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Meiofauna versus macrofauna as a food resource in a tropical intertidal mudflat

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21

22 **Abstract**

23 Evaluations of the functioning of benthic marine food webs could be improved by
24 quantifying organic matter fluxes from the meiofauna to higher trophic levels. In this study,
25 we measured the simultaneous ingestion of meiofauna and macrofauna by common dwellers
26 of a tropical intertidal mudflat on the coast of Amazonia. The meiofauna and macrofauna
27 (tanaid) communities of a tropical intertidal mudflat of French Guiana were separately
28 enriched with ^{15}N and ^{13}C , respectively. The enriched preys were then used as tracers during
29 feeding experiments with common predators of different sizes and feeding mechanisms: a
30 Portunidae crab (*Callinectes bocourti*), a Penaeidae shrimp (*Farfantepenaeus subtilis*) and a
31 Gobiidae fish (*Gobionellus oceanicus*). In feeding experiments with all predators except
32 crabs, feeding rates increased with the availability of meiofauna and macrofauna food
33 sources. The ability of consumers to ingest their food selectively was evaluated by calculating
34 the differences in the ratio of macrofauna to meiofauna between the *i*) ingested material and
35 *ii*) that available in the environment. Larger predators showed a higher degree of preferential
36 macrofauna ingestion than smaller predators, consistent with the optimal foraging theory. For
37 large predators, the meiofauna would be important only during early life or in the absence of
38 large food items.

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41 **Introduction**

42 Marine sediments constitute one of the largest environments in the world, in terms of
43 the area covered. They form the habitat of the meiofauna, a discrete group of small (passing
44 through a 0.5 mm-mesh sieve), highly diverse and abundant organisms (Giere 2009).
45 Meiofauna biomass varies considerably between habitats. It is generally smaller than that of
46 other benthic components, but the meiofauna could play a key role in this ecosystem, due to
47 its high levels of production and activity (Schwinghamer et al. 1986, Moens et al. 2013). The
48 meiofauna move through the sediment and construct burrows, thereby conveying oxygen and
49 nutrients vertically and increasing organic matter mineralization and nutrient cycling (Aller &
50 Aller 1992, Coull 1999, Bonaglia et al. 2014). The meiofauna also supplies ecosystem
51 services, such as nutrient cycling and waste processing, and it plays an important role in food
52 webs (Schratzberger & Ingels 2018). The meiofauna is highly diverse, with a large array of
53 feeding strategies, resulting in the consumption of a broad spectrum of food sources,
54 including microphytobenthos (Middelburg et al. 2000, Moens et al. 2002) and, to a lesser
55 extent, bacteria (van Oevelen et al. 2006, Pascal et al. 2009). The meiofauna may, therefore,
56 represent a major link between small food items and higher trophic levels (Coull 1999). The
57 meiofauna is a high-quality food source, as the animals in this population can biosynthesize
58 and accumulate highly unsaturated fatty acids (Fleeger 2007, Leduc et al. 2009, De Troch et
59 al. 2012, Braeckman et al. 2015) that most metazoans are unable to produce. Numerous
60 studies have demonstrated the importance of the meiofauna in the diet of epibenthic predators
61 (Coull 1990), such as fishes (Fitzhugh & Fleeger 1985, Henry & Jenkins 1995), shrimps (Bell
62 & Coull 1978, Nilsson et al. 1993) and crabs (Scherer & Reise 1981). Many predators present
63 developmental shifts in food preference, with the young preferentially ingesting meiofauna
64 and adults preferentially ingesting larger food items (Coull 1990, 1999, Nilsson et al. 1993).

65 The criteria governing the selection of meiofauna *versus* macrofauna by predators, as a
66 function of the respective availabilities of these two food sources, remain unclear

67 The simplest approach to determining trophic linkages between a consumer and its prey
68 is the direct observation of feeding behavior (Majdi et al. 2018). However, such observations
69 are particularly difficult in the fine sediment of the benthic environment, due to the high
70 turbidity of the overlying water, enhanced by from the suspension of sediment due to the
71 movements of foraging consumers (Kneib 1985). As an alternative approach, a visual analysis
72 can be performed on the gut contents of consumers, but such studies are subject to biases due
73 to differences in digestion rates between food items (Alheit & Scheibel 1982, Scholz et al.
74 1991). The overall impact of predation on the meiofauna can be evaluated by excluding
75 predators over small (Hall et al. 1990) or large scales (Carpenter et al. 1995, Deegan et al.
76 2007). However, the effects of predation are confounded with indirect effects, such as
77 depletion of the meiofaunal food source (Ólafsson et al. 1993) and/or physical disturbance
78 due to regular bioturbation by predators (Austen & Widdicombe 1998, Schratzberger &
79 Warwick 1999, Ólafsson 2003, Fleeger et al. 2008). The use of stable isotopes is considered
80 to be a powerful tool for determining nutrient sources for consumers, as stable carbon and
81 nitrogen ratios are largely determined by diet (Fry 2006). The full potential of stable isotopes
82 is closely linked to the discrimination of potential food sources in terms of isotopic
83 composition. Stable isotopes can also be used as tracers, after the artificial enrichment of
84 preys. This approach has been used to evaluate the ingestion of bacteria and
85 microphytobenthos by meiofauna (Moodley et al. 2002, Pascal et al. 2008b, Pascal et al.
86 2008c), macrofauna (Pascal et al. 2008a, Leroy et al. 2012) and fishes (Como et al. 2018). A
87 similar approach has also been used to measure the consumption of macroalgae (Pascal &
88 Fleeger 2013, Legrand et al. 2018). However, to our knowledge, this approach has never been
89 used to assess the ingestion of meiofauna and macrofauna by predators.

90 Improvements in our understanding of the complexity of benthic marine food webs
91 require both *i*) improvements in the quantification of the fraction of the meiofauna transferred
92 to higher trophic levels and *ii*) evaluations of potential variations of this trophic flux
93 according to the availability of other food sources. The aim of this study was to measure the
94 simultaneous ingestion of meiofauna and macrofauna by common dwellers of the tropical
95 intertidal mudflat of the coast of Amazonia.

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Materials and methods

99

Study site

100 This study was performed in the intertidal mudflat of Awala-Yalimapo (05°44'44"N,
101 53°55'36"W), in Western French Guiana, 850 km away from the mouth of the Amazon River
102 (Fig 1). The study site has a humid tropical climate, with a wet season from January to July
103 and a dry season from August to the end of December. This coast is subject to a semidiurnal
104 tidal cycle, with a tidal range of 0.8 m (neap tides) to 2.9 m (spring tides). Over the course of
105 the year, mud temperature oscillates between 29 and 33°C, sediment pore water salinity varies
106 between 12 and 46 and sediment organic content fluctuates between 5.6 and 6.8% (Nguyen et
107 al. 2018). The sampling station was located in the upper area of the intertidal mudflat, in very
108 fluid mud adjacent to an area of consolidated mud with young mangrove trees.

109 In this area, meiofaunal abundance fluctuates between 1.7×10^6 and 4.4×10^6 ind.m⁻²,
110 equivalent to dry weights of 3.3 and 8.3 g m⁻², respectively, and the community is dominated
111 by nematodes, with harpacticoid copepods and other groups (Ostracods, Platyhelminthes and
112 Molluscs) accounting for only 26% and less than 1%, respectively, of the benthic meiofauna
113 (Dupuy et al. 2015). The term “macrofauna” is used here for animals with a length of 0.5 mm
114 to 20.0 mm. The macrofauna is not very diverse and is dominated by a small number of few
115 taxa, such as tanaids, with the species *Halmyrapseudes spaansi* accounting for 84% of
116 macrofauna specimens, with mean abundances from 2,600 ind.m⁻² to up to 73,000 ind.m⁻²
117 corresponding to a maximum dry weight of 12.1 g m⁻² (Jourde et al. 2017; Nguyen et al.
118 2018). The macrofauna also includes members of the Polychaetes and, to a lesser extent,
119 Gastropods and Nemertea (Jourde et al. 2017). The macrofaunal community is dominated by
120 small species, such as *H. spaansi*, which never exceeds 6.4 mm in length (Nguyen et al.
121 2018). In this study, organisms of more than 20 mm in length, with the potential to ingest
122 meiofauna and macrofauna, are considered to be predators. We focused on the most common

123 predators at this site, collected locally: the crab *C. bocourti*, the shrimp *F. subtilis* and the
124 highfin goby *G. oceanicus*. The abundances of *C. bocourti* and *F. subtilis* have never been
125 evaluated in the study area. The abundance of the high fin goby *G. oceanicus* was previously
126 estimated from benthic cores, which showed this species to have a patchy distribution, with
127 densities of up to 50 ind. m⁻² (Jourde et al. 2017). All feeding experiments were performed
128 during the dry season, in November 2015.

129 *Predator sampling*

130 The uppermost centimeter of the sediment was collected from the mudflat at low tide,
131 with a large rectangular scoop. The sediment was sieved with 63 µm and 500 µm meshes, to
132 extract the meiofauna and macrofauna, respectively. *C. bocourti* and *F. subtilis* were collected
133 at high tide, with a 500 µm-mesh landing net, *G. oceanicus* specimens were collected by
134 hand, from their burrows, at low tide.

135 *Preparation of enriched preys*

136 The study site has two advantages for studies of this type: *i*) easy extraction of the
137 meiofauna and macrofauna by sieving, because the sediment consists primarily of particles of
138 less than 63 µm in diameter (Dupuy et al. 2015) and *ii*) ease of experimental manipulation of
139 the macrofaunal community, due to its low diversity, dominated by a species of small tanaids
140 (Jourde et al. 2017, Nguyen et al. 2018). Sediment was sampled as previously described. For
141 the accurate control of prey availability, sediment depleted of as many meiofauna and
142 macrofauna as possible was required. The sediment was therefore sieved, and the fraction
143 passing through a 63 µm mesh was allowed to settle overnight, after which the overlying
144 water was removed (Fig. 2). A 1 cm layer of this deposited sediment and 1 liter of local
145 seawater, filtered through a 50 µm-mesh sieve, were placed in each 200 cm² aquarium used
146 for feeding experiments (*n*=16 and control (*n*=1); Table 1). Enriched ¹³C glucose and ¹⁵N
147 ammonium were added separately to the sediment to label the bacteria and/or
148 microphytobenthos for the secondary labeling of their grazers: the meiofauna and

149 macrofauna. For the preparation of labeled meiofauna, the sediment was sieved and the
150 fraction passing through a 500 μm mesh was allowed to settle overnight. This fraction of
151 deposited sediment was mixed with $^{15}\text{NH}_4\text{Cl}$ (99% ^{15}N -enriched NH_4Cl ; Euriso-top) at a final
152 concentration of 4 g m^{-2} and incubated. For the preparation of labeled macrofauna, the
153 collected sediment was mixed directly with ^{13}C -glucose (99% ^{15}N -enriched glucose; Euriso-
154 top) at a final concentration of 2.5 g m^{-2} and incubated. Each type of sediment was *i*) placed in
155 a separate large plate, at a thickness of 0.5 cm, *ii*) incubated under local conditions of
156 temperature (29-33°C (Nguyen 2018)) and irradiance ($2000 \text{ kW m}^{-2} \text{ y}^{-1}$ (Elana 2017)), and *iii*)
157 regularly sprayed with freshwater to compensate for evaporation. After four days of
158 incubation, each type of sediment was independently sieved through separate meshes to
159 collect ^{15}N -enriched meiofauna (63 μm) and ^{13}C -enriched macrofauna (500 μm). Each of the
160 16 aquaria (200 cm^2) used for feeding experiments was filled with 1 L of seawater and a 1 cm
161 layer of fauna-free sediment, mixed with variable amounts of enriched meiofauna (^{15}N)
162 and/or macrofauna (^{13}C) and one type of target predator. Species community compositions of
163 enriched preys (meiofauna and macrofauna) were similar in all experiments. First, we
164 increased the abundance of one resource (meiofauna or macrofauna), whilst making the other
165 resource unavailable. Secondly both preys were available simultaneously, in different
166 proportions (table 1). One gram (dry weight) of prey corresponds to 4.6×10^6 meiofauna
167 specimens and 6.1×10^3 macrofauna specimens.

168 *Feeding experiments*

169 Predators were sampled as described above. All predators were kept for less than six
170 hours in a large tank containing oxygenated local seawater and sediment with associated
171 fauna before feeding experiments, to prevent starvation. We released 6 *C. bocourti*, 15 *F.*
172 *subtilis* or 15 *G. oceanicus* specimens into each of the experimental aquaria. In the control
173 aquarium, containing the highest abundance of each enriched prey, 15 specimens of *G.*
174 *oceanicus* were placed in a cage closed with a 63 μm mesh, to obtain control predators unable

175 to ingest enriched preys. All incubations with predators were performed in oxygenated
176 aquaria, for 2 hours, under local temperature and irradiance conditions. At the end of the
177 incubation period, the predators were collected in an aquarium fish net and immediately
178 frozen (-18°C).

179 *Isotope analyses and calculations*

180 For the meiofauna, each stable isotope sample consisted of 700 nematodes or 300
181 copepods picked at random, by hand, under a dissecting microscope, after extraction from
182 sediment by sieving through a 63 µm mesh and Ludox HS40 centrifugation, and pooled
183 (Jonge & Bouwman 1977). Macrofauna were extracted from sediment by sieving through a
184 500 µm mesh, and six tanaid specimens per sample were pooled. For each set of conditions,
185 three pools of two *C. bocourti*, five *F. subtilis* and five *G. oceanicus* specimens, selected at
186 random, were homogenized in an Ultra-Turrax blender, frozen and freeze-dried.

187 The nitrogen and carbon isotopic compositions of the various organisms sampled (preys
188 and predators) were determined by EA-IRMS (Isoprime, Micromass, UK). The nitrogen and
189 carbon isotope ratios are expressed in the delta notation $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, as follows: $\delta X =$
190 $[(R_{\text{Reference}}/ R_{\text{Sample}}) - 1] \times 1000$, where $X = \delta^{15}\text{N}$ or $\delta^{13}\text{C}$ and R is the ratio $^{15}\text{N}: ^{14}\text{N}$ or $^{13}\text{C}: ^{12}\text{C}$
191 in the sample and in the reference material. Results are expressed relative to atmospheric
192 nitrogen for N and to Vienna Pee Dee Belemnite (VPDB) for C, and are expressed in units of
193 ‰ ± standard deviation (SD).

194 An excess of ^{15}N , above background levels (natural ^{15}N of predator without enrichment)
195 was considered to constitute ^{15}N enrichment, and is expressed in terms of specific uptake (I). I
196 was calculated as the product of excess ^{15}N (E) and the previously measured N biomass per
197 predator (Table 2). I was converted into meiofaunal or macrofaunal carbon ingested, with the
198 C/N ratio of each prey. E was defined as the difference between the background ($F_{\text{background}}$)
199 and sample (F_{sample}) ^{15}N fractions: $E = F_{\text{sample}} - F_{\text{background}}$, with $F = ^{15}\text{N}/(^{15}\text{N}+^{14}\text{N}) = R / (R +$
200 $2)$ and $R =$ the nitrogen isotope ratio. For $F_{\text{background}}$, we used values measured with predators,

201 without enrichment. R was derived from the measured $\delta^{15}\text{N}$ values: $R = [(\delta^{15}\text{N}/ 1000) + 1] \times$
202 R_{airN_2} . Prey intake was calculated as $[I \times (\text{C/N ratio of enriched prey}) / (F_{\text{enriched prey}} \times$
203 incubation time)] (Pascal et al., 2008).

204 The incorporation of ^{13}C was calculated in a similar manner, with $F = ^{13}\text{C} / (^{13}\text{C} + ^{12}\text{C}) =$
205 $R / (R+1)$, R_{airN_2} replaced by $R_{\text{VPDB}} = 0.0112372$ and $\text{Uptake} = I / (F_{\text{enriched predator}} \times \text{incubation}$
206 time)

207 *Data analyses*

208 One-way analysis of variance (ANOVA) with Tukey post hoc tests was used to analyze
209 the differences between ingestion rates. The normality of the data was first checked in a
210 Shapiro-Wilk test, and homoscedasticity was checked with a Bartlett test. The nonparametric
211 Kruskal-Wallis test was used to assess the differences in isotopic composition ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$)
212 of preys and predators. The selectivity of prey ingestion was evaluated by fitting a linear
213 model to the data for the ratio of the biomasses of macrofauna to meiofauna ingested, with a
214 95% confidence interval. All statistical analyses were performed with R. Values are presented
215 as means \pm standard deviation (SD) unless otherwise specified.

216

217

218 Results

219 The individual dry weight, carbon and nitrogen contents of each type of prey and
220 predator are presented in table 2. Tanaids had a mean individual dry weight 750 times higher
221 than that of nematodes and 300 times higher than that of copepods. The natural isotopic
222 compositions of preys and predators are presented in figure 3. Before enrichment, $\delta^{15}\text{N}$ and
223 $\delta^{13}\text{C}$ levels were similar in the meiofauna and macrofauna (Tanaidacea) (Kruskall-Wallis, $p >$
224 0.05). After enrichment, the $\delta^{15}\text{N}$ levels of the nematodes and copepods used during feeding
225 experiments were not significantly different (Kruskall-Wallis, $p > 0.05$), with respective
226 enrichment values (δ after enrichment minus δ at T0) of $261.0 \pm 44.5 \text{ ‰}$ ($n = 6$ samples of
227 700 specimens) and $268.0 \pm 24.9 \text{ ‰}$ ($n = 6$ samples of 300 specimens). Tanaids had a mean
228 $\delta^{13}\text{C}$ content of $2789.5 \pm 65.6 \text{ ‰}$ ($n = 3$ samples of 6 specimens each).

229 *C. bocourti* was the predator with the lowest individual weight, followed by *F. subtilis*
230 and *G. oceanicus* (Tab. 2). *C. bocourti* had a mean width of $1.3 \text{ cm} \pm 0.4$ ($n = 42$) whereas *F.*
231 *subtilis* and *G. oceanicus* were $4.4 \text{ cm} \pm 0.9$ ($n = 210$) and $5.0 \text{ cm} \pm 2.0$ ($n = 180$) long,
232 respectively. The natural isotopic compositions of all predators (Fig. 3) were similar for $\delta^{13}\text{C}$
233 (Kruskall-Wallis, $p > 0.05$), whereas *F. subtilis* and *G. oceanicus* had significantly different
234 $\delta^{15}\text{N}$ levels (Kruskall-Wallis, $p < 0.01$).

235 *G. oceanicus* caged in the aquarium with the highest abundances of each of the enriched
236 preys had significantly higher ^{13}C and ^{15}N levels than the natural isotopic composition
237 samples (Kruskall-Wallis, $p < 0.05$), by 1.5 ± 0.5 and $2.1 \pm 0.7 \text{ ‰}$, respectively ($n=3$). These
238 enrichment levels correspond to 2.7% for ^{13}C and 7.1% for ^{15}N relative to free specimens of
239 *G. oceanicus* able to ingest enriched preys in similar incubation conditions.

240 Meiofauna ingestion by *C. bocourti* was not significantly affected by meiofauna
241 abundance, and the values obtained ranged from 11.8 to 18.9 $\text{mgC}_{\text{prey}} \text{ gC}_{\text{predator}}^{-1} \text{ h}^{-1}$, which is

242 equivalent to 3584 to 5766 nematode ind⁻¹ h⁻¹ (Fig. 4). By contrast, the ingestion of
243 meiofauna by *F. subtilis* and *G. oceanicus* increased with meiofauna abundance and was
244 significantly higher at the highest meiofauna abundance tested (Fig. 4), at reaching 12.7 ± 1.0
245 $\text{mgC}_{\text{prey}} \text{gC}_{\text{predator}}^{-1} \text{h}^{-1}$ (6342 ± 516 nematode ind⁻¹ h⁻¹) and 4.6 ± 0.5 $\text{mgC}_{\text{prey}} \text{gC}_{\text{predator}}^{-1} \text{h}^{-1}$
246 (3120 ± 363 nematodes ind⁻¹ h⁻¹), respectively.

247 The ingestion of macrofauna by *C. bocourti* was not significantly affected by prey
248 abundance and ranged from 1.2 to 4.5 $\text{mgC}_{\text{prey}} \text{gC}_{\text{predator}}^{-1} \text{h}^{-1}$, equivalent to 2.0 to 2.9 tanaid
249 ind⁻¹ h⁻¹ (Fig. 5). By contrast, the ingestion of macrofauna by *F. subtilis* and *G. oceanicus*
250 increased significantly with macrofauna abundance, reaching 5.6 ± 0.2 $\text{mgC}_{\text{prey}} \text{gC}_{\text{predator}}^{-1} \text{h}^{-1}$
251 (5.7 ± 0.2 tanaid ind⁻¹ h⁻¹) and 3.8 ± 0.4 $\text{mgC}_{\text{prey}} \text{gC}_{\text{predator}}^{-1} \text{h}^{-1}$ (5.4 ± 0.5 tanaid ind⁻¹ h⁻¹),
252 respectively (Fig. 5).

253 The ability of predators to ingest their food in a selective manner was evaluated by
254 calculating the differences between the ratios of macrofauna to meiofauna ingested and ratios
255 of macrofauna to meiofauna available in the environment (Fig. 6). If these two ratios were
256 similar, it was concluded that there was no selection, whereas differences between these ratios
257 were interpreted as indicating the preferential ingestion of meiofauna or macrofauna. For each
258 predator, we fitted a linear model with a 95% confidence interval to the data (Fig. 6). For *C.*
259 *bocourti*, this confidence interval included all theoretical values for non-selective ingestion,
260 reflecting an absence of selection in feeding behavior. For *F. subtilis* and *G. oceanicus*, the
261 lowest values of the 95% confidence interval were always higher than the theoretical values,
262 implying a preferential ingestion of macrofauna over meiofauna by both these predator
263 species.

264

Discussion

267 The aim of this study is improve our understanding of benthic marine food webs by
268 the quantification of ingestion of meiofauna and macrofauna by higher trophic levels in a
269 tropical intertidal mudflat on the coast of Amazonia

Meiofauna predation

271 The effect of top-down control on the meiofauna is unclear. Several studies have
272 suggested that predation on the meiofauna is negligible due to the ability of the meiofauna to
273 disperse (Giere 2009) and fast turnover times, whereas predators are comparatively rare
274 (Gibbons 1988, Shaw & Jenkins 1992, Coull 1999). On the contrary, other studies have
275 concluded that predation affects meiofauna abundance (Danovaro et al. 2007, Fleeger et al.
276 2008) and community composition (Li et al. 1996, O'Gorman et al. 2008). These
277 discrepancies may reflect biases associated with the different methods used to evaluate
278 trophic fluxes (see below in the part *Methodological considerations*). Differences in the
279 conclusions drawn may also reflect differences in trophic links between study sites.

280 Estimations of the top-down effect of predators require knowledge of their abundance.
281 In the study area, the abundances of *C. bocourti* and *F. subtilis* have unfortunately never been
282 evaluated. However, abundances of the high fin goby *G. oceanicus* have been estimated from
283 measurements in benthic cores, revealing a patchy distribution, with densities reaching 50 ind.
284 m⁻² (Jourde et al. 2017). For evaluation of the maximum top-down effect, daily ingestion was
285 calculated, taking into account the highest abundance of fish and lowest abundance of
286 meiofauna (Dupuy et al. 2015), and the highest ingestion rate measured in this study. This
287 area of the mudflat is submerged and exposed to fish predation for only six hours per day (24
288 h). This maximum daily ingestion would therefore reach 56% of the standing stock of
289 meiofauna in Awala. However, this assumption must be viewed with caution, because *i*)

290 grazers, such as shrimps and crabs, were not considered, as their natural abundances remain
291 unknown and *ii*) gobies have a patchy distribution and are not realistically sampled by benthic
292 cores. However, our results nevertheless suggest that the meiofauna community could be
293 regulated by predation, at least during the limited periods during which predators are
294 abundant as previously suggested by other studies (Danovaro et al. 2007, Fleeger et al. 2008).

295 *Meiofauna predators*

296 Body size is an important determinant of many physiological processes, and maximal
297 ingestion rate is generally inversely correlated with body size (Peters, 1983). This assumption
298 was confirmed in this study, as maximum rates of meiofauna ingestion decreased with
299 increasing predator weight, from crab to fish. In shrimp, the maximum daily meiofauna
300 ingestion rate corresponded to 30% of the predator's body weight. This rate is higher than that
301 estimated for the shrimp *Crangon crangon*, which eats 8-16% (del Norte-Campos &
302 Temming 1994, Feller 2006) or 10-12% (Pihl & Rosenberg 1984) of its own body weight
303 daily. This higher level of ingestion activity may be due to different evaluation techniques or
304 to the higher temperature in the tropical environment of *F. subtilis* than in the habitat of *C.*
305 *crangon*.

306 Theoretically, food uptake by a consumer should increase with food abundance.
307 However, beyond a certain threshold prey density, uptake rates remain constant, according to
308 Holling's prey-dependent type II functional response (Holling 1959), as reported for shrimp
309 (Gregg & Fleeger 1998). The threshold value was not reached here for *F. subtilis* and *G.*
310 *oceanicus*. As the natural abundance of the meiofauna (Dupuy et al. 2015) and macrofauna
311 (Nguyen et al. 2018) can exceed the abundances tested here, ingestion rates could be higher
312 than the measured values, for both preys.

313 The meiofauna constitutes a potentially high-quality food source, due to the high
314 levels of unsaturated fatty acids in these animals (Fleeger 2007, Leduc et al. 2009, De Troch
315 et al. 2012, Braeckman et al. 2015). The meiofauna is strongly associated with sediment

316 particles. When consuming the meiofauna, predators can *i*) ingest bulk sediment, which
317 entails a high cost in terms of the rejection of non-digestible material or *ii*) selectively ingest
318 the meiofauna, which entails a high cost in food selection. In this study, the three predators
319 have different feeding mechanisms for selecting their food. Juvenile crabs of the genus
320 *Callinectes* selectively ingest microbes rather than bulk detritus (Fantle et al. 1999). Penaid
321 shrimps feed selectively, with their chelate pereopods grasping and transporting acceptable
322 morsels of food to the mouth (Hindley & Alexander 1978). Gobies graze more or less
323 indiscriminately on sediment, in addition to predating on larger preys on sight (Fitzhugh &
324 Fleeger 1985, Hamerlynck & Cattrijsse 1994). The predators studied have different weight
325 ranges, with the crab *C. bocourti* smaller than the goby *G. oceanicus* by a factor of 1.6.
326 According to optimal foraging theory, that the greatest rewards per unit effort are obtained by
327 predating on the largest graspable prey items (Krebs 1978). Development shifts in diet, from
328 smaller meiofauna to larger macrofauna, have been reported for the crab *Carcinus maenas*
329 (Reise 1978, Scherer & Reise 1981). The shrimp *Crangon crangon* displays a similar dietary
330 shift when its total body length exceeds 20 mm (Pihl & Rosenberg 1984, Gee 1987).
331 Similarly, in our study, the shrimp *F. subtilis*, with a mean length of 44 mm, also
332 preferentially ingested macrofauna. For fish, the switch from meiofauna to macrofauna
333 appears to occur at a threshold total length of 3-4 cm (Gee 1989), as previously reported for
334 several goby species from the Adriatic Sea (Kovačić & la Mesa 2008), Baltic Sea (Aarnio &
335 Bonsdorff 1993), North Sea (Schückel et al. 2013) and Atlantic Ocean (D'Aguillo et al. 2014).
336 The results reported here are consistent with this assumption, as gobies of 5 cm or more in
337 length preferentially ingested macrofauna.

338 The experiments reported here suggest an important role of the macrofauna and
339 meiofauna in the diet of *G. oceanicus*, but natural isotopic composition revealed limited $\delta^{15}\text{N}$
340 enrichment between the preys and the goby, suggesting that other food items not considered
341 here, such as detritus or microphytobenthos, might play a role in the diet of these fish. Despite

342 preferential macrofauna ingestion, large *G. oceanicus* specimens continued to ingest
343 meiofauna, unlike other goby species of similar size (de Morais & Bodiou 1984). Gobies can
344 be opportunist predators with a diet reflecting variations in the food available (D'Aguillo et al.
345 2014). In the Awala mudflat, the abundance of tanaids varies by a factor of 10^3 , depending on
346 the season (Nguyen et al. 2018). The meiofauna may, therefore, play an important role in the
347 diet of the predator in conditions of lower macrofauna availability. Such seasonal variations in
348 the trophic role of the meiofauna have already been suggested for fish (Schückel et al. 2013).
349 Gobies switch to the ingestion of smaller items when in competition for food resources or if
350 the availability of large preys decreases (Henry & Jenkins 1995). Fluxes from the meiofauna
351 to higher trophic levels appeared complexes and likely variable along the year suggesting that
352 a temporal survey would be useful to clarify the trophic role of meiofauna. Despite those
353 potential variations, the present study provides quantitative fluxes embeddable in ecological
354 models of benthic food webs.

355 *Methodological considerations*

356 The potential of stable isotopes for studies of this kind depends heavily on the
357 difference in isotopic composition between the food sources to be distinguished. In this study,
358 the meiofaunal community and tanaids had similar isotopic compositions, rendering
359 interpretation of the patterns obtained with natural isotopes difficult and necessitating the use
360 of enrichment experiments.

361 Predator abundance in the study area had been determined only for *G. oceanicus*
362 (Jourde et al. 2017). For the purpose of feeding, the predators studied perform tidal
363 migrations, following the rising tide by swimming or walking over the sediment on the
364 bottom (Gibson, 2003). They can reach very high densities during this migration, and the
365 shrimp (*F. subtilis*) and crab (*C. bocourti*) species studied were chosen on the basis of their
366 high abundance and availability at the time of the experiments. Incubations were performed

367 with high abundances of predators, potentially affecting predator interactions and feeding
368 behavior, resulting in a possible underestimation of ingestion rates.

369 Copepods have a caloric value 35% higher than those of most members of the
370 meiofauna (Gee 1989). Copepods generally dwell closer to the sediment surface than
371 nematodes, and display emergence behavior relative to the water column (Giere 2009). This
372 differential distribution would facilitate predation on copepods by shrimps (Pihl & Rosenberg
373 1984, Gee 1987) and fishes (Coull 1990, McCall & Fleeger 1995). However, it was not
374 possible to differentiate between copepods and nematodes in this study, because these two
375 groups were labeled similarly. The availability of sediment in the aquarium constituted
376 realistic incubation conditions, because the sediment serves as a refuge, reducing the risk of
377 predation for meiofauna and macrofauna (Arnold 1984, Lipcius & Hines 1986, Gregg &
378 Fleeger 1998). Feeding experiments were run over a short period of two hours and did not,
379 therefore, necessarily yield results representative of feeding behavior over longer time scales,
380 as the feeding activity of the predators studied is known to fluctuate over the day (Hagerman
381 & Østrup 1980, Ryer 1987, Kanou et al. 2005). However, short incubation times were used
382 here, to limit *i*) label exchange between meiofaunal and macrofaunal preys and *ii*) the
383 excretion of ingested label by predators. This excretion bias would be limited, as feeding
384 experiments lasted two hours and gut retention time would not exceed this duration for
385 Portunidae crabs (Serrano 2012) or Gobiidae fish (Kanou et al. 2005). However, this bias
386 could be larger for Penaidae shrimps, which have gut retention times of between one and four
387 hours (Hoyt et al. 2000).

388 The isotopic compositions of predators changed slightly following their transfer to a
389 mesh cage in an aquarium containing enriched preys. This finding suggests that any bias due
390 to the inefficient removal of unincorporated label by rinsing would be limited, and that the
391 enrichments observed with free predators were due principally to trophic processes. The mud
392 sediment of French Guiana is dominated by silt (70-85%) and clay (10-15%), and mean

393 particle size is below 63 μm (Dupuy et al. 2015). The fauna thus represents a large portion of
394 the material remaining on the 63 μm mesh after sieving. However, a small fraction of detritus
395 would also have been present and the associated bacteria would have taken up glucose- ^{13}C or
396 ammonium- ^{15}N during the enrichment process. The ingestion of this enriched detritus by
397 predators would then lead to an overestimation of the ingestion of meiofauna and macrofauna.
398 This bias should be borne in mind when interpreting the results. Despite this shortcoming, the
399 method used here has several advantages: *i*) the measurement of ingestion fluxes, *ii*) dual
400 labeling of preys, making it possible to evaluate feeding preferences and, *iii*) ease of use, with
401 incubations possible even at remote sites with limited technical resources.

402 **Conclusion**

403 The use of stable isotope-enriched meiofauna and macrofauna in feeding experiments
404 is an appropriate method for evaluating preferential ingestion. In these experiments, feeding
405 rates increasing with the availability of meiofauna and macrofauna food for all predators other
406 than the crabs, suggesting that rates of ingestion of both preys may actually be higher than
407 measured. All three predators studied ingested meiofauna, but the contribution of the
408 meiofauna to the diet decreased with increasing predator size (*C. bocourti* > *F. subtilis* > *G.*
409 *oceanicus*), whereas no such relationship to size was observed for the macrofauna. Larger
410 predators preferentially ingested macrofauna to a greater extent than smaller predators, in
411 accordance with optimal foraging theory. For larger predators, the meiofauna is an important
412 component of the diet only at early stages of development or in the absence of large food
413 items.

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Figure and table

417 Table 1. Measured prey abundances (dry weights of meiofauna and macrofauna in g m^{-2}) in

418 dual-prey feeding experiments in 16 independent aquariums. Each letter refers to a predator.

419 A: *C. bocourti* ($n = 4$), B: *F. subtilis* ($n = 6$) and C: *G. oceanicus* ($n = 6$)

		Meiofauna (g m^{-2})		
		3.7	9.1	22
	0.9		A, B, C	
	1.3	A, B	A, B	
Macrofauna (g m^{-2})	1.8	C	B, C	C
	3.7		A, B, C	
	7.3		B, C	

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423 Table 2. Dry weight, carbon and nitrogen weights per specimen of prey (nematode, copepod,
424 Tanaidacea) or predator (*C. bocourti*, *F. subtilis*, *G. oceanicus*) (mean \pm SD, *n*: number of
425 samples and number of specimens per sample used to evaluate these weights).

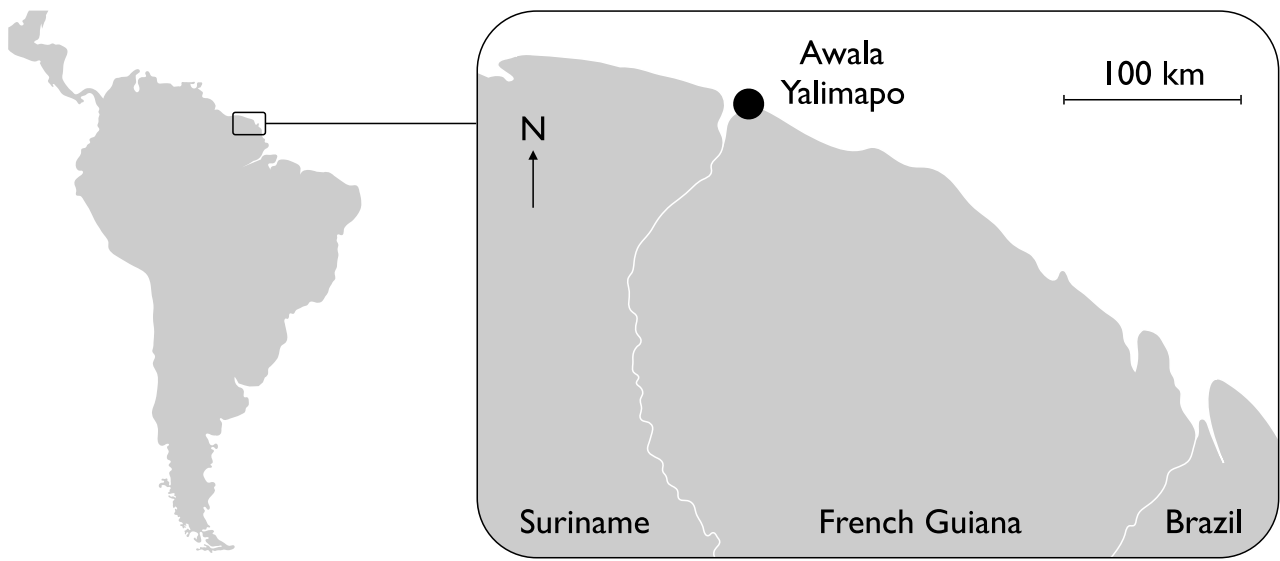
	Individual dry weight	Individual carbon weight	Individual nitrogen weight	n	Specimens per sample
Nematoda	217 \pm 61 ng	94 \pm 29 ng	23 \pm 8 ng	6	700
Copepoda	534 \pm 92 ng	209 \pm 31 ng	47 \pm 7 ng	6	300
Tanaidacea	162 \pm 45 μ g	46 \pm 11 μ g	10 \pm 2 μ g	6	6
<i>C. bocourti</i>	95 \pm 36 mg	29 \pm 13 mg	6 \pm 3 mg	45	2
<i>F. subtilis</i>	122 \pm 41 mg	47 \pm 18 mg	13 \pm 5 mg	57	5
<i>G. oceanicus</i>	156 \pm 92 mg	65 \pm 41 mg	18 \pm 11 mg	54	5

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431 Figure 1. Location of the Awala-Yalimapo study site in French Guiana

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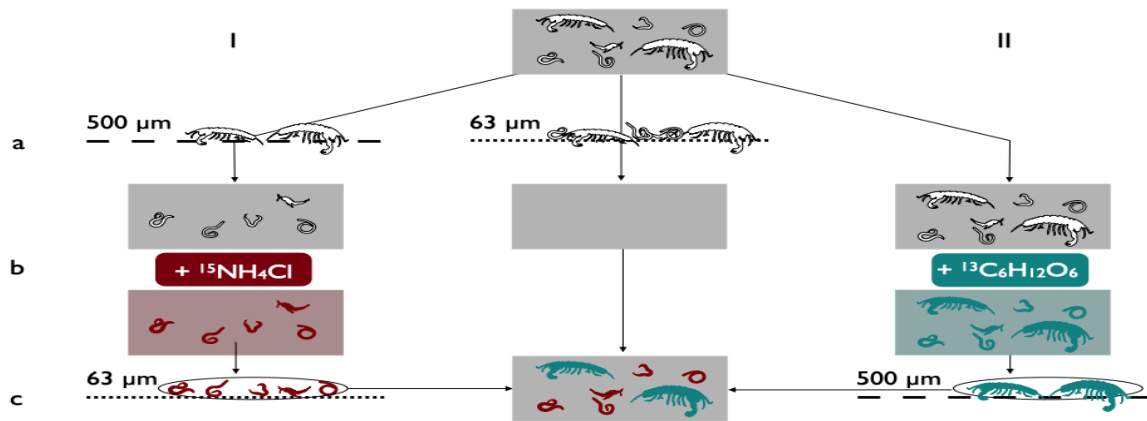


Figure 2

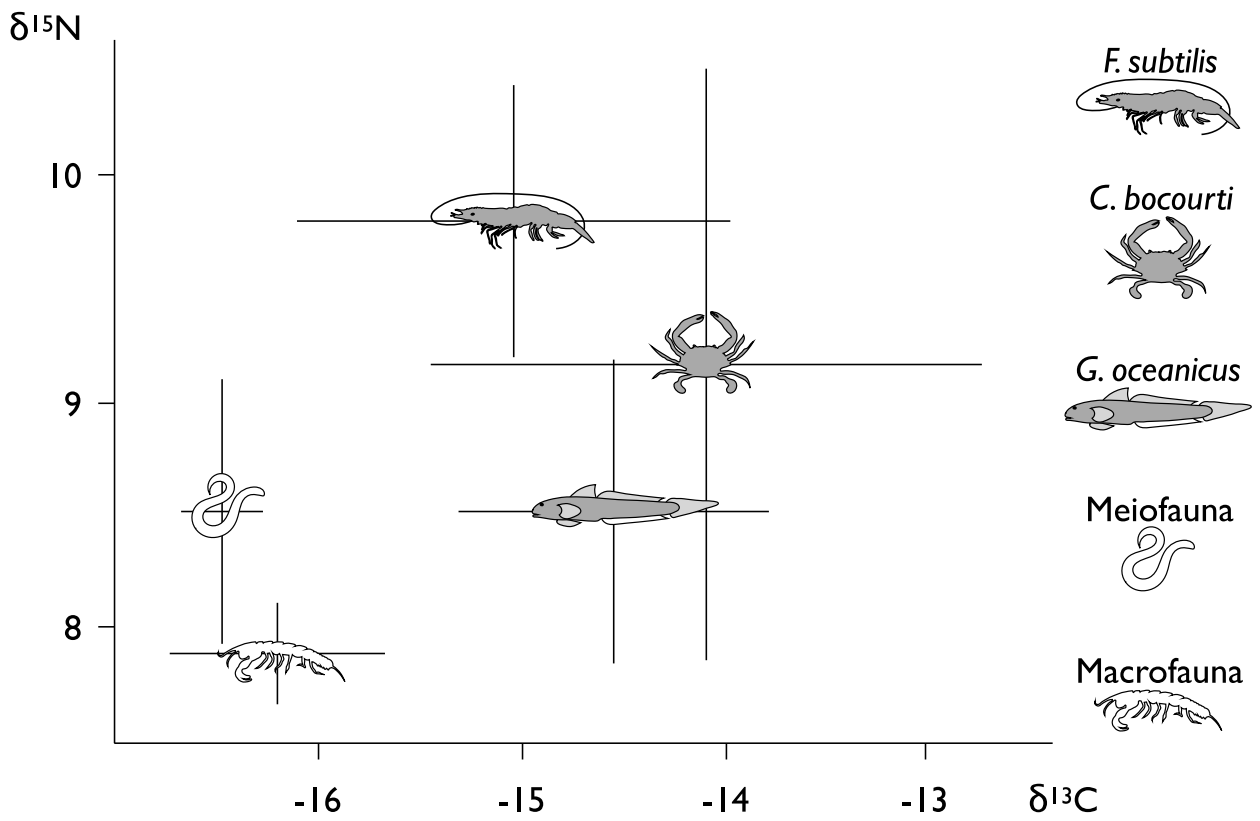
435

436 Figure 2. Diagram of the protocol for enrichment of the meiofauna (I) and macrofauna (II):
437 the sediment was a) passed through a 500 µm mesh for I and left untreated for II, b) mixed
438 with $^{15}\text{NH}_4\text{Cl}$ for I and ^{13}C -glucose for II and incubated for four days, c) passed through
439 meshes of 63 µm for I and 500 µm for II, to collect the ^{15}N -enriched meiofauna and ^{13}C -
440 enriched macrofauna, respectively. The enriched fauna was mixed with non-enriched
441 sediment devoid of fauna obtained with a 63 µm-mesh sieve

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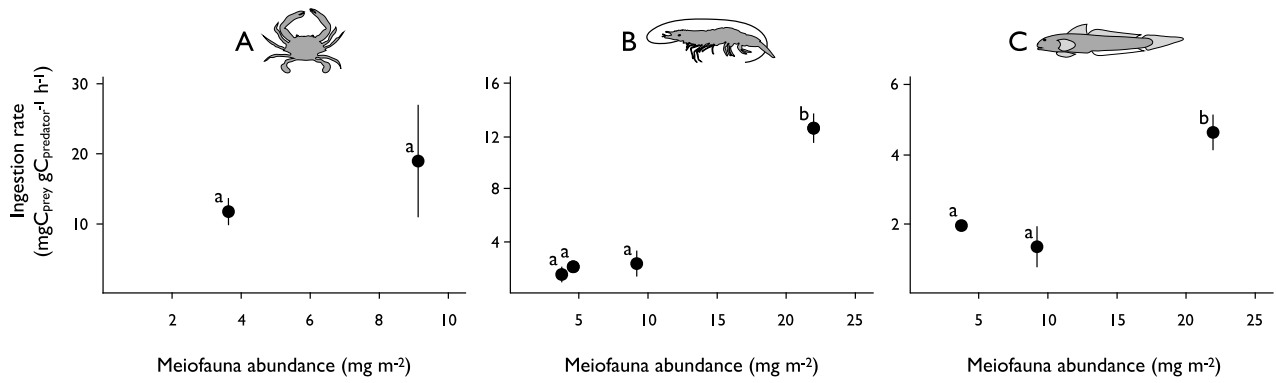


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446 Figure 3. Natural isotopic composition ($\delta^{15}\text{N}$ as a function of $\delta^{13}\text{C}$, \pm SD, $n= 6$) of preys

447 (meiofauna and macrofauna) and predators (*C. bocourti*, *F. subtilis* and *G. oceanicus*)

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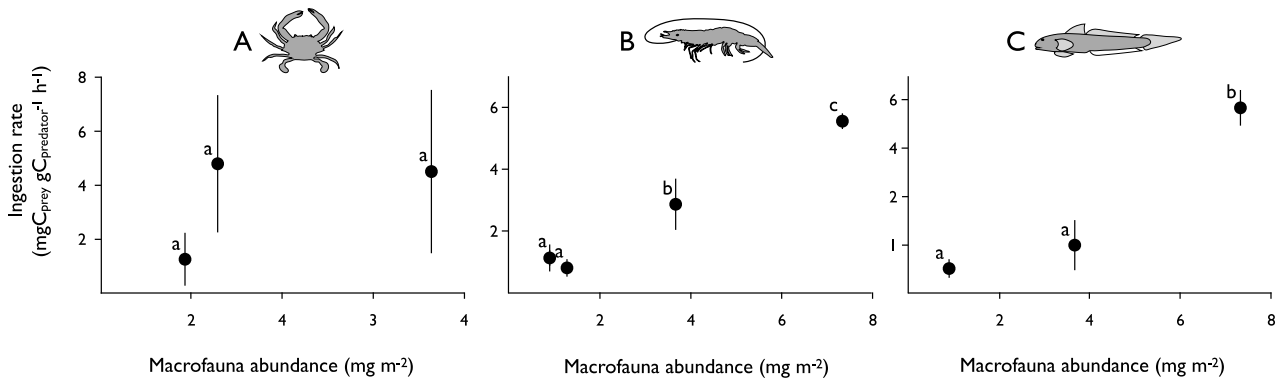
451 Figure 4. Ingestion of meiofauna ($\text{mgC}_{\text{prey}} \text{gC}_{\text{predator}}^{-1} \text{h}^{-1}$; $\pm \text{SD}$, $n=3$) by *C. bocourti* (A), *F.*

452 *subtilis* (B) and *G. oceanicus* (C) as a function of dry meiofauna biomass (mg m^{-2}). Different

453 lower-case letters indicate significant differences between the tested abundances (ANOVA,

454 Tukey test, $p < 0.005$)

455



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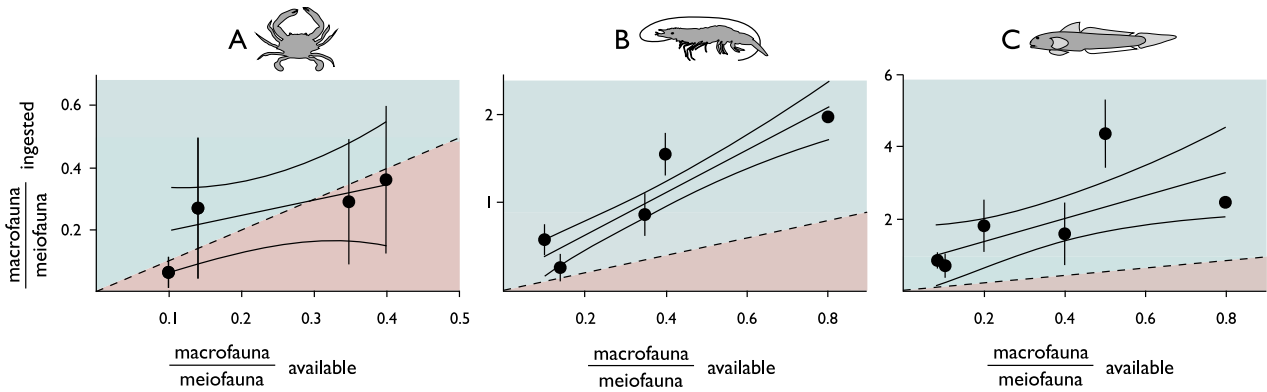
458 Figure 5. Ingestion of macrofauna ($\text{mgC}_{\text{prey}} \text{mgC}_{\text{predator}}^{-1} \text{h}^{-1}$; \pm SD, $n=3$) by *C. bocourti* (A),

459 *F. subtilis* (B) and *G. oceanicus* (C) as a function of dry macrofauna biomass (mg m^{-2}).

460 Different lower-case letters indicate significant differences between the tested abundances

461 (ANOVA, Tukey test, $p < 0.005$).

462



464
 465 Figure 6. Ratio of the biomasses of macrofauna and meiofauna ingested plotted against the
 466 ratio of biomasses of macrofauna and meiofauna available (\pm SD, $n=3$), for *C. bocourti* (A),
 467 *F. subtilis* (B) and *G. oceanicus* (C). The dotted line corresponds to a theoretical absence of
 468 selection. Points above (blue part) or below (red part) the dotted line indicate the selective
 469 ingestion of macrofauna and meiofauna, respectively. The linear models fitted to the data are
 470 presented as solid lines with 95% confidence intervals

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Compliance with ethical standards

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Conflict of interest: The authors declare that they have no conflict of interest

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Human and animal rights statement: This article does not contain any studies with human participants performed by any of the authors. All applicable international, national and/or institutional guidelines for the care and use of animals were followed. All procedures performed in the study involving animals were in accordance with the ethical standards of French law regarding maintaining animal welfare in research.

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