiatoa* biomass was considerably lower than the average biomass of all bacteria
217and diatoms, as evaluated through PLFA analyses, reaching respectively $11.5 \pm 6.4 \text{ g C m}^{-2}$
218and $5.4 \pm 4.1 \text{ g C m}^{-2}$, respectively ($n = 27$) (Tab. 1). Biomass of *Beggiatoa* was not related to
219all bacteria and algal biomass as p -values of Spearman correlation analysis were not
220significant.

221 Among potential food items of mangrove sediment, *Beggiatoa* were always more
222depleted in ^{13}C (Fig. 2). Along the year, they presented a mean $\delta^{13}\text{C}$ of $-28.9 \pm 3.2\text{‰}$ whereas
223all bacteria, diatoms and bulk detritus had a higher $\delta^{13}\text{C}$ with respectively: $-25.4 \pm 1.5\text{‰}$,
224 $-25.8 \pm 4.3\text{‰}$ and $-25.2 \pm 0.5\text{‰}$ ($n = 27$). *Beggiatoa* $\delta^{13}\text{C}$ was not significantly correlated with
225 $\delta^{13}\text{C}$ of all bacteria, diatoms and detritus (Tab. 2). Also $\delta^{13}\text{C}$ of all bacteria and diatom were
226not linked ($r_s = 0.558$, n.s.), whereas $\delta^{13}\text{C}$ of detritus and all bacteria were slightly correlated
227($r_s = 0.405$, $p < 0.05$). Detritus presented lower variability in their ^{13}C composition than other

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

230 The PCA performed on characteristics of food items that potentially influence grazers
231 (Fig. 4), showed that spatial and week variations appeared to be lower than seasonal
232 variations. The F1 and the F2 axes together explained 62% of observed variability and data
233 points clustered according to seasons (Fig. 5). The cyclonic period was characterized by high
234 $\delta^{13}\text{C}$ of all food items (*Beggiatoa*, all bacteria, diatom and detritus) and wet season was
235 characterized by high abundance of all bacteria and diatoms whereas dry season samples
236 showed high C:N ratio and higher abundance of *Beggiatoa* (Fig. 5).

237 Grazers

238 Individual weights of grazers were derived from stable isotope samples ($n = \text{specimen}$
239 $\text{per sample} \times \text{replicates}$). The weight per specimen (means \pm SD) was 115.7 ± 96.3 ng for
240 rotifers ($n = 1500 \times 18$), 449.3 ± 334.3 ng for nematodes ($n = 600 \times 27$), 2.8 ± 2.1 μg per
241 *Ceratocephale* sp ($n = 100 \times 27$) and 10.6 ± 10.4 μg for *Macrostomum* sp. ($n = 100 \times 24$).

242 Along the survey ($n = 27$), in the surficial centimeter of sediment, most abundant
243 grazers were rotifers ($269 \pm 230 \text{ } 10^3 \text{ ind/m}^2$) followed by nematodes ($242 \pm 181 \text{ } 10^3 \text{ ind/m}^2$),
244 polychaete ($46 \pm 34 \text{ } 10^3 \text{ ind/m}^2$) and copepods ($11 \pm 12 \text{ } 10^3 \text{ ind/m}^2$). Fluctuations of grazer
245 biomass are presented in Table 1. Among grazers, polychaete represented the highest biomass
246 ($56 \pm 42 \text{ } 10^3 \text{ mg C/m}^2$) followed by nematodes ($51 \pm 38 \text{ } 10^3 \text{ mg C/m}^2$), rotifers ($13 \pm 11 \text{ mg}$
247 C/m^2) and copepods ($4 \pm 4 \text{ mg C/m}^2$).

248 None of the grazer biomass data were correlated with all bacteria and diatom biomass
249 (Tab. 3). However, biomass of rotifers ($r_s = -0.535$, $p < 0.01$) and polychaetes ($r_s = -0.477$,
250 $p < 0.05$) were negatively correlated with *Beggiatoa* biomass (Tab. 3).

251 Among grazers, rotifers presented the $\delta^{13}\text{C}$ value with the lowest variability ($\delta^{13}\text{C} =$
252 $-24.6 \pm 0.3\text{‰}$, $n = 16$). ^{13}C compositions of other grazers presented higher standard deviation

253 among samples: nematode ($\delta^{13}\text{C} = -24.5 \pm 2.5\text{‰}$, $n = 27$), *Macrostomum* sp. ($\delta^{13}\text{C} = -22.3 \pm$
254 2.5‰ , $n = 23$) and polychaete ($\delta^{13}\text{C} = -22.0 \pm 2.4\text{‰}$, $n = 27$) (Fig. 2). Measurement of $\delta^{15}\text{N}$
255 was not possible for rotifer and *Macrostomum* sp. due to low sample amount. Mean $\delta^{15}\text{N}$ ($n =$
256 27) was $6.6 \pm 0.7\text{‰}$ for nematode community and $5.1 \pm 1.4\text{‰}$ for polychaete (Fig. 4).

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

263

264 **Discussion**

265 A) Methodological considerations

266 The abundance of *Beggiatoa* varies over different time scales (Bernard and Fenchel,
267 1995). Biomass displays seasonal variation (Bernard and Fenchel, 1995; Jørgensen, 1977) but
268 can also change rapidly due to the migration behavior of this bacteria (Fenchel and Bernard,
269 1995; Garcia-Pichel et al., 1994; Nelson and Castenholz, 1982) and to unusual weather
270 conditions (Elliott et al., 2006; Grant and Bathmann, 1987; Jørgensen, 1977). This survey
271 suggests that the abundance of *Beggiatoa* varies more at the weekly than at the seasonal scale
272 although multivariate analyses revealed a greater fluctuation of general environmental
273 conditions over the seasonal time scale. Sampling strategy designed to explore variations at
274 both the weekly and seasonal time scales should, therefore, cover a large range of
275 environmental conditions.

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

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

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

289 food webs in estuaries and oceans (Boecklen et al., 2011; Layman et al., 2012). The stable
290 isotope compositions of consumers differ from those of their food source in a predictable
291 manner and can therefore be used to evaluate dietary composition (Fry, 2006). However,
292 stable isotopes are more useful in studies of systems with food sources presenting different
293 isotope values (Moncreiff and Sullivan, 2001). In the mangrove environment studied,
294 *Beggiatoa* present a $\delta^{13}\text{C}$ lower than that of other food sources due to its chemoautotrophic
295 growth (Güde et al., 1981). Enrichment experiments artificially enhance difference in isotopic
296 compositions of food items and were previously used to confirm that stable isotopes are
297 reliable for evaluation of the contribution of *Beggiatoa* to the diet of grazers from the studied
298 mangrove (Pascal et al., 2014). We determined the isotopic composition of bacterial and
299 diatom communities by measuring the $\delta^{13}\text{C}$ of specific phospholipid-derived fatty acids
300 (PLFA) (Boschker and Middelburg, 2002). Strong trophic links between a prey and a grazer
301 result in parallel fluctuations in their isotopic compositions. In this survey, we evaluated the
302 correlation between the $\delta^{13}\text{C}$ of prey and grazers. A lack of covariation between $\delta^{13}\text{C}$ of the
303 different 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
305 separated by 10 m. $\delta^{13}\text{C}$ of food sources and grazers appeared to be highly variable, with
306 considerable differences between sites (Fig. 2). Nevertheless, this approach was found to be
307 suitable for the evaluation of trophic links as it highlighted the role of particular food sources
308 in the diet of consumers, revealing the importance of diatoms in the diet of nematodes, for
309 example.

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

313obtained may differ between approaches. However, both approaches yielded similar results in
314our study: *Beggiatoa* mats made only a minor contribution to the diet of grazers.

315 2) Diet of grazers

316 Rotifers were the most abundant members of the meiofauna in this survey. Rotifers are
317common members of the benthic and pelagic communities in fresh and brackish waters,
318whereas they are thought to be rare in marine environments (Fontaneto et al., 2006; Schmid-
319Araya, 1998). Nevertheless, rotifers can occasionally dominate the marine benthos in terms of
320both abundance (Sommer et al., 2007; Sommer et al., 2003) and biomass (Johansson, 1983).
321They have been found in sulfide-rich sediments containing *Beggiatoa* in coastal (Bernard and
322Fenchel, 1995; Fenchel and Riedl, 1970) and deep sea areas (Sommer et al., 2007; Sommer et
323al., 2003). Bdelloid rotifers have different modalities of food collection: suspension feeding,
324scraping or browsing (Melone et al., 1998). They can consume diverse type of prey (bacteria,
325algae and yeasts) and are able to ingest their prey in a selective manner (Mialet et al., 2013).
326The possible uptake of sulfur-oxidizing bacteria by rotifers has already been suggested
327(Fenchel and Riedl, 1970) and isotope enrichment experiments confirmed that *Beggiatoa* was
328ingested by rotifers in the mangrove studied (Pascal et al., 2014). However, rotifers were
329unlikely to be very dependent on this food resource as they were also present in sediments
330adjacent to mats in the mangrove (Pascal et al., 2014) and in deep-sea habitats without
331*Beggiatoa* (Sommer et al., 2003). The weak links observed between *Beggiatoa* and rotifers in
332the present survey also suggest that these bacteria are not the principal component of the
333rotifer diet.

334 *Macrostomum* spp were shown to ingest sulfur-oxidizing bacteria in a ¹³C labeling study
335(Pascal et al., 2014). *Macrostomum lignano* is a turbellarian species that is cultured with
336diatoms in experimental conditions (Ladurner et al., 2005). Our results suggest that, in natural

337environments, *Macrostomum* spp. have a mixed diet not dominated by a single item such as
338diatoms or *Beggiatoa*.

339 The ingestion of sulfur-oxidizing bacteria by nematodes has been observed (Bernard and
340Fenchel, 1995) and detected on the basis of isotopic composition (Pascal et al., 2014; Spies
341and DesMarais, 1983; Van Gaever et al., 2006). Some deep-sea nematode species feed
342exclusively on *Beggiatoa* (Spies and DesMarais, 1983), whereas the nematodes in this study
343appeared to be less dependent on these bacteria as a food source. The correlation between
344 $\delta^{13}\text{C}$ of diatoms and nematodes revealed a strong trophic role of algae. Benthic diatoms can
345develop in environments with high sulfide concentrations (Admiraal and Peletier, 1979;
346Round, 1979). Compared to adjacent sediments, *Beggiatoa* mats can host diatoms with
347similar (Montagna and Spies, 1985) and even higher abundances (Powell et al., 1986) as
348already reported for the mangrove studied (Pascal et al., 2014). Stable isotope composition
349studies have revealed that the microphytobenthos is the principal food source of the nematode
350community in temperate intertidal mudflats (Moens et al., 2002; Montagna et al., 1995b;
351Riera et al., 1996; Rzeznik-Orignac et al., 2008). However, the contribution of these algae
352may be smaller in other environments such as salt marshes (Riera et al., 1999), in which other
353where other food sources are available such as detritus from marine phanerogams (Couch,
3541989) or allochthonous stranded macroalgae (Riera and Hubas, 2003). Mangrove and saltmarsh
355ecosystems have similar profiles of organic carbon sources in their surface sediments
356(Middelburg et al., 1997). In mangroves, microalgae are generally considered to have only a
357small input, due to light limitation and inhibition by tannins (Alongi, 1994). However, despite
358this minor contribution to the total productivity of the ecosystem, the microphytobenthos can
359represent a major source of carbon for the benthic macrofauna (Bouillon et al., 2004; Bouillon
360et 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. $\delta^{13}\text{C}$ 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 (Grippio 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

411content of the bacteria (Fagerbakke et al., 1996). *Beggiatoa* has a large central vacuole and its
412confined cytoplasm accounts for less than 16% (Jannasch et al., 1989) or 2% of the total
413biovolume (Schulz and Jørgensen, 2001), depending on the study considered. This
414“hollowness” of *Beggiatoa* (Larkin and Henk, 1990) decreases its dry-matter content.
415Consistently, an analysis of PLFA content along a transect in the mangrove studied revealed
416that total bacterial abundance in the uppermost centimeter of sediment was not significantly
417higher in *Beggiatoa* mat sediments than in adjacent sediment without mats (Pascal et al.,
4182014). *Beggiatoa* thus accounted for a much smaller amount of dry matter than suggested by
419its volume (Bernard and Fenchel, 1995) and the biomass of *Beggiatoa* would therefore have
420been smaller than that of other bacteria and other food sources. This lower organic matter
421content may have reduced its nutritive value and attractiveness for grazers.

422 In the mangrove studied, a spatial approach revealed that the presence of mats of sulfur
423bacteria had no effect on the general structure of the benthic food web and the role of bacteria
424in the diet of grazers (Pascal et al., 2014). This survey revealed that this conclusion was valid
425throughout the year, as the trophic role of *Beggiatoa* was limited at all sampling times,
426regardless of the fluctuations in available food sources. Thus, in habitat in which food
427resources are not limiting, the spatial concentration of bacteria in mats does not make them
428more attractive than other food resources.

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1 Tables

Season Week	Cyclonic			Wet			Dry		
	1	2	3	1	2	3	1	2	3
Carbon / Nitrogen of sediment	10.1 ±								
	1.4								
<i>Beggiatoa</i> mat biomass (mg C m ⁻²)	79.5 ±	102.1 ±	139.6 ±	136.5 ±	107.4 ±		127.1 ±		138.9 ±
						116.0 ± 4.4		116.7 ± 23.1	
	4.6	14.8	25.4	14.6	23.9		23.7		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
	19.2 ±	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
Rotifer community biomass (mg C m ⁻²)									
	4.1								
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
<i>Ceratocephale</i> 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

2Table 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

	<i>Beggiatoa</i> 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
<i>Ceratocephale</i> 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

	<i>Beggiatoa</i> 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
<i>Ceratocephale</i> 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

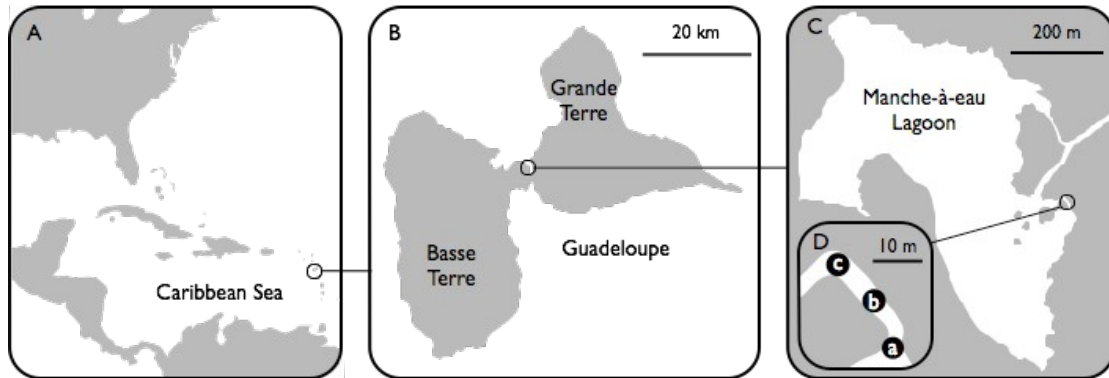


Figure 1. A: location of Guadeloupe archipelago in the Caribbean Sea, B: location of Manche-à-Eau lagoon in Guadeloupe, C: location of sampling area, D: location of sampling stations (a, b, c)

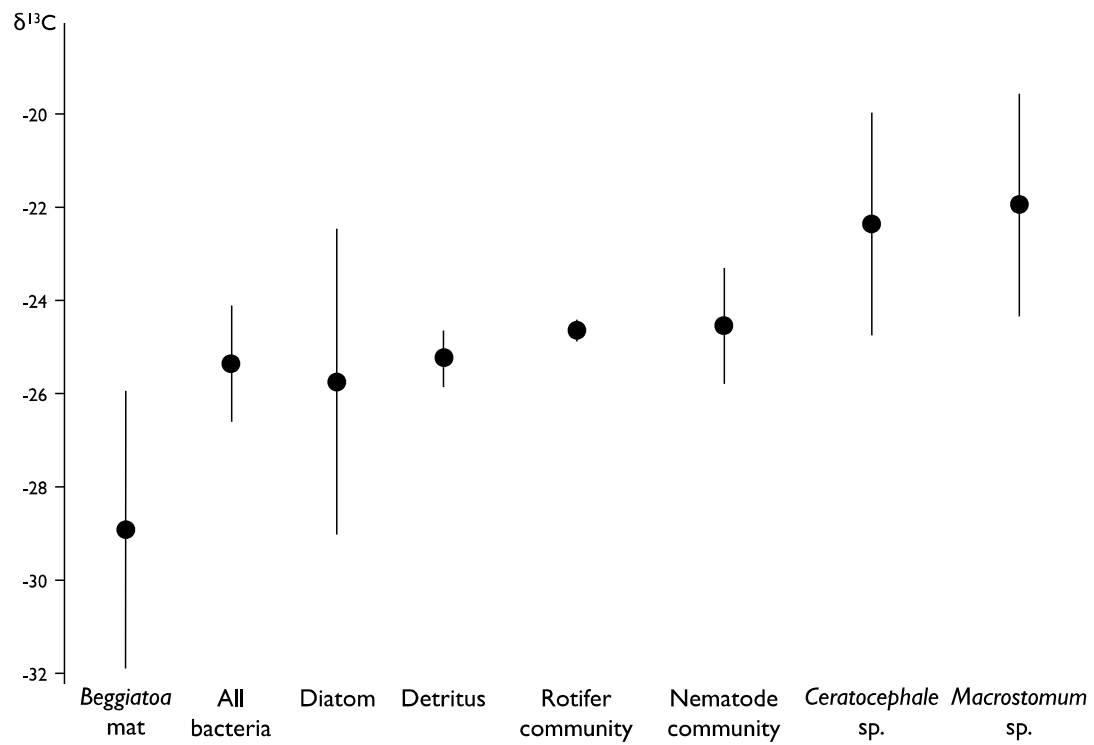


Figure 2. Mean carbon isotopic composition (‰) of food sources (*Beggiatoa* mat, all bacteria, diatom and detritus) and grazers (rotifer community, nematode community, *Ceratocephale* sp. and *Macrostomum* sp.) along the year (means \pm SD, $n = 27$ except for rotifer community $n = 18$)

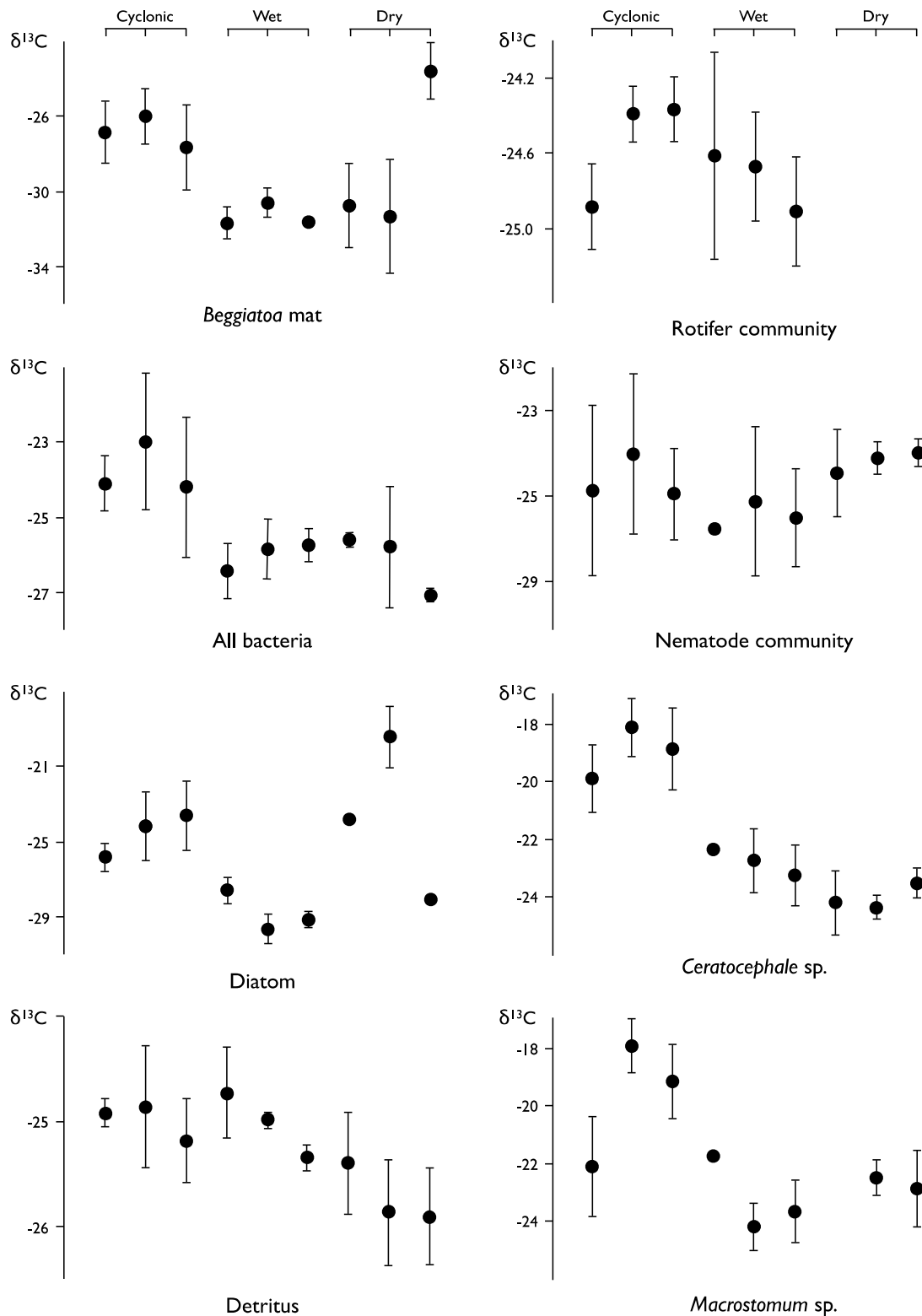


Figure 3. Carbon isotopic composition (‰) of food sources (*Beggiatoa mat*, all bacteria, diatom and detritus) and grazers (rotifer community, nematode community, *Ceratocephale sp.* and *Macrostomum sp.*) during each sampling session (means \pm SD, $n = 3$)

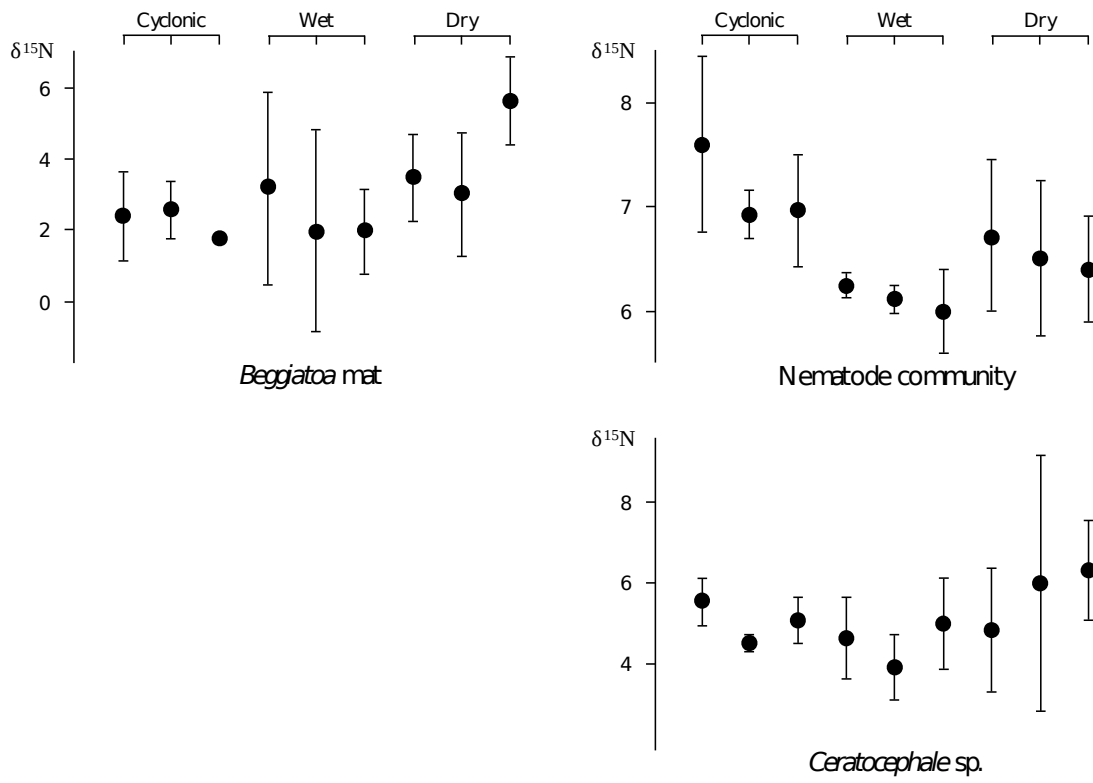


Figure 4: Nitrogen isotopic composition (‰) of *Beggiatoa mat*, nematode community and *Ceratocephale sp.* during each sampling session (means \pm SD, $n = 3$)

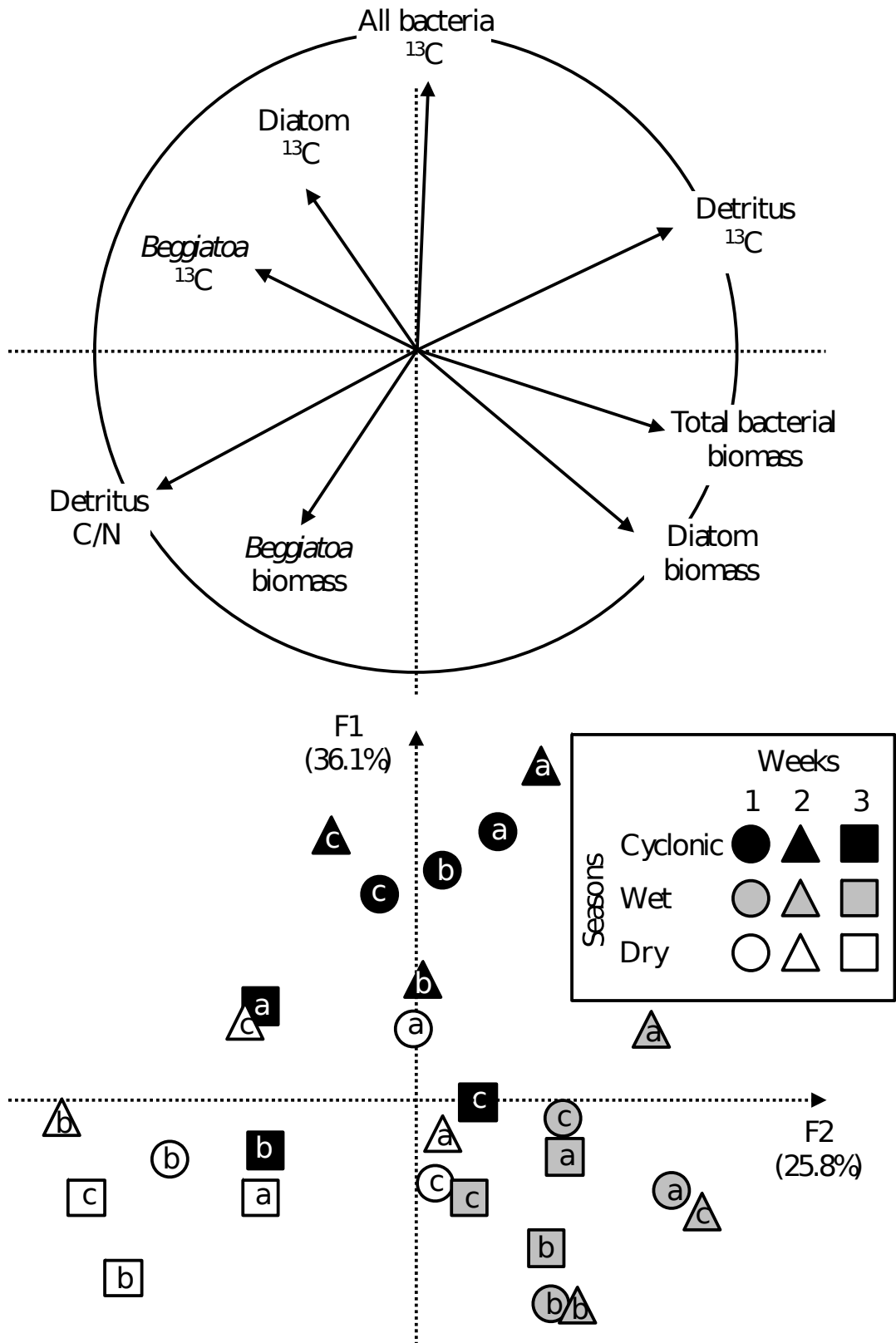


Fig 5. PCA calculated using 27 observations (replicates a, b and c during 3 weeks during 3 seasons) and 8 variables. For each variable, the circle of correlation is reported