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# Trophic role of large benthic sulfur bacteria in mangrove sediment

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**Abstract :**

Large filamentous sulfur-oxidizing bacteria belonging to the Beggiatoacae family can cover large portions of shallow marine sediments surrounding mangroves in Guadeloupe (French West Indies). In order to assess the importance of Beggiatoa mats as an infaunal food source, observations were conducted of the area within mats and at increasing distances from mats. We used natural isotopic compositions and a C-13 enrichment study. Both revealed an ingestion of bacterial mats by associated meiofauna, dominated by rotifers and to a smaller extent by small polychaetes and nematodes. Compared to adjacent sites, sediment covered by bacterial mats presented a higher abundance of diatoms, whereas the total biomass of bacteria did not vary. This constant bacterial abundance suggests that the proportion of organic matter represented by sulfur bacteria is limited compared to the fraction of total bacteria. There was no significant difference in infaunal abundance in mats, suggesting that the availability of this chemosynthetic food resource had a limited local effect. Grazers presented a delta C-13 value increasing with distance from the mat. However, isotopic composition of phospholipid-derived fatty acids specific for diatoms and bacteria revealed that this change is related to modifications of delta C-13 dietary components rather than to changes in diet composition. These complementary methods revealed that the occurrence of sulfur-oxidizing bacterial mats does not necessarily affect grazer abundance and importance of bacteria in their diet. Despite its wide occurrence, Beggiatoa mats would consequently have a minor influence on the structure of the mangrove food web.

**Keywords** : Beggiatoa, Mangrove, Benthic food web, Sulfur bacteria, Meiofauna, Nematode, Rotifers, Stable isotope

# Introduction

Bacteria are very important for the structure and the functioning of all ecosystems due to their role in organic matter degradation and nutrient cycling. Bacteria can also be grazed and may play a major role in food webs as a food source (Sherr et al. 1987). This trophic role has been well established in pelagic environments but due to technical difficulties the trophic role of bacteria is less well known in benthic systems (Kemp 1990). Outside of hydrothermal vent systems, studies focusing on the benthic bacterial compartment suggest that grazing is less than 30% of the bacterial production in several marine environments such as intertidal mudflats (van Oevelen et al. 2006a, Pascal et al. 2009), shallow-water sands (Sundbäck et al. 1996) and deep-sea sediments (Gontikaki et al. 2011). The bacterial contribution to the grazers diet has also received little attention. This role is potentially limited as meiofauna would derive less than 10 % of their total carbon demand from bacteria in estuarine (van Oevelen et al. 2006a, van Oevelen et al. 2006b) and in deep sea environments (Gontikaki et al. 2011). The majority of studies suggested a role lower than 11% for macrofauna (van Oevelen et al. 2006b) even if a contribution of 50% were assessed for deep sea macrofauna (Gontikaki et al. 2011). Previous grazing experiments performed simultaneously with dual labeled food items (bacteria and diatoms) allowed the evaluation of ingestion selectivity by meio- and macro-grazers; small meiofauna appeared to have a better selection efficiency due to their size and to preferentially ingest benthic microalgae as compared to less selective macrofauna (Pascal et al. 2008, Pascal et al. 2013).

Several reasons potentially explain why bacteria do not constitute a major food resource and are not preferentially ingested by benthic browsers. Firstly, bacteria may lack essential components such as fatty acids that are present in diatoms and other microalgae (Zhukova & Kharlamenko 1999). Secondly, bacteria and diatoms can differ in their spatial distribution and ultimately in their availability. Most studies were performed in the intertidal environment

69 with benthic microalgae concentrated at the air-sediment interface during low tide whereas
70 bacteria are distributed more homogenously along a vertical gradient (Joint et al. 1982).
71 Finally, most benthic bacteria are attached to sediment particles in contrast to benthic
72 microalgae and feeding on the microalgal biofilm would hence save energy by *i*) selecting
73 food particles for selective feeders and *ii*) rejecting non-digestible material for non-selective
74 feeders. Contrariwise, feeding on bacteria would cost more energy for all grazer feeding
75 modes.

76 As they form filaments reaching 200 µm in diameters, the white sulfur-oxidizing bacteria
77 belonging to the family of *Beggiatoaceae* are among the largest prokaryotic organisms
78 (Larkin et al. 1994). High concentrations of sulfide are produced in their habitat and
79 *Beggiatoa* cells obtain their energy from the oxidation of sulfide to sulfate. They can also
80 produce elemental sulfur stored as internal granules mostly located in the periplasm
81 explaining their white appearance (Schulz & Jørgensen 2001). In order to perform this
82 chemical reaction, these bacteria inhabit the interface between anoxic sediments and oxic
83 water and form mats that can reach 3 cm in thickness and are characterized by a patchy spatial
84 distribution (Lloyd et al. 2010) and are typically located in quiet waters, in sediment with high
85 organic matter loading or at sulfide seeps (Montagna & Spies 1985). They are found in a large
86 variety of freshwater as well as marine environments: in deep sea mud volcanoes and
87 hydrothermal vents, around seeps of hydrocarbons and methane, below productive upwelling
88 areas and they have also been observed in shallow waters in polar (Van Gaever et al. 2006)
89 and temperate (Fenchel & Bernard 1995) environments, where they have been regarded as an
90 indicator of organic enrichment (Elliott et al. 2006).
91 *Beggiatoa* are highly vacuolated and represent a small amount of dry matter (Bernard &
92 Fenchel 1995). Despite this apparently unfavorable characteristic, *Beggiatoa* would play an
93 important role in the food web as many protozoan species depend on sulfur-oxidizing bacteria

for food and ciliates are assumed to be the main grazers of *Beggiatoa* (Bernard & Fenchel 1995). Isotopic composition and high abundances of meiofaunal grazers in bacterial mats both suggest an ingestion of sulfur bacteria in numerous deep sea environments (Spies & DesMarais 1983, Van Gaever et al. 2006, Pape et al. 2011). In contrast to deep-sea environments, the importance of bacterial mats for meio- and macrofauna in coastal food webs remains to be investigated (Bernard & Fenchel 1995).

The aim of the present study was to determine if bacterial consumption by benthic organisms was increased when bacteria were concentrated in a *Beggiatoa* mat. The importance of bacteria as a potential food source for meiofauna and macrofauna was estimated here in a Caribbean mangrove forest using complementary methods. Abundance of infauna was evaluated as well as natural carbon and nitrogen isotopic composition of potential grazers and their food source along a spatial gradient of increasing distance from *Beggiatoa* mats. $^{13}C$ enrichments were made to enhance differences in isotopic compositions between *Beggiatoa* mat and other food items. To our knowledge, this study is the first observation of *Beggiatoa* in mangrove environments. Due to their fragility, most meiofaunal taxa do not resist sieving, fixation or freezing techniques. Permanent access to the study site allowed us to work with living animals and to consider those organisms largely neglected in food web studies.

# Material and method

*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 a mean tidal amplitude of 30 cm (tide gauge of Pointe-à-Pitre, REFMAR®). Temperature and salinity at more than 0.5 m depth are relatively constant

118 with average values of respectively 28°C and of 35.

119 The lagoon is bordered by a mangrove forest dominated by *Rhizophora mangle*. The
120 sediment (< 1 m depth) between mangrove tree roots is anoxic and contains high sulfide
121 concentrations (Maurin 2009). In some places, the sediment is covered by large patches of
122 dense and conspicuous (20-60 µm diameter) filamentous white sulfur bacteria visible with the
123 naked eye (Fig. 2, almost exclusively large *Beggiatoa* spp.). The size of those bacterial
124 patches is temporally highly variable with a diameter measuring a few centimeters to several
125 meters. High numbers of interstitial organisms such as ciliates, nematodes and turbellarians
126 are associated with the mats.

127 Samples were collected by snorkeling in October 2011 at four different locations along
128 a transect: inside a *Beggiatoa* mat (hereafter called 0 m station) and 1, 10 and 200 m away
129 from the mats. Water depth along the transect ranged between 0.5 (at the mat) and 2 m (200 m
130 away) (Fig. 1). When collected, bacterial patches measured approximately 1 m width and
131 were located 1 m away from the edge of mangrove forest. At each location, 3 replicate
132 samples were randomly collected. For stable isotope and abundance analyses, each sample
133 consisted of pooled 0-1 cm layers collected with syringe of 10 cores gently pushed into the
134 sediment to avoid sediment suspension (inside core diameter = 5.5 cm). For abundance, each
135 sample was sieved and the fraction remaining on 63 µm mesh was equally separated in
136 different aliquots using Motoda splitting box (Motoda 1959). This protocol allows reporting
137 the results per unit surface area.

138 *Species identification*

139 The most abundant meiofaunal species were isolated and gathered according to
140 morphology. When morphological traits were unconspicuous using a dissecting scope,
141 species were pooled. This study is consequently integrating different taxonomic levels.
142 Abundant colonial ciliates were identified as the family Vorticellidae (hereafter called

143 vorticel). Nematodes and copepods were identified respectively to phylum and sub-class
144 levels. Rotifer and gnathostomulida were identified using morphological traits as *Rotaria* sp.
145 and *Haplognathia ruberrima*. The two abundant platyhelminthe species were identified using
146 molecular approaches as *Macrostomum* sp. and *Polycanthus* sp.; DNA was extracted from
147 freshly collected specimens using DNeasy Blood and tissue kit (Qiagen) according to the
148 manufacturer's instructions. The 18S rDNA markers were amplified using primers 1F and 5R.
149 PCR products were purified with QIAquick PCR purification kit (Qiagen) and directly
150 sequenced by Genoscreen. The 18S rDNA gene sequences obtained were compared with the
151 National Center of Biotechnology information (NCBI) (http://www.ncbi.nlm.nih.gov).

152 *Abundance and isotopic composition*

153 Sediment was freeze-dried and phospholipid-derived fatty acids (PLFA) were extracted
154 and their isotopic composition was determined using a gas-chromatograph combustion-
155 interface isotope-ratio mass spectrometer (GC-c-IRMS) following protocol in Boschker *et al*.
156 (1999). Concentrations and $\delta^{13}C$ PLFA specific to bacteria (i14:0, i15:0, ai15:0, i16:0,
157 C18:1ω7c and cy19:0), diatoms (C20:4ω6, C20:5ω3, C22:5ω3 and C22:6ω3) and
158 cyanobacteria (C18:2ω6c, C18:3ω3, C18:4ω3) were used to estimate the relative contribution
159 of these groups to the total PLFA pool and their weighted-average $\delta^{13}C$ composition. Carbon
160 content of bacteria and diatom was evaluated using carbon PLFA / carbon biomass ratios of
161 0.056 and 0.035, respectively (Boschker & Middelburg 2002).

162 Polychaetes, nematodes, copepods, and rotifers were extracted from sediment using
163 Ludox HS40 (de Jonge & Bouwman 1977). For abundance evaluations, samples were fixed
164 with 2% formalin and stained with Rose Bengal. For stable isotope analysis, sediment was
165 frozen and 150 *Nereididae* sp., 700 nematodes, 100 copepods and 1500 rotifers were
166 haphazardly removed from each sample. Several protocols were applied to extract potential
167 preys and infauna from the sediment. Sediment sampled from *Beggiatoa* mats was allowed to

168 settle few minutes in the lab until the formation of a new bacterial biofilm; diatoms and
169 filamentous sulfur-oxidizing bacteria were individually picked alive and cleaned of debris
170 under dissecting microscope. A similar protocol was used to collect 150 *Macrostomum* sp.
171 and 60 *Haplognathia ruberrima* and 2000 vorticels. In sediment without bacterial mats, white
172 specimens of *Polycanthus* sp. were easily identified against the dark sediment and for each
173 sample ≥150 specimens were live picked using glass pipette. Macrofaunal specimens of
174 ragged sea hare (*Bursatella leachii*) were collected in the field and starved overnight to clear
175 gut contents. For each sample, 12 specimens were homogenized using a blender, freeze-dried,
176 and a fraction of the sample was used for stable isotope analyses. Carbon/nitrogen ratio and
177 isotopic composition of bulk sediment containing bacteria and diatom was determined for
178 each sample from untreated sub-samples for $^{15}N$ content and from acid (1 M HCl) treated sub-
179 samples for $^{13}C$ content. Using mass-balance equations, isotopic compositions and
180 abundances of bacteria and diatom evaluated with PLFA were used to calculate isotopic
181 composition of detritus free of bacteria and diatom.

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

186 $$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 10^3$$

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

189 *Enrichment experiment*

190 To further investigate the consumption of *Beggiatoa* by sediment fauna, we designed a
191 $^{13}C$ labeling experiment where chemoautotrophic bacterial mats were selectively labeled in

192 the dark. Sediment from the bacterial mat environment was sampled in January 2012 and
193 placed in 3 circular mesocosms (internal diameter = 23.5 cm with a sediment height of 25
194 cm). A recirculating system of 4 L water allowed sediment of each tank to be covered by 1
195 cm of oxygenated lamellar running water. $NaH^{13}CO_3$ (>99% $^{13}C$-enriched) was added to
196 reach a final concentration of $1 g.m^{-2}$ (Middelburg et al. 2000). Incubations were realized in
197 the dark, at 25°C, salinity 35 and during 4 days. At the end of the incubation, isotopic
198 composition of bacteria, nematode and rotifer were measured with methods previously
199 described.

200 *Data analyses*

201 One-way analysis of variance (ANOVA) was used to test for differences in
202 carbon/nitrogen ratio of sediment, biomass of bacteria and diatom and abundance of
203 meiofauna (rotifer, polychaete, copepod and nematode). Normality of residuals was tested
204 using Shapiro-Wilk tests before performing ANOVA. When overall ANOVA tests were
205 significant, Tukey tests were used for *post hoc* comparisons. Unless specified, values are
206 presented as means ± standard deviations (SD).

207 A Bayesian isotopic mixing model was used to determine possible contributions of
208 different food items to the diet of infauna found in *Beggiatoa* mats. Isotopic compositions of
209 diatom and bulk organic matter from sediment were not discriminated from $\delta^{13}C$
210 compositions and were averaged into one food source called BOM (Bulk Organic Matter).
211 SIAR (Stable Isotope Analysis in R; Parnell et al. 2010) incorporates the variability of
212 consumers and trophic enrichment factors (TEFs) to produce a mean and a 95% confidence
213 interval of the percent contribution of each source to a consumer. As *H. ruberrima* graze
214 mainly, if not exclusively on *Beggiatoa* mats (Pascal et al. in press), we used the *a-posteriori*
215 isotopic signature of the gnathostomulids to calculate a TEF of -1.5 ± 1.0‰ for $\delta^{13}C$ of

*Beggiatoa* bacteria. For $\delta^{13}C$ of BOM, a TEF of 1.1 ± 0.3‰ (McCutchan et al. 2003) and for $\delta^{15}N$ of all food sources, a TEF of 3.4 ± 1.1‰ were used (Minagawa & Wada 1984).

# Results

The *Beggiatoa* mat environment

One species of Platyhelminthe was identified as *Macrostomum sp.* as it shows 99.2% of similarity with *Macrostomum lignano* (550 bp) and the other species as *Polycanthus sp*. as it presents 98.0% of similarity with *Polycanthus torosus* (500 bp). Using morphological traits, the most abundant polychaete was identified as *Ceratocephale sp.* (Glasby, pers. comm.), which was supported by the 18S rDNA sequence analysis.

Individual weight of infauna was derived from the stable isotope samples (Table 1). In the surficial sediment, mean percentage contributions of PLFA specific for bacteria, diatoms and cyanobacteria are presented in Table 2. Expressed in abundances per surface unit, the biomass of bacteria was higher than the biomass of algae (Fig. 3). Meiofauna presented highly variable abundances in mats environment (Fig. 4). Among meiofauna enumerated in the samples, rotifers were dominant in biomass (101.7 ± 96.1 mg C. $m^{-2}$), followed by *Nereididae sp.* (71.0 ± 75.6 mg C. $m^{-2}$), nematodes (15.4 ± 9.1 mg C. $m^{-2}$) and copepods (1.5 ± 2.5 mg C. $m^{-2}$).

Of all food sources, *Beggiatoa* were the most depleted in $^{13}C$ whereas diatoms were the most enriched (Fig. 5). Sediment detritus had a carbon isotopic composition close to diatoms and among potential grazers, *H. ruberrima* was the most $^{13}C$ depleted whereas *B. leachii* was the most enriched. All other meiofaunal members presented a $\delta^{13}C$ varying between -26.2 and -21.9 ‰. Diatoms were the food source with the lowest $\delta^{15}N$ value while detritus and *Beggiatoa* were more enriched in $^{15}N$. All fauna were enriched in $^{15}N$ compared to the food sources with $\delta^{13}C$ isotope signatures ranging between 4.06 and 8.94 ‰ (Fig. 5).

240 The diet composition of *B. leachii* could not be resolved based on isotope compositions.
241 SIAR outputs suggested that all other meiofaunal grazers were ingesting *Beggiatoa*, but in
242 different proportions. Grazers with the highest contribution of the bacterial mats in their diet
243 were *H. rubberima*, copepods, rotifers, and nematodes with respective mean percentages of
244 86, 41, 28 and 22%. *Nereididae sp*., vorticels, and *Macrostomum* sp. ingested less *Beggiatoa*
245 material with respective mean percentages of 16, 12 and 5% (Fig. 6).
246 Complementary enrichment experiment with $NaH^{13}CO_3$ led to $^{13}C$ enrichment of
247 *Beggiatoa* with $\delta^{13}C$ increasing from -31.7 to 1693 ‰ (Table 3). Nematodes and rotifers
248 incubated with those enriched bacteria both showed an increase in $^{13}C$ content. Isotopic
249 compositions of potential grazers and food sources in $^{13}C$-enriched conditions were also used
250 to run a SIAR mixing model. Model outputs with enrichment conditions confirmed a
251 contribution of *Beggiatoa* in grazer diets. This contribution was analogous in enriched vs.
252 control conditions for nematodes (23 *vs*. 24%) and rotifer (27 *vs*. 28%). Similarly
253 contributions of other food items to the diet did not differ between control and enriched
254 conditions (Table 3).
255 Environments adjacent to *Beggiatoa* mats
256 Along the transect at 1, 10, and 200 meters from *Beggiatoa* mats, the total biomass of
257 bacteria was not significantly affected by the presence of *Beggiatoa* mats (Fig. 3).
258 Conversely, microalgal biomass was significantly higher in *Beggiatoa* mats than in all other
259 stations (Fig. 3). Cyanobacteria were always less abundant than bacteria and diatoms (Table
260 2). Differences in detritus C/N ratios were not significant between stations.
261 Abundances of nematodes and copepods tended to increase whereas abundances of
262 rotifers tended to decrease with increasing distance from mats. However none of those
263 differences were significant except that nematodes were significantly less abundant in mats
264 (Fig. 4). The variability in rotifer, polychaete, copepod and nematode abundances were higher

265 in mats where SD reached 106% of the mean value. Individual biomasses of grazers were
266 derived from weights of stable isotope samples and were not significantly different among
267 stations for nematodes, copepods, *Polycanthus* sp. and *Bursatella leachii*. There was no clear
268 trend in nitrogen isotopic composition of grazers along transect (Fig. 7). Carbon isotopic
269 compositions in all grazers decreased with increasing distances from mats (Fig. 7). Difference
270 in grazer $\delta^{13}C$ between 200 m and mats stations was higher for copepods (9.3‰) and
271 nematodes (4.4‰) but was lower for *B leachii* (0.6‰) (Fig. 7). Isotopic composition of PLFA
272 revealed gradual $^{13}C$ enrichment of both bacteria and diatoms along transect away from the
273 mat (Fig. 7). The decrease in $\delta^{13}C$ from the 200 m station to the mat station was smaller for
274 bacteria (6.9 ‰) than for algae (13.3 ‰) (Fig. 7). $\delta^{13}C$ of bacteria and $\delta^{13}C$ of meiofaunal
275 grazers covaried. They both showed similar increases in $^{13}C$ with respect to distances from the
276 *Beggiatoa* mat (Fig. 8).

277 # Discussion

278 The simplest approach to determine trophic linkages between bacteria and grazers is to
279 compare their respective distributions in natural environments. Interpretation of these results
280 can be difficult as grazers potentially affect bacterial dynamics through processes other than
281 grazing. For instance, nematodes were reported to favor development of *Beggiatoa* mats as
282 they increase oxygen penetration and nutrient diffusion into bacterial mats (Salvadó et al.
283 2004). The use of stable isotopes is an increasingly used alternative approach to investigate
284 trophic interactions. The full potential of stable isotopes is tightly linked to the discrimination
285 of potential food sources in terms of isotopic compositions. In the studied mangrove
286 environment, *Beggiatoa* are distinct from diatoms as they present a lower $\delta^{13}C$ due to their
287 specific pathways for carbon metabolism (Güde et al. 1981). One way to increase the power
288 of stable isotope is to artificially enhance differences of isotopic compositions of food items
289 for a better determination of their contribution in food webs (van Oevelen et al. 2006a, van

290 Oevelen et al. 2006b, Galván et al. 2008). In the present study, the sediment contains
291 mangrove tree detritus mostly coming from *Rhizophora mangle* bordering the mangrove
292 forest seaward and this tree material is depleted in $^{13}C$ with values reaching -30‰ (Mothet,
293 personal communication). $\delta^{13}C$ of mat bulk sediment does not express variability in
294 composition of each detrital compound as it presents an average value of -24‰. A selective
295 ingestion of depleted detritus by browsers would overestimate the contribution of depleted
296 *Beggiatoa* in their diet. To increase the power of discrimination among sources, an
297 enrichment experiment was performed in the dark to modify isotopic composition of bacteria
298 whereas diatoms and detritus remained unchanged.

299 Natural isotopic compositions revealed an ingestion of *Beggiatoa* by all studied grazers
300 with a variable contribution of this food item according to infaunal species. For two of those
301 grazers, this conclusion is corroborated by enrichment experiment revealing similar
302 contribution rates of *Beggiatoa* in their diets.

303 Meiofauna dwelling in *Beggiatoa* mats was largely dominated in both abundance and biomass
304 by rotifers. This dominance was observed throughout a year round survey (Pascal et al.
305 unpublished data). This result is unexpected as most species of benthic rotifers were described
306 in freshwater and limno-terrestrial environments (Schmid-Araya 1998) but rotifers in marine
307 environments have received far less attention. Rotifer species were reported in a hypersaline
308 brine channel of the Artic Sea ice suggesting their ability to colonize extreme environments
309 (Friedrich & deSmet 2000). Their occasional occurrence in anoxic and sulfidic marine
310 environment was previously observed (Fenchel & Riedl 1970, Bernard & Fenchel 1995).
311 More recently high rotifer abundances were observed at 800 m water depth colonizing
312 surficial gas hydrates (Sommer et al. 2003, Sommer et al. 2007) where oxidation of methane
313 leads to the production of large amounts of sulfide, which ultimately favors the growth of
314 sulfidic bacteria like *Beggiatoa*. Similarly to deep-sea gas hydrates, rotifers of the present

315 study dominate the meiofaunal community when sulfide concentrations are high and
316 presented a high average abundance: 5.3 $10^5$ (Sommer et al. 2003) *vs*. 6.4 $10^5$ ind. $m^{-2}$ in the
317 present study. However, other deep sea investigations of methane seeps revealed absence
318 (Pape et al. 2011) or marginal (Hauquier et al. 2011) density of rotifers. Guilini et al. (2012)
319 considered that rotifers observed in Sommer et al. (2003, 2007) studies might result from
320 artificial contamination by tap water. Such contamination is unlikely in present study as
321 rotifer specimens were observed directly in untreated sediment. Sommer et al. (2007)
322 suggested that high variations in rotifer abundances could be explained by migration between
323 oxygenated surface sediment and deeper zones to escape predation by nematodes. Little is
324 known about the feeding ecology of marine rotifers and most species have a ventral ciliated
325 field used to scrape the biofilm of bacteria, fungi and diatoms (Schmid-Araya 1998). Uptake
326 of sulfur-oxidizing bacteria by rotifers in sulfidic environment has been previously suggested
327 (Fenchel & Riedl 1970) and their highest abundance in *Beggiatoa* mats have been explained
328 by sulfur-oxidizing bacteria consumption (Sommer et al. 2007). In our study, isotopic
329 compositions under both natural-abundance and enriched conditions suggested a substantial
330 contribution of *Beggiatoa* in the rotifers diet. *Beggiatoa* would not be an obligatory feeding
331 resource as rotifers were found in environments adjacent to *Beggiatoa* mats where they could
332 depend on organic carbon from overlying water column (Sommer et al. 2007).

333 Polychaetes dwelling in *Beggiatoa* mats of mangrove sediments are members of the
334 meiofauna and their stable isotopic composition also suggests potential ingestion of sulfur-
335 oxidizing bacteria. Consumption of filamentous sulfur-oxidizing bacteria from methane seeps
336 by macrofaunal dorvilleid polychaetes were previously revealed by direct observation of gut
337 content and stable isotope analysis (Levin & Michener 2002).

338 Nematodes are the third dominant members of meiofauna in *Beggiatoa* mats. Our stable
339 isotope analyses in natural and enriched conditions support the consumption of sulfur bacteria

340 by the nematode community. According to previous investigations, nematodes are the
341 dominant taxonomic group in *Beggiatoa* mats of shallow sediment (Montagna et al. 1989,
342 Bernard & Fenchel 1995) as well as in deep sea environments (Van Gaever et al. 2006, Pape
343 et al. 2011). Ingestion of filamentous sulfur-oxidizing bacteria by nematodes was observed
344 (Bernard & Fenchel 1995) and also revealed by their isotopic composition (Spies &
345 DesMarais 1983). At an Arctic mud volcano, the proliferation of a single species of nematode
346 in *Beggiatoa* mats was attributed to the feeding on sulfur bacteria with a trophic specialization
347 uncommon among meiofaunal organisms (Van Gaever et al. 2006).

348 Copepods usually represent less than 1 % of total meiofauna in bacterial sulfide-
349 oxidizing mats (Fenchel & Riedl 1970, Bernard & Fenchel 1995) whereas their dominance is
350 higher in adjacent habitats (Montagna & Spies 1985, Powell et al. 1986, Van Gaever et al.
351 2006, Sommer et al. 2007). Similarly, copepods present lower abundances in the present
352 study. This limited abundance of copepods is probably due to a low tolerance to anoxia and
353 sulfide (Levin et al. 1991).

354 In sulfide seeps, group of plathylminthes, aschelminths and gnathostomulids constitute
355 a high fraction of the meiofaunal community whereas this contribution is limited in adjacent
356 non sulfidic sediments (Powell et al. 1986). Abundances of those groups were not evaluated
357 in the present study but their stable isotope compositions suggested a contribution of
358 *Beggiatoa* to their diets. The high $^{13}C$ depletion of the gnathostomulidae *Haplognathia*
359 *ruberrima* would not be due to endo- or ectosymbioses with sulfur-oxidizing bacteria but
360 would be related to a selective ingestion of sulfur-oxidizing bacteria (Pascal et al. in press).
361 *Macrostomum lignano* can easily be cultured with diatoms in experimental conditions
362 (Ladurner et al. 2005) and this turbellarian species is a model organism classically used to
363 investigate hermaphroditic reproduction, developmental biology and ageing research (Schärer
364 et al. 2004). In the present study, *Macrostomum* sp. are not strictly herbivores as they were

365 seen consuming large filamentous sulfur-oxidizing bacteria and their stable isotope
366 composition suggests this is not an uncommon feeding behavior (Pascal PY, personal
367 observation).

368 The ragged sea hare (*Bursatella leachii*) is a key benthic component of the macrofaunal
369 community of mangrove habitats. They have a daily rhythm and an aggregative distribution in
370 shallow subtidal waters (Ramos et al. 1995). *B. leachii* is a generalist grazer of a wide variety
371 of macroalgae and benthic cyanobacteria (Ramos et al. 1995). In the Manche à Eau system,
372 their abundance was highly variable with temporal peak densities showing individuals grazing
373 upon *Beggiatoa* mats as well as surficial sediment in adjacent benthic environment (Pascal
374 PY, personal observation). The very heavy $\delta^{13}C$ signal of *B. leachii* revealed that this
375 gastropod is migrating and feeding outside the mangrove forest given their more enriched
376 $\delta^{13}C$ composition (Finlay & Kendall 2007). Sulfur bacteria may represent one of the potential
377 food source ingested by *B. leachii* but may possibly be only consumed ephemerally when this
378 mollusk is swarming in the mangrove environment.

379 The variability in infauna abundance in the studied mangrove mats was higher than in
380 the adjacent sediments. Similarly, high variations in meiofaunal abundances were revealed in
381 other bacterial mats from seeps in coastal (Montagna & Spies 1985) and deep sea
382 environments (Van Gaever et al. 2006). Our results support the idea that sulfide systems are
383 heterogeneous environments characterized by highly variable geochemistry.

384 *Beggiatoa* mat sediments were characterized by a higher abundance of diatoms than in
385 adjacent sediments. Most studies focusing on free-living sulfur-oxidizing bacteria like
386 *Beggiatoa* were done in deep-sea environments where primary producers are absent. Bacterial
387 mats in a coastal petroleum seep (15 m water depth) also present high chlorophyll-*a*
388 concentrations, even if the dominance of phaeophytin-*a* indicates stressed and decaying
389 microalgal populations (Montagna & Spies 1985). Similarly, high abundance of diatoms were

390 reported in sulfur-oxidizing bacterial mats in shallow water (6.5 m water depth) sediments of
391 Denmark (Bernard & Fenchel 1995) and in deeper sediments (60 m water depth) in the gulf
392 of Mexico (Powell et al. 1986). These high abundances may reflect the tolerance of benthic
393 diatoms to relatively high sulfide concentrations (Admiraal & Peletier 1979) and possibly
394 higher nutrient availability at mat sites given the very high mineralization rates in mangrove
395 sediments (Bouillon et al. 2008).

396 The transect investigated in this study showed that bacterial biomass is not significantly
397 higher in *Beggiatoa* mat sediments compared to those without these mats. The limited
398 contribution of *Beggiatoa* to total bacterial carbon is also suggested by differences in their
399 respective $\delta^{13}C$ values. Unlike other bacteria, *Beggiatoa* cells only have 2% of their
400 biovolume consisting of active cytoplasm (Schulz & Jørgensen 2001) and as they are strongly
401 vacuolated, they represent a considerably smaller amount of dry matter than suggested by
402 their volume (Bernard & Fenchel 1995). *Beggiatoa* biomass is consequently negligible
403 compared to the total amount of bacteria found in the surficial sediment.

404 Concentration of bacteria in mats makes them likely easier to feed upon for grazers.
405 However, none of the studied infauna species exhibited a significantly higher abundance in
406 *Beggiatoa* mat sediments. This constant abundance could hide changes in community
407 composition with increased abundance of species specialized in *Beggiatoa* consumption.
408 However compartments linked with bacteria remains unchanged and the general food web
409 structure is not strongly influenced by the presence of *Beggiatoa*. Similar enrichment in $^{13}C$ of
410 bacteria and $^{13}C$ of meiofauna suggests a constant contribution of bacteria to the diet of
411 meiofauna along the transect. Consequently, complementary approaches of natural and
412 enriched stable isotopes suggests that the global bacterial food role is not increased by the
413 presence of *Beggiatoa*. Most studies suggest that deep sea microbial mats increase standing
414 stocks of micro-, meio- and macrobenthic communities (Levin 2005). Isotopic data have

415 revealed that the contribution of chemosynthetic carbon to the diet of benthic species
416 increases with depth and the absence of photosynthetic primary production (Levin &
417 Michener 2002, Levin 2005). Despite this relationship with depth, sulfur-oxidizing bacteria
418 can constitute an important food source in some shallow continental shelf systems (Powell et
419 al. 1983, Montagna & Spies 1985). Mangrove forests are overall highly productive with a
420 large number of organic matter sources, such labile leaf detritus and primary producers like
421 diatoms and cyanobacteria. The mangrove system reveals that the additional trophic resource
422 constituted by *Beggiatoa* does not influence infaunal abundances or the contribution of
423 bacteria to their diet.
424 Infauna can be influenced by toxicity of bacterial mat environments. *Beggiatoa* can create
425 anoxic conditions as they can consume up to 70% of total oxygen of the sediment (Fenchel &
426 Bernard 1995). Moreover, *Beggiatoa* are found in sediments rich in sulfide which is toxic at
427 low concentrations for many aerobic metazoans as it blocks the cytochrome *c* oxidase of their
428 respiratory chain (Bagarino 1992). This toxicity is particularly high for small-sized grazers
429 where diffusional fluxes of sulfide into body tissue are extremely fast (Jahn et al. 1997). Some
430 meiofaunal species have developed sulfide detoxification system based on an oxidation in
431 their body wall (Fenchel & Findlay 1995). However, this tolerance is restricted to some
432 species (Pape et al. 2011) and the diversity observed in bacterial mats is consequently often
433 lower than in adjacent sediment (Van Gaever et al. 2006). As a result, we suggest that in the
434 studied marine mangrove systems, eukaryotic species able to tolerate this toxicity do not
435 necessarily have a higher contribution of bacteria to their diet than species dwelling in
436 adjacent sediment.

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# Tables

Table 1. Individual infaunal weight derived from weight of stable isotope samples.

| | Number of specimen examined | Individual weight per specimen |
|---|---|---|
| Rotifer | 3 X 1500 | 158 ± 70 ng |
| Copepod | 3 X100 | 685 ±233 ng |
| Nematode | 3 X 700 | 789 ± 241 ng |
| *Macrostomum* sp. | 3 X 150 | 2.79 ± 0.12 µg |
| *Nereididae* sp. | 3 X 100 | 2.98 ± 0.86 µg |
| *Haplognathia ruberrima* | 3 X 60 | 3.94 ± 2.65 µg |
| *Bursatella leachii* | 3 X12 | 2.02 ± 0.33 g |

595 Table 2. Contribution of PLFA specific for bacteria, diatoms and cyanobacteria to total fatty

596 acid methyl esters along transect stations (% means ± SD, n = 3).

| | Mat | 1 m | 10 m | 200 m |
|---|---|---|---|---|
| Bacteria | 25.1 ± 2.0 | 27.1 ± 2.6 | 21.1 ± 3.2 | 25.1 ± 0.4 |
| Diatoms | 8.1 ± 2.0 | 6.5 ± 0.8 | 6.6 ± 1.3 | 3.5 ± 1.0 |
| Cyanobacteria | 2.4 ± 0.3 | 2.5 ± 0.2 | 2.2 ± 0.2 | 1.7 ± 0.0 |

597

598 Table 3. Isotopic composition ($\delta^{13}C$) in enrichment experiment (means ± SD). Mean
599 contribution (%) and 95% confidence intervals of different food items (*Beggiatoa*, diatom and
600 detritus) to the diet of nematode and rotifer based on SIAR mixing model.

| | Control | Enrichment experiment |
|---|---|---|
| $\delta^{13}C$ (‰) | | |
| *Beggiatoa* | -31.7 ± 0.9 | 1693.2 ± 275.5 |
| Nematode | -22.3 ± 0.3 | 338.8 ± 65.9 |
| Rotifer | -26.2 ± 0.6 | 389.3 ± 95.9 |
| | | |
| Nematode diet composition (%) | | |
| *Beggiatoa* | 24 (0-68) | 23 (11-38) |
| Diatom and detritus | 75 (31-100) | 77 (62-89) |
| | | |
| Rotifer diet composition (%) | | |
| *Beggiatoa* | 28 (18-38) | 27 (6-51) |
| Diatom and detritus | 71 (61-81) | 72 (49-94) |

601

# Figure caption

**Figure 1.** A: Location of Guadeloupe island in the Caribbean Sea, B: location of Manche-à-eau lagoon in Guadeloupe, C: location of sampling transect and D: schematic view of 4 sampling points along the transect, *i. e.* inside *Beggiatoa* mats and 1, 10 and 200 m away from mats (not drawn to scale).

**Figure 2.** Mats of white benthic filamentous sulfur bacteria between roots of mangrove tree (water depth = 1 meter).

**Figure 3.** Biomass of bacteria and diatom (in g $C.m^{-2}$) and Carbon/Nitrogen ratio of surficial sediment (1 cm) along transect stations (means ± SD, n = 3). Significant differences ($p < 0.01$; ANOVA; Tukey test) indicated with *.

**Figure 4.** Abundances of meiofauna (rotifer in $10^6.m^{-2}$ and polychaete, copepod and nematode in $10^3.m^{-2}$) in surficial sediment (1 cm) along transect stations (means ± SD, n = 3), with significant differences ($p < 0.01$; ANOVA; Tukey test) indicated by *.

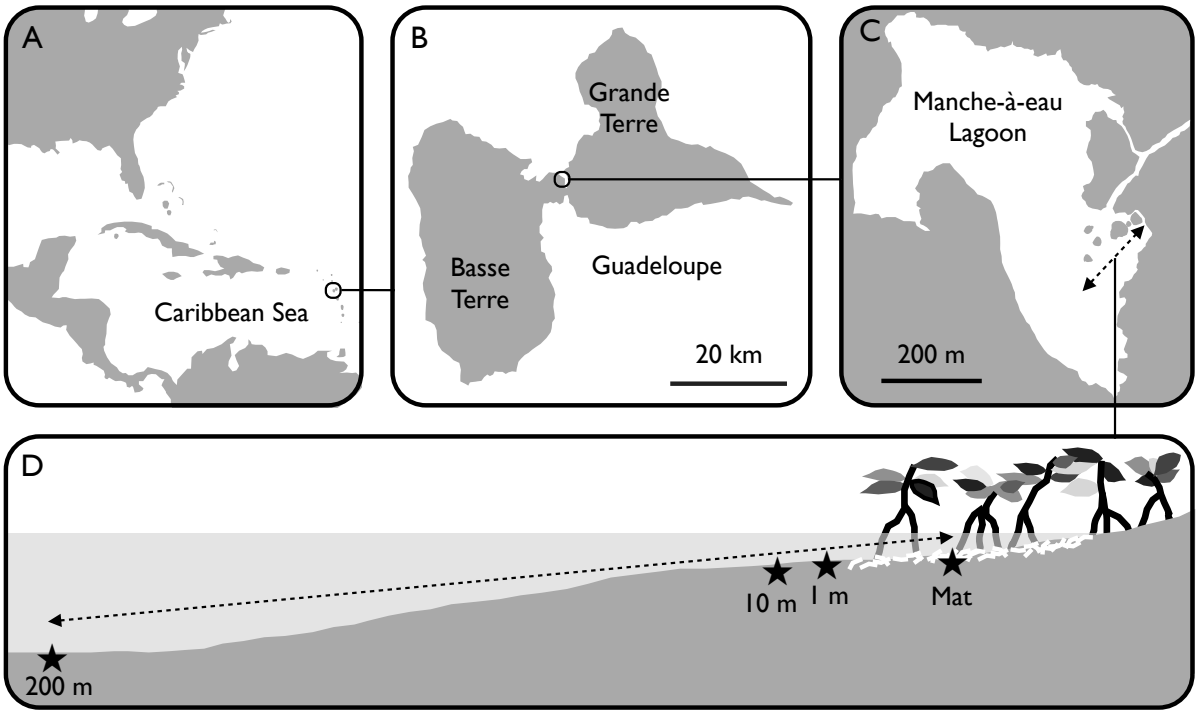
**Figure 5.** Natural isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) of food sources (*Beggiatoa*, diatom and bulk sediment (detritus)), meiofaunal (rotifer, vorticel, *Macrostomum* sp., nematode, copepod, *Nereididae* sp., *H. ruberrima*) and macrofaunal potential grazers (*Bursatella leachii*). Means ± SD (n = 3) are reported.

**Figure 6.** Contribution (%) of different food items (*Beggiatoa* in white and BOM in grey) to the diet of meiofaunal grazers (gnathostomulid *H. ruberrima*, copepod, rotifer, nematode, polychaetes *Nereididae* sp., vorticel, plathyhelminthe *Macrostomum* sp.). Results were issued with the SIAR mixing model. For each source 95%, 75% and 25% credibility intervals of probability distributions were reported.

**Figure 7.** Natural isotopic composition of bacterial and algal PLFA ($\delta^{13}C$) and potential grazers ($\delta^{13}C$ and $\delta^{15}N$ of nematode, copepod, *Polycanthus* sp. and *B. leachii*) along transect stations (means ± SD, n = 3).

**Figure 8.** Carbon natural isotopic compositions of meiofauna (white symbols for copepod and black symbols for nematode) according to $\delta^{13}C$ of bacterial PLFA along transect stations. The theoretical line represents variation of identical amount between bacteria and meiofauna.

633 **Figure**




634
635 Figure 1

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638 Figure 2

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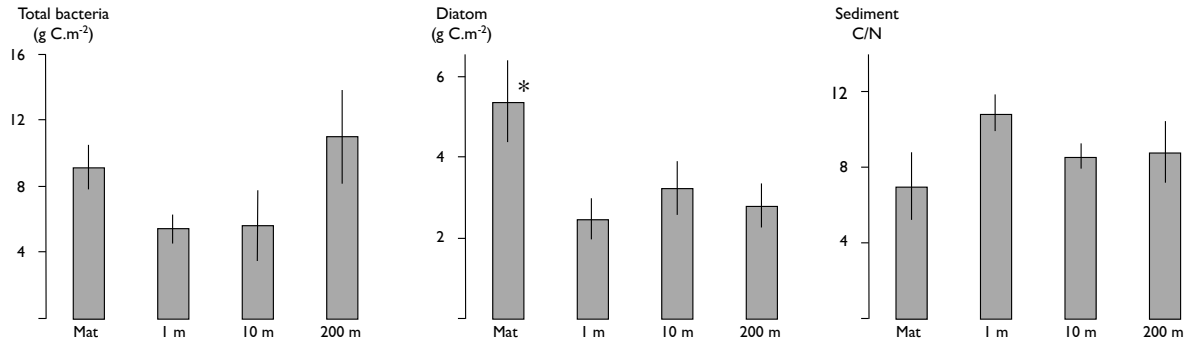


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641 Figure 3

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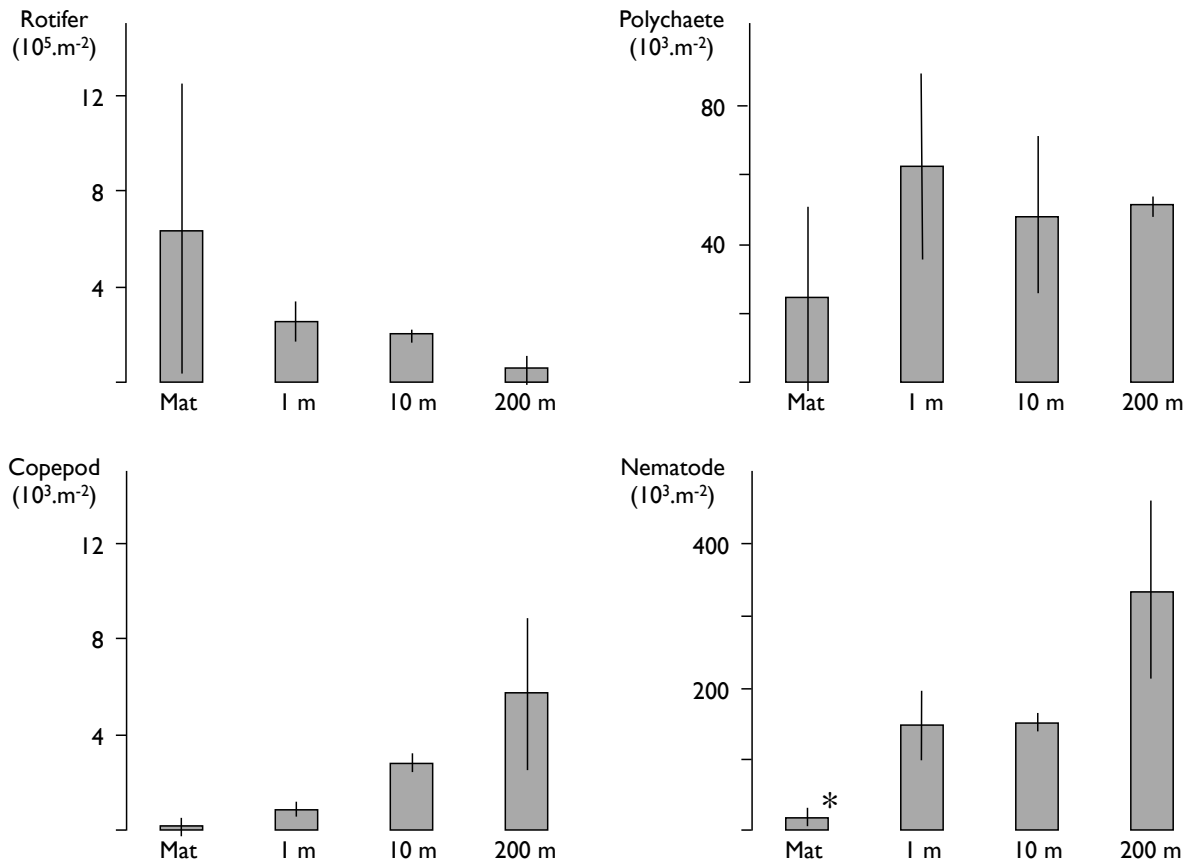


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644 Figure 4

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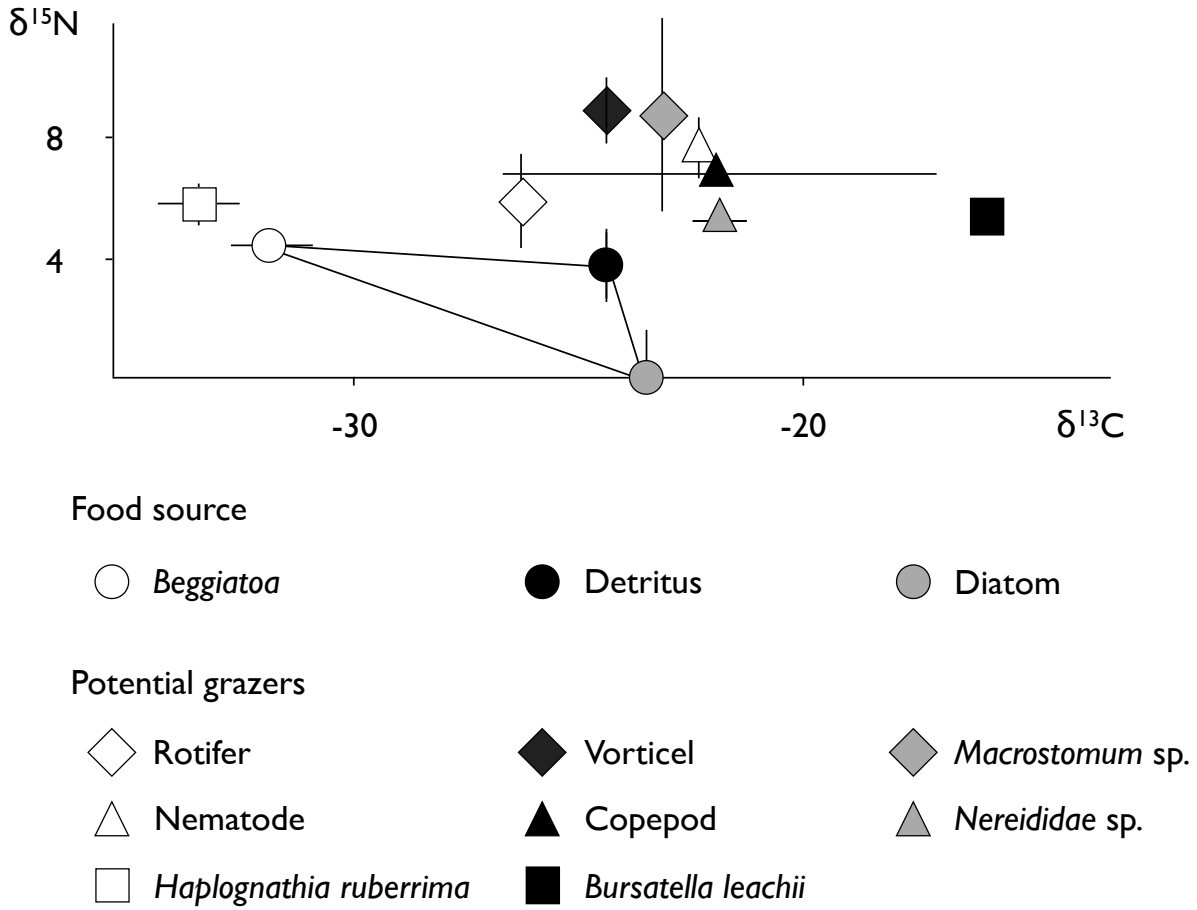


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647 Figure 5

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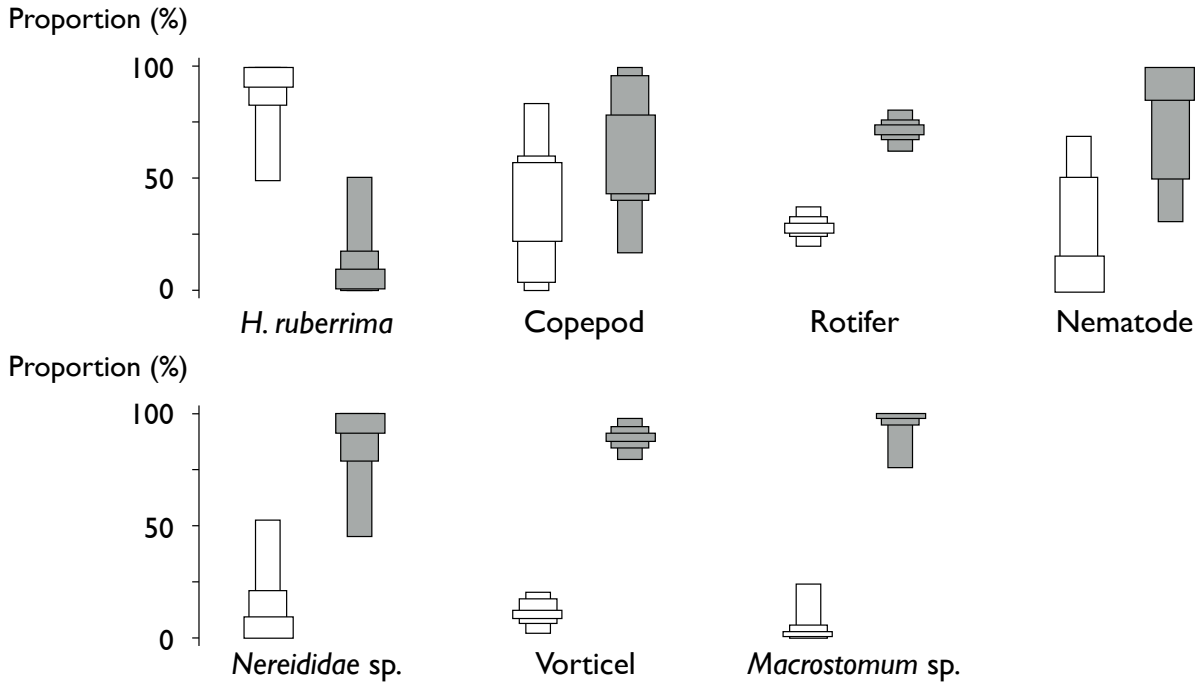


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651 Figure 6

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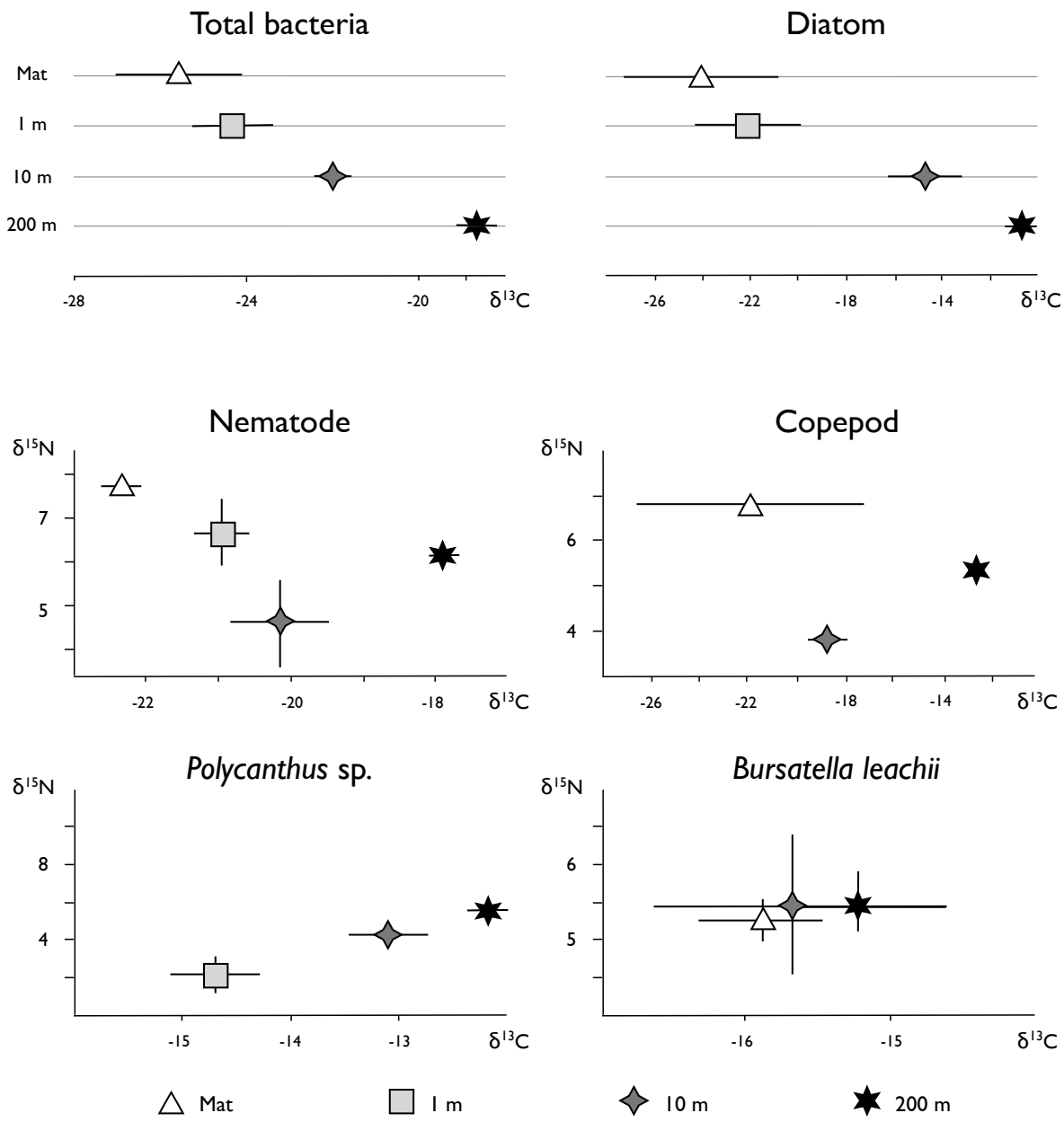


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655 Figure 7.

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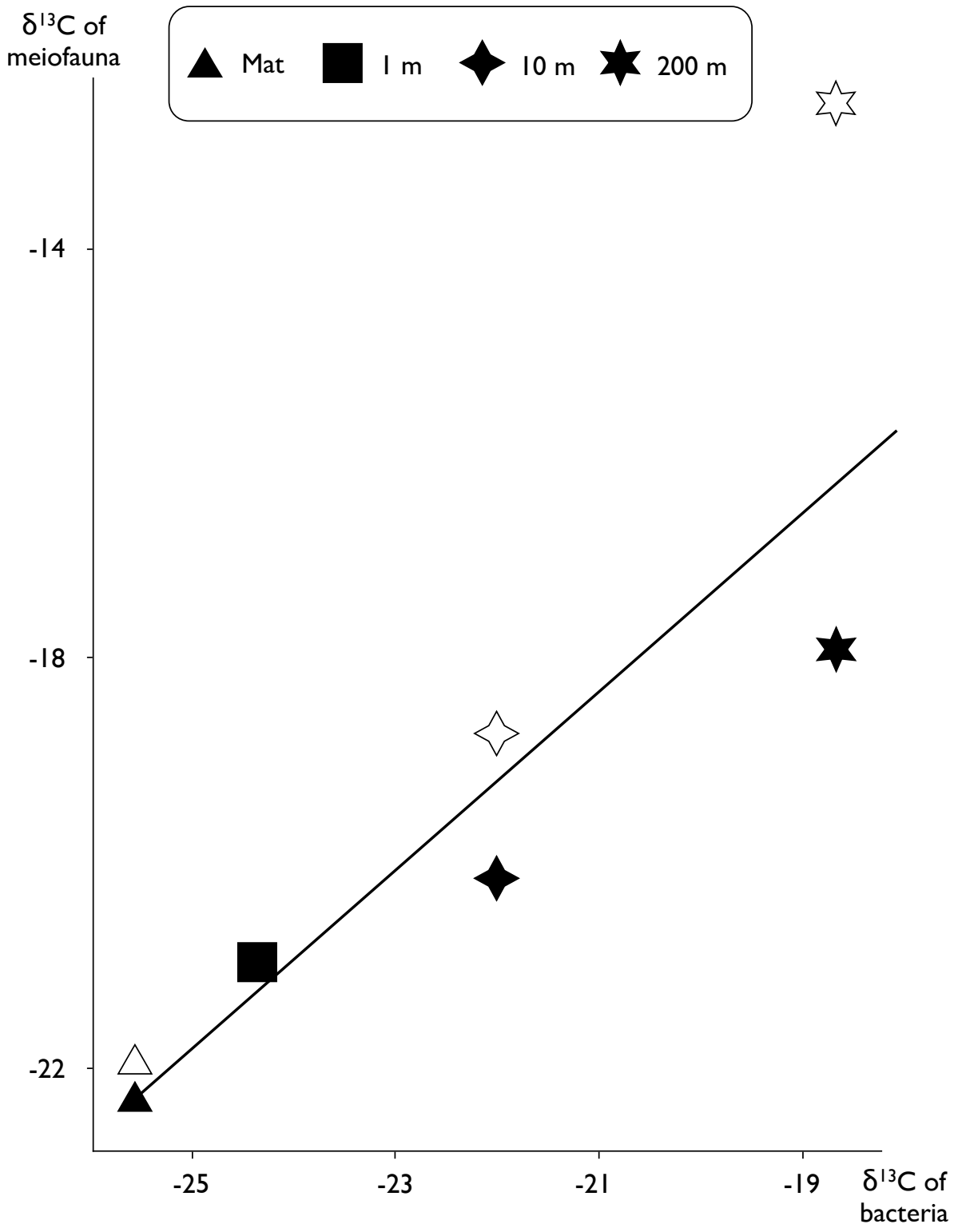


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658 Figure 8.