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Influence of environment factors on bacterial ingestion rate of the deposit-feeder *Hydrobia ulvae* and comparison with meiofauna

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26 *tepida*. *Hydrobia ulvae* ingested bacteria at a higher rate than smaller meiofaunal grazers and
27 seemed to have a lower ability to selectively ingest diatoms than meiofaunal grazers.

28 **Key-Words**

29 Deposit-feeding, *Hydrobia ulvae*, gastropod, bacteria, grazing, environmental factors,
30 *Ammonia tepida*, nematodes, mudflat

31 **Introduction**

32 In pelagic environments, bacteria are heavily grazed and consequently play a major role in
33 food webs (Azam et al., 1983). In the benthic environment, bacteria are generally 1000 times
34 more abundant than in pelagic systems, reaching abundances of about 10^9 cells cm^3 (Schmidt
35 et al., 1998). However, microbial food web research in sediment is in its infancy and the
36 trophic significance of benthic bacteria remains elusive (Review in Kemp, 1986).

37 The deposit-feeder *Hydrobia ulvae* is one of the most abundant species of macrofauna
38 inhabiting intertidal mudflats in Western Europe (Bachelet and Yacine-Kassab, 1987; Barnes,
39 1990; Sola, 1996). Deposit feeders typically process at least one body weight of sediment
40 daily (Lopez and Levinton, 1987). This sediment includes highly digestible and nutritious
41 microphytobenthos and bacteria, less digestible plant debris and completely indigestible
42 refractory detritus (Rice and Rhoads, 1989). Diatoms have been found to be a major source of
43 nutrition for *H. ulvae* (Fenchel et al., 1975; Jensen and Siegismund, 1980; Lopez and Cheng,
44 1983a; Bianchi and Levinton, 1984; Haubois et al., 2005a). However bacteria have also been
45 found as food for *Hydrobia* species (Cammen, 1980; Jensen and Siegismund, 1980; Bianchi
46 and Levinton, 1981; Levinton and Bianchi, 1981). Due to high abundances of *H. ulvae* in
47 intertidal mudflats, carbon flow from bacteria to snails may be a significant pathway in this
48 type of environment.

49 The objective of the present study was to quantify the bacterial ingestion rate of *H. ulvae*
50 and to investigate how this rate varies with abiotic (temperature, salinity and luminosity) and

51 biotic (bacterial and algal abundance) factors. Intertidal mudflats are subject to large and
52 quick changes in many environmental factors at short time scales (circadian and tidal cycles)
53 (Guarini et al., 1997) and these variations may significantly influence snail feeding behaviour.
54 Bacterivory of *H. ulvae* was then compared to that of other grazers of different sizes and
55 feeding modes, the foraminifera *Ammonia tepida* and a nematode community from surficial
56 sediment of an intertidal mudflat (Brouage-Marennes Oléron-France). Bacterial ingestion of
57 both grazers have been previously described (Pascal et al., 2008b; Pascal et al., In press). All
58 grazing experiments were performed simultaneously in similar conditions using stable isotope
59 enriched prey (¹³C enriched algae and ¹⁵N enriched bacteria).

60 **Experimental procedure**

61 *Study site*

62 The Brouage intertidal mudflat is located in the eastern part of the Marennes-Oléron Bay
63 (Atlantic coast of France). Meteorological conditions exhibit a strong seasonality typical of a
64 temperate climate. Range of temperature and salinity in emerged sediments are more extreme
65 during summer tidal cycles (Guarini et al., 1997). Minimum and maximum mud temperatures
66 are 5°C and 34°C respectively. The maximum daily range of mud temperature due to
67 emersion and immersion cycle reaches 18°C (Guarini et al., 1997). Salinity of overlaying
68 water is controlled by the Charente River freshwater input, ranging from 25 to 35 over the
69 year (Héral et al., 1982). Salinity of the upper layers of sediment may also decrease with
70 rainfall. The sediment surface irradiance shifts from dark during submersion and night
71 emersions to high levels of incident light during daytime emersions. This irradiance can reach
72 2000 μM of photons $\text{m}^{-2} \text{s}^{-1}$ (Underwood and Kromkamp, 2000). Details of numerous benthic
73 organisms and processes are available concerning this intertidal zone (gathered in Leguerrier
74 et al., 2003; Leguerrier et al., 2004; Degré et al., 2006).

75 *Preparation of ¹⁵N enriched bacteria*

76 Superficial sediment (1 cm depth) was collected on the Brouage mudflat (45,55,074 N;
77 1,06,086 W). One cm³ of the collected sediment was added to 20 cm³ of bacterial liquid
78 culture medium and kept in darkness for 24 hours at 13°C. The composition of this culture
79 medium was previously described in Pascal et al. (2008a). This primary culture was then
80 subcultured for 24 hours under the same conditions to get approximately 2×10^9 cells cm³.
81 Finally, bacteria were collected in 0.2 µm filtered seawater after 3 centrifugations (3500 g, 10
82 mn, 20°C), frozen in liquid nitrogen and kept frozen at -80°C until grazing experiments.

83 *Preparation of ¹³C enriched algae*

84 An axenic clone of the diatom *Navicula phyllepta* (CCY 9804, Netherlands Institute of
85 Ecology NIOO-KNAW, Yerseke, The Netherlands), the most abundant diatom species in the
86 study area (Haubois et al., 2005b), was cultured in medium described by Antia and Cheng
87 (1970) and containing NaH¹³CO₃ (4 mM). Diatoms were concentrated by centrifugation
88 (1500 g, 10 mn, 20 °C), washed three times to remove the ¹³C-bicarbonate, and freeze-dried.

89 *Quantification of bacteria and algae abundance*

90 In order to determine the ratio between enriched and non-enriched preys in microcosms,
91 abundances of bacteria and algae were assessed. To separate bacteria from sediment particles,
92 incubation in pyrophosphate (0.01M for at least 30 min) and sonication (60 W) were
93 performed. Bacteria from both sediment and culture were labelled using 4.6-diamidino-2-
94 phenylindole dihydrochloride (DAPI) (2500 µg l⁻¹), filtered onto 0.2 µm Nucleopore black
95 filter (Porter and Feig, 1980) and then counted by microscopy. We verified the absence of
96 ciliates and flagellates in the bacterial culture during this microscope observation step. The
97 abundance of diatoms in the sediment was assessed using Chl *a* as a proxy, measured using
98 fluorometry (Lorenzen, 1966).

99 *Grazing experiments*

100 The top centimeter of sediment was collected during ebb tide from the same study area at
101 midday on March 13, 2006. It was sieved on 500 μm , 200 μm and 50 μm in order to
102 concentrate respectively *H. ulvae*, *A. tepida* and nematodes. Before sieving, snails were
103 placed on natural sediment and kept for 24 h at 20°C in the dark. Time between sieving and
104 the start of the grazing experiment never exceeded two hours in order to avoid starvation bias
105 in feeding behavior (Calow, 1975). Seventeen handpicked specimens of *H. ulvae* were placed
106 in polypropylene Petri dishes ($\varnothing = 9$ cm). This density was chosen in order to avoid a density-
107 dependence effect on the individual ingestion due to space limitation (Blanchard et al., 2000).
108 A fraction of the sediment passing through the 50 μm mesh was mixed with the ^{15}N enriched
109 bacteria. This slurry contained 10.5×10^8 bacteria cm^3 , ^{15}N enriched bacteria being twice as
110 abundant as non-enriched ones. Four cm^3 of this slurry were put into each microcosm. Each
111 experiment was carried out in triplicate, along with at least one control. Control samples were
112 frozen (-80°C) in order to kill any grazers.

113 The calculation of bacterial ingestion rate relies on the assumption that enriched preys
114 accumulate in snail's gut at a constant rate, and that no egestion of labelled materials occurs
115 during incubation time. A kinetic study was run for 1 to 12 hours including the 2 hour run that
116 was used for all other experiments. Incubations were made under the following standardized
117 conditions that were close to the mean values recorded on the study site: temperature (20°C),
118 salinity (31), luminosity (darkness), bacterial abundance (10.5×10^8 bacterial cells cm^3) and
119 algal abundance ($15 \mu\text{gChla g dry sediment}^{-1}$). For each experiment to determine the effects
120 of environmental factors, only one incubation factor was modified so as to determine its effect
121 on *H. ulvae*'s grazing activity. After the sieving step, snails were transferred without
122 acclimation into different microcosms to simulate short-term changes of environmental
123 factors. To test the effect of temperature, the snails were placed at 5°C, 15°C, 30°C and 40°C:
124 these temperatures are in the range of those measured in the study area (Guarini et al., 1997).

125 The effect of salinity was investigated by placing *Hydrobia* in microcosms with a salinity of
126 18. To decrease salinity, cultured bacteria were rinsed with 0.2 μm filtered-sea-water diluted
127 with 0.2 μm filtered distilled water. Such decrease in salinity can occur in field conditions
128 when sediment is exposed to heavy rainfall. The light effect was tested with a light intensity
129 of 83 μM of photons $\text{m}^{-2} \text{s}^{-1}$. Bacterial abundance was modified adding various quantities of
130 bacteria enriched in ^{15}N . Bacterial abundances (total enriched and non-enriched) tested were
131 4, 7 and 17 cells $\text{cm}^3 \text{wt sed}^{-1}$ with respectively the following ratio between abundance of total
132 and enriched bacteria: 6.1, 2.0 and 1.3. Algal abundance was modified by adding various
133 quantities of cultured *N. phyllepta* enriched in ^{13}C while bacterial abundances (total enriched
134 and non-enriched) were kept constant at 10×10^8 cells cm^3 . Algal abundance (total enriched
135 and non-enriched) were 26, 64 and 114 $\mu\text{gChla g dry sed}^{-1}$ with respectively the following
136 ratio between abundance of total and enriched algae: 2.4, 1.3 and 1.2.

137 Incubations were stopped by freezing microcosms at -80°C . Samples were thawed and *H.*
138 *ulvae* were separated by hand from their shell and the 17 specimens of each microcosm were
139 pooled and homogenized using a Potter-Eveljhem.

140 *Isotope analysis and calculations*

141 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of prey (bacteria and algae) and grazers were measured using an EA-IRMS
142 (Isoprime, Micromass, UK). Nitrogen isotope composition is expressed in the delta notation
143 ($\delta^{15}\text{N}$) relative to air N_2 : $\delta^{15}\text{N} = [((^{15}\text{N}/^{14}\text{N})_{\text{sample}} / (^{15}\text{N}/^{14}\text{N})_{\text{reference}}) - 1] \times 1000$. Carbon isotope
144 composition is expressed in the delta notation ($\delta^{13}\text{C}$) relative to Vienna Pee Dee Belemnite
145 (VPDB): $\delta^{13}\text{C} = [((^{13}\text{C}/^{12}\text{C})_{\text{sample}} / (^{13}\text{C}/^{12}\text{C})_{\text{reference}}) - 1] \times 1000$.

146 Incorporation of ^{15}N is defined as excess above background ^{15}N (control experiment) and
147 is expressed in terms of specific uptake (*I*). *I* was calculated as the product of excess ^{15}N (*E*)
148 and biomass of N per grazer. *I* was converted to bacterial carbon grazed using the C/N ratio of
149 bacteria. *E* is the difference between the background ($F_{\text{background}}$) and the sample (F_{sample}) ^{15}N

150 fraction: $E = F_{\text{sample}} - F_{\text{background}}$, with $F = {}^{15}\text{N} / ({}^{15}\text{N} + {}^{14}\text{N}) = R / (R + 2)$ and R = the nitrogen
151 isotope ratio. For the $F_{\text{background}}$, we used control values measured with killed grazers (frozen).
152 For *H. ulvae* we used the highest value measured in control ($\delta^{15}\text{N} = 12.42$ and $\delta^{13}\text{C} = -13.72$).
153 R was derived from the measured $\delta^{15}\text{N}$ values as: $R = ((\delta^{15}\text{N}/1000)+1) \times R_{\text{airN}_2}$ where R_{airN_2}
154 $= 7.35293 \times 10^{-3}$ (Mariotti, 1982). The uptake of bacteria was calculated as $\text{Uptake} = (I \times (\%$
155 $\text{C}_{\text{enriched bacteria}} / \% \text{N}_{\text{enriched bacteria}})) / (F_{\text{enriched bacteria}} \times \text{incubation time})$. This uptake was
156 multiplied by the ratio between the abundance of total and enriched bacteria determined by
157 DAPI counts.

158 Incorporation of ^{13}C was calculated analogously, with $F = {}^{13}\text{C} / ({}^{13}\text{C} + {}^{12}\text{C}) = R / (R + 1)$,
159 R_{airN_2} is replaced by $R_{\text{VPDB}} = 0.0112372$ and $\text{Uptake} = I / (F_{\text{enriched bacteria}} \times \text{incubation time})$.
160 The uptake measured was multiplied by the ratio between the abundance of total and enriched
161 diatom, determined from fluorometrical measurements.

162 Enriched *N. phyllepta* carbon consisted of $22.95 \pm 0.54\%$ ^{13}C . The C/N ratio of enriched
163 bacteria was 3.49 and bacterial nitrogen consisted of $2.88 \pm 0.03\%$ ^{15}N . The individual
164 average weight of *H. ulvae* was 0.54 ± 0.08 mg and each specimen was composed on average
165 of 184 ± 19 μgC and 43 ± 4 μgN ($N = 72$ samples of at least 17 specimens each). Ingestion
166 rate as $\text{gC}_{\text{bacteria}} \text{gC}_{\text{H. ulvae}}^{-1} \text{h}^{-1}$ was obtained by dividing ingestion rate of bacteria ($\text{gC ind}^{-1} \text{h}^{-1}$)
167 by *H. ulvae* mean weight (gC ind^{-1}).

168 Variations of uptake rates according to salinity and irradiance were tested using bilateral
169 independent-samples two-tailed tests. One-way analyses of variance (ANOVA) were used in
170 order to test the impact of temperature and algal and bacterial abundance on uptake rates of
171 bacteria and algae. The Tukey test was used for post-hoc comparisons.

172 **Results**

173 The kinetic experiment showed that accumulation of bacteria in *H. ulvae* increased linearly
174 during the first two hours of incubation and then levelled off (Fig. 1). The linear regression

175 slope for the first two hours indicated an uptake rate of $1149 \text{ ngC ind}^{-1} \text{ h}^{-1}$ equivalent to 6.43
176 $10^{-3} \text{ gC}_{\text{bacteria}} \text{ gC}_{H. \text{ulvae}}^{-1} \text{ h}^{-1}$ ($r^2 = 0.98$). The linear regression slope between five and twelve
177 hours was more than seven times lower than for the two first hours and indicated an uptake
178 rate of $145 \text{ } \mu\text{gC ind}^{-1} \text{ h}^{-1}$ equivalent to $0.81 \cdot 10^{-3} \text{ gC}_{\text{bacteria}} \text{ gC}_{H. \text{ulvae}}^{-1} \text{ h}^{-1}$ ($r^2 = 0.98$).

179 Ingestion of bacteria increased from 462 to $1277 \text{ ngC ind}^{-1} \text{ h}^{-1}$ when temperature increased
180 from 5°C to 30°C , and then decreased reaching $1059 \text{ } \mu\text{gC ind}^{-1} \text{ h}^{-1}$ at 40°C (Fig. 2). Ingestion
181 rate of bacteria by *H. ulvae* was significantly decreased at 5°C ($F = 10$; $p < 0.01$), but ingestion
182 rates observed at 10 , 20 , 30 and 40°C were not significantly different.

183 The ingestion rate measured for a salinity of 31 ($1149 \pm 285 \text{ ngC ind}^{-1} \text{ h}^{-1}$) was similar to
184 the one measured for a salinity of 18 ($1085 \pm 58 \text{ ngC ind}^{-1} \text{ h}^{-1}$) (two-tailed test, $p = 0.20$).

185 The ingestion rate observed under light conditions ($1478 \pm 246 \text{ ngC ind}^{-1} \text{ h}^{-1}$) was similar
186 to the one observed in darkness ($1149 \pm 285 \text{ ngC ind}^{-1} \text{ h}^{-1}$) (two-tailed test, $p = 0.72$).

187 Ingestion rates of bacteria were significantly linked to bacterial abundance in microcosms
188 ($F = 38$; $p < 0.001$) (Fig. 3). Ingestion rate increased linearly from 38 ± 13 to $1117 \pm 93 \text{ ngC}$
189 $\text{ind}^{-1} \text{ h}^{-1}$) when bacterial concentrations increased from 4 to $10 \times 10^8 \text{ cells cm}^3$ and increased,
190 though not significantly to $1604 \pm 366 \text{ ngC ind}^{-1} \text{ h}^{-1}$ for a bacterial concentration of 17×10^8
191 cells cm^3 .

192 Dual labeling of prey allowed simultaneous assessment of the ingestion of bacteria and
193 algae. When algal concentration increased from 15 to $114 \text{ } \mu\text{gChla g}^{-1}$ with constant bacterial
194 abundance ($10.5 \times 10^8 \text{ cells cm}^3$), the ingestion rate of algae remained constant ($F = 3.3$; $p =$
195 0.11) (Fig. 4). However, ingestion rate of bacteria remained constant for algal concentration
196 in the sediment between 15 and $64 \text{ } \mu\text{gChla g dry wt sed}^{-1}$ but significantly decreased at the
197 highest algal concentration of $114 \text{ } \mu\text{gChla g dry wt sed}^{-1}$ ($F = 4.4$; $p < 0.05$). As a result, when
198 algal abundance increased, the fraction of algae in the diet of *H. ulvae* increased.

199 Grazing experiments were simultaneously performed with two other grazers: the
200 foraminifera *A. tepida* and a nematode community. Feeding behaviour of *A. tepida* (Pascal et
201 al., 2008b) and nematodes (Pascal et al., In press) has been previously described. All grazing
202 incubations were conducted at the same time and in similar conditions, making comparisons
203 between grazers possible. The effects of environmental factors (temperature, salinity and
204 luminosity) on ingestion rates of bacteria are summarized in Table 1. Among the different
205 grazers tested, *A. tepida* was the most affected by salinity and temperature. Light only
206 affected nematodes and increased their feeding activity. Classification of grazers according to
207 their maximal ingestion rates of bacteria and algae reported per grazer weight gave the
208 following list arranged in ascending order: *A. tepida*, nematode community and *H. ulvae*
209 (Table 1). For the dual labelling experiment, ratios between algae and bacteria ingested were
210 measured for each grazer, at each algal concentration. Comparison of those ratios between
211 grazers reflected their respective ability to discriminate between food sources (*i.e.* algae and
212 bacteria). At the three algal concentrations tested, *A. tepida* and nematodes showed a higher
213 ratio of algae:bacteria ingested than *H. ulvae*, suggesting a better ability to preferentially
214 ingest algae over bacteria compared to the gastropod (Fig. 5).

215 **Discussion**

216 *Kinetic experiment*

217 During the 12 hour incubation, *H. ulvae* first accumulated the enriched bacteria linearly
218 over 2 hours (Fig. 1). This suggests that ingestion rate of bacteria was constant and that no
219 egestion of recently ingested labelled material occurred during this period. After 4 hours of
220 incubation, the accumulation rate of bacteria by *H. ulvae* decreased. This may have two
221 nonexclusive origins: egestion of labelled bacteria and a decrease in feeding activity over
222 time. As all other grazing experiments were performed during two hours, they consequently
223 reflected the ingestion rates of *H. ulvae*.

224 Linear accumulation of labelled diatom or bacteria by *H. ulvae* had been previously
225 recorded from 45 min (Fenchel et al., 1975) to 2 hours (Blanchard et al., 2000; Haubois et al.,
226 2005a). Molluscs have complex digestive tracts allowing partitioning of food particles within
227 the gut. Relatively indigestible material passes quickly to the intestine and is subjected to
228 extracellular digestion. More nutritious material like bacteria and algae is diverted to the
229 digestive gland where it undergoes intracellular digestion. For *Hydrobia totteni*, gut residence
230 time is 30-40 min (Lopez and Cheng, 1983b) whereas digestive gland residence time is 5
231 hours (Kofoed et al., 1989). Assuming a similar situation for *H. ulvae*, the absence of egestion
232 during the two hour long incubations would mean that all bacteria are diverted to the digestive
233 gland. In their grazing experiment with enriched diatoms, Sokolowski et al. (2005) observed
234 that during the first 4 h phase of experiment, accumulation rate was 3 times higher than
235 during the last 12 h phase. We observed exactly the same ratio between accumulation rates
236 found during the grazing periods 0-2 h and 0-12 h. Those similar results suggest that digestive
237 processes for bacteria and algae may be similar.

238 *Range of ingestion rates*

239 To our knowledge, there is no data dealing with the ingestion rate of bacteria by *Hydrobia*
240 to compare with our values. However, concerning algal ingestion our data are consistent with
241 those previously measured. In the present study, ingestion rates fluctuated between 1.2-1.8
242 $\mu\text{gC ind}^{-1} \text{ h}^{-1}$. In the literature, ingestion rates of snails fed with diatoms are 0.5-2.9 $\mu\text{gC ind}^{-1}$
243 h^{-1} for *Hydrobia truncata* (Forbes and Lopez, 1989) and 1.2 (Sokolowski et al., 2005), 1.12-
244 1.33 (Blanchard et al., 2000) and 0.04-2.08 (Haubois et al., 2005a) for *H. ulvae*.

245 The maximal ingestion rates of algae and bacteria by *Hydrobia ulvae* were higher than
246 meiofaunal rates. Nevertheless, individual weight of *H. ulvae* is more than one hundred and
247 one thousand times higher than *A. tepida* and nematodes respectively (Table 1). Body size is
248 an important determinant of many physiological processes and maximal ingestion rate is

249 generally inversely correlated to body size (e. g. Moloney and Field, 1989). The present study
250 focuses only on two potential prey, bacteria and algae, although other food sources are
251 available in sediment. For instance Dissolved Organic Material may constitute an important
252 food supply for nematodes (Lopez et al., 1979; Meyer-Reil and Faubel, 1980; Montagna,
253 1984; Jensen, 1987) and foraminifera (Schwab and Hofer, 1979). Nematodes and foraminifera
254 may be principally dependent on those other resources and present consequently low
255 ingestion rates of bacteria and algae.

256 *Effect of abiotic factors on bacterial ingestion rate*

257 The general trend showed a temperature effect with an optimum around 30°C. However,
258 except at the lowest temperature (5°C), differences between feeding rates of *H. ulvae*
259 observed in the present study were not significant, indicating a limited influence of
260 temperature. In a similar manner, Barnes (2006) did not detect changes in feeding activity of
261 *H. ulvae* during *in situ* experiments with the same range of temperature. Ingestion rates
262 observed at salinities of 18 and 31 were not significantly different in the present study.
263 Grudeno & André (2001) also observed that shell growth of juvenile *H. ulvae* was unaffected
264 by salinity in the range of 15-30. Light did not affect the ingestion of bacteria by *H. ulvae*.
265 The literature gives conflicting results concerning the effect of light. Barnes (1986) found that
266 crawling activity of snails was higher in darkness whereas Orvain & Sauriau (2002) observed
267 an increase of *H. ulvae* crawling activity with light. However in Orvain & Sauriau's
268 experiment, light may have induced formation of algal biofilm, affecting microphytobenthic
269 distribution and thus indirectly affecting snail activity levels.

270 In intertidal mudflats, the surficial centimeter of sediment is subjected to fast and large
271 environmental variations. The ability of a grazer to sustain feeding activity when
272 environmental conditions fluctuate can be interpreted as an adaptation to this habitat. All
273 compared grazers in the present study came from the top centimeter of sediment of the same

274 study area and grazing incubations were performed in similar conditions. Compared to other
275 grazers, the feeding response of the foraminifera *A. tepida* presented the largest ranges of
276 variation indicating that they may present a low adaptation to rapid environmental changes
277 (Table 1). Nevertheless, *A. tepida* is considered as one of the most tolerant species of
278 foraminifera to temperature and salinity variations (Bradshaw, 1961; Walton and Sloan, 1990)
279 and more generally to environmental changes (Samir, 2000; Armynot du Chatelet et al., 2004;
280 Bouchet et al., 2007). *A. tepida* may be able to survive starvation when the environment is
281 unfavourable and may await optimal conditions to feed and develop. An alternate explanation
282 could be that when conditions are hostile, foraminifera move from the top layers of sediment
283 to deeper layers (Severin and Erskian, 1981; Severin, 1987; Groß, 2002). Feeding activity of
284 nematodes and *H. ulvae* appeared to be more independent of environmental variables. The
285 nematode community was mainly composed of three species, *Chromadora macrolaima*,
286 *Daptonema oxycerca* and *Ptycholaimellus jacobi* (Pascal et al., In press), known to dwell and
287 feed in surface sediment. Moreover, *H. ulvae* is considered the most environmentally tolerant
288 of Northwest European *Hydrobia* (Hylleberg, 1975; Lassen and Kristensen, 1978). However
289 caution must be taken in interpretation of our results because the effects of each
290 environmental factor on feeding behaviour of snails were studied independently whereas in
291 natural environment, all these factors covary. Moreover, seasonal acclimatising capacity was
292 not taken into account (Barnes, 2006).

293 *Feeding response to bacterial and algal abundances*

294 In fine grained environments, *Hydrobia* ingests mouthfuls of sediment containing organic
295 food source, including bacteria and microalgae (Kofoed, 1975; Lopez and Cheng, 1983b;
296 Levinton et al., 1984). Due to high size and feeding mode of *H. ulvae*, the snail probably has a
297 very low ability to ingest selectively very small preys such as bacterial cells. In opposition,

298 larger preys such as diatom cells can be selectively ingested from sediment by *Hydrobia*
299 (Fenchel, 1975; Lopez and Levinton, 1978; Lopez and Kofoed, 1980).

300 Indiscriminant ingestion of bacteria by *H. ulvae* implies that bacterial ingestion is
301 exclusively dependent on ingestion rate of sediment and the concentration of bacteria in
302 sediment. This type of feeding indicates that relationships between bacterial ingestion and
303 bacterial concentration in sediment can be described by (i) a power law relation, (ii) a linear
304 increase or (iii) null or decreasing relation. Those relations mean that when prey concentration
305 increases, ingestion rate of sediment respectively (i) increases, (ii) remains constant or (iii)
306 decreases. In the present study, the ingestion rate of bacteria first increased linearly with
307 bacterial concentration and then levelled off at the highest concentration (Fig. 3). This relation
308 may involve a constant ingestion rate of sediment at the lowest concentration of bacteria and a
309 decrease of ingested sediment at the highest bacterial concentration.

310 Ingestion of algae by snails was not influenced by algal concentration in the range of
311 concentration tested (Fig. 4). Contrarily, *Hydrobia* had been found previously to have
312 increasing algal ingestion rate when algal concentration increased in a similar range of values
313 (Forbes and Lopez, 1986; Forbes and Lopez, 1989; Haubois et al., 2005a). The ability of a
314 deposit feeder to alter its ingestion rate depends on its sensory capacity to recognize food
315 quality (Taghon, 1982). This perception may differ between the freeze-dried diatoms in the
316 present study and live diatoms in other studies, which could explain the different responses
317 observed.

318 The ratio between algae and bacteria ingested denotes grazer ability to select diatoms from
319 the sediment/bacteria aggregate. At each algal concentration, this ratio was always higher for
320 *A. tepida* and nematodes, indicating higher algal selection efficiency. The nematode
321 community was composed mainly of epigrowth feeders (75%) and non selective deposit
322 feeders (21%). Epigrowth feeders puncture diatom cells with their teeth to ingest cell

323 contents. Consequently, they are mainly dependant on algal resources (Jensen, 1987). *A.*
324 *tepida* uses a network of pseudopodia to gather and ingest food particles. This feeding mode
325 allows foraminifera to be highly selective in ingested food (Lee et al., 1966; Lee and Muller,
326 1973). *Ammonia* may also greatly depend on algal resources, as this foraminifera was found
327 to ingest rapidly and with high efficiency fresh algal deposits (Moodley et al., 2000).
328 Montagna and Yoon (1991) also observed that nematodes demonstrate a high efficiency in
329 selective ingestion of algae in comparison with other meiofaunal groups. *H. ulvae* appeared
330 less proficient in algal selection than meiofaunal grazers. *N. phyllepta*, the algal species used
331 in the present study may have been too small (<30 µm) to allow selective ingestion by *H.*
332 *ulvae*, but this hypothesis can reasonably be rejected as *Hydrobia* is not able to select diatoms
333 according to the cell size (Levinton, 1987; Haubois et al., 2005a). In sandy sediment,
334 *Hydrobia* presents epipsammic browsing activity by taking particles into the buccal cavity,
335 scraping off attached microorganisms and then spitting out the particles (Lopez and Kofoed,
336 1980). As a result, gut contents and even fecal pellets of *Hydrobia* can contain more diatoms
337 than the offered sandy sediment (Fenchel et al., 1975; Lopez and Levinton, 1978).
338 Conversely, in fine grained sediment, *Hydrobia* ingests mouthfuls of sediment containing
339 organic food, including microalgae (Kofoed, 1975; Lopez and Cheng, 1983b; Levinton et al.,
340 1984). Results of the present study also suggest that *H. ulvae* feeding on muddy sediment
341 present a limited ability to discriminate between algae and the sediment/bacteria aggregate.
342 Taghon and Jumars (1984) pointed out that for animals having limited particle selection
343 ability, foraging strategies are mainly a function of ingestion and digestion processes. Indeed,
344 in the present study *H. ulvae* appeared to decrease the rate of ingested sediment at high algal
345 and bacterial concentrations. In the present study, labelled prey were distributed
346 homogeneously in sediment. Feeding rates and feeding behaviour of *H. ulvae* may be
347 different when algae are condensed in biofilm.

348 In the Brouage mudflat, *H. ulvae* and meiofauna are present, on average, in similar
349 biomasses throughout the year (Degré et al., 2006). The present study suggests that *H. ulvae*
350 ingests bacteria at a higher rate than meiofaunal do. In the study area, benthic bacteria would
351 therefore be grazed to a higher extent by macrofauna than by meiofauna.

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- 526
- 527

528 **Figure captions**

529 **Figure 1.** Bacteria uptake by *H. ulvae* (mean \pm SD, N =3) as function of incubation time
530 (h).

531 **Figure 2.** Bacterial ingestion rate by *H. ulvae* (mean \pm SD, N =3) as function of
532 temperature ($^{\circ}$ C). Different letters above bars indicate significant differences between
533 incubation conditions (ANOVA; Tukey test).

534 **Figure 3.** Bacterial ingestion rate by *H. ulvae* (mean \pm SD, N =3) as function of bacterial
535 abundance (10^8 cells cm^3). Different letters above bars indicate significant differences
536 between incubation conditions (ANOVA; Tukey test).

537 **Figure 4.** Ingestion rates of algal carbon O (mean \pm SD) and bacterial carbon λ (mean \pm
538 SD) by *H. ulvae* ($\text{ngC ind}^{-1} \text{h}^{-1}$) as a function of algal abundance ($\mu\text{gChla g dry wt sed}^{-1}$).
539 Bacterial abundance was kept constant (1.05×10^9 cells cm^3). * above bars indicate
540 significant differences between incubation conditions (ANOVA; Tukey test).

541 **Figure 5.** Ratio between algae and bacteria taken up by three different grazers (the
542 foraminifera *A. tepida*, Brouage mudflat nematode community and the gastropod *H. ulvae*) as
543 a function of algal abundance ($\mu\text{gChla g dry wt sed}^{-1}$). Bacterial abundance was kept constant
544 (1.05×10^9 cells cm^3).

545 **Table captions**

546 **Table 1.** Comparison of the feeding activity of three different grazers (the foraminifera *A.*
547 *tepida*, the Brouage mudflat nematode community and the gastropod *H. ulvae*).

	Meiofauna		Macrofauna
	<i>Ammonia tepida</i>	Nematode community	<i>Hydrobia ulvae</i>
Individual weight (gC_{organic} ind⁻¹)	1.0×10^{-6}	1.3×10^{-7}	1.8×10^{-4}
Effect of environmental factors on ingestion rate of bacteria			
Ratio between ingestion rates of bacteria at 30 and 10°C	3.6	1.6	1.5
Effect of salinity (18 against 31 ‰)	Negative	None	None
Effect of luminosity (Darkness against 83 μM of photons m⁻² s⁻¹)	None	Positive	None
Maximal ingestion rates of bacteria and algae			
Maximal ingestion rate of bacteria (10⁻³ gC_{bacteria} gC_{grazer}⁻¹ h⁻¹)	0.06	0.92	7.45
Maximal ingestion rate of algae (10⁻³ gC_{algae} gC_{grazer}⁻¹ h⁻¹)	0.94	5.08	9.56

Table 1

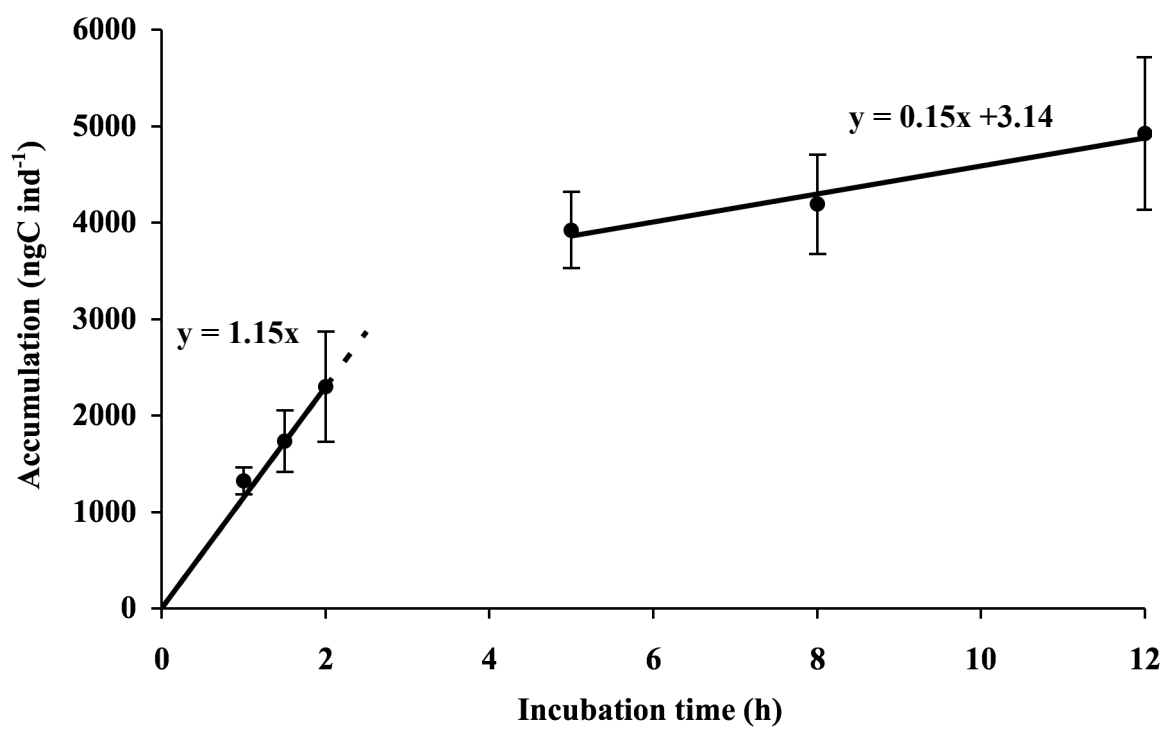


Fig. 1

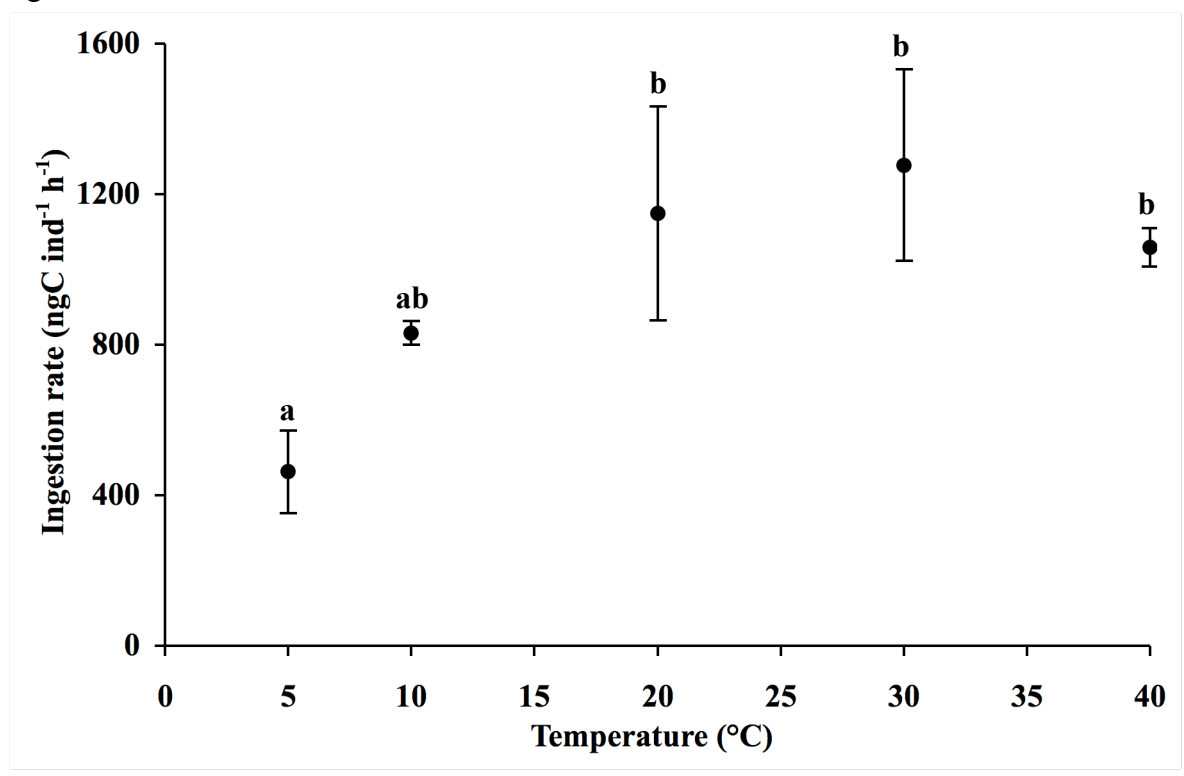


Fig. 2

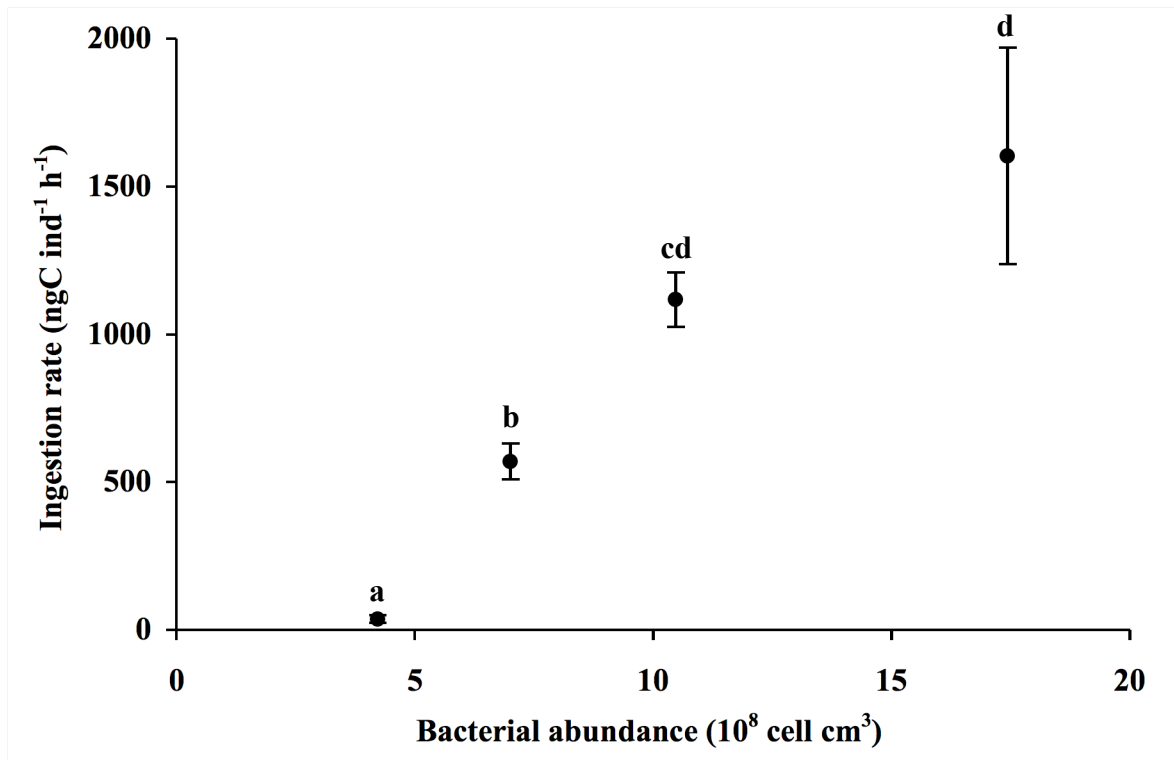


Fig. 3

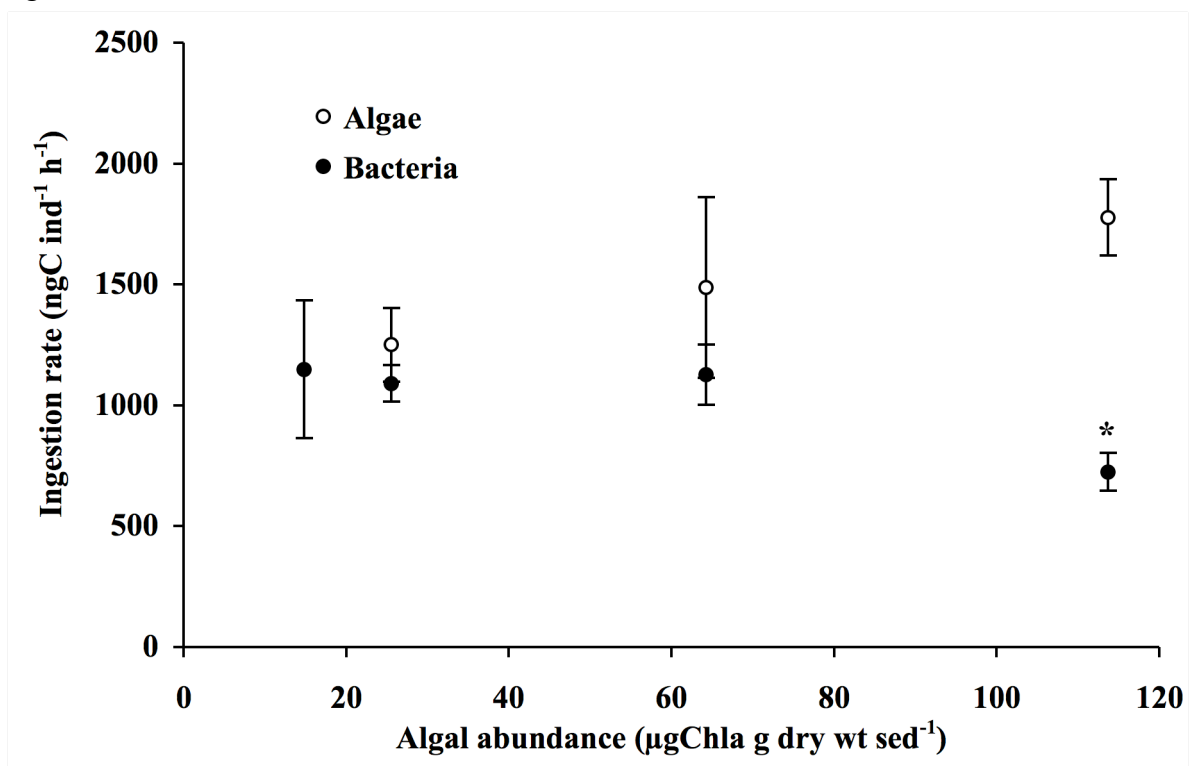


Fig. 4

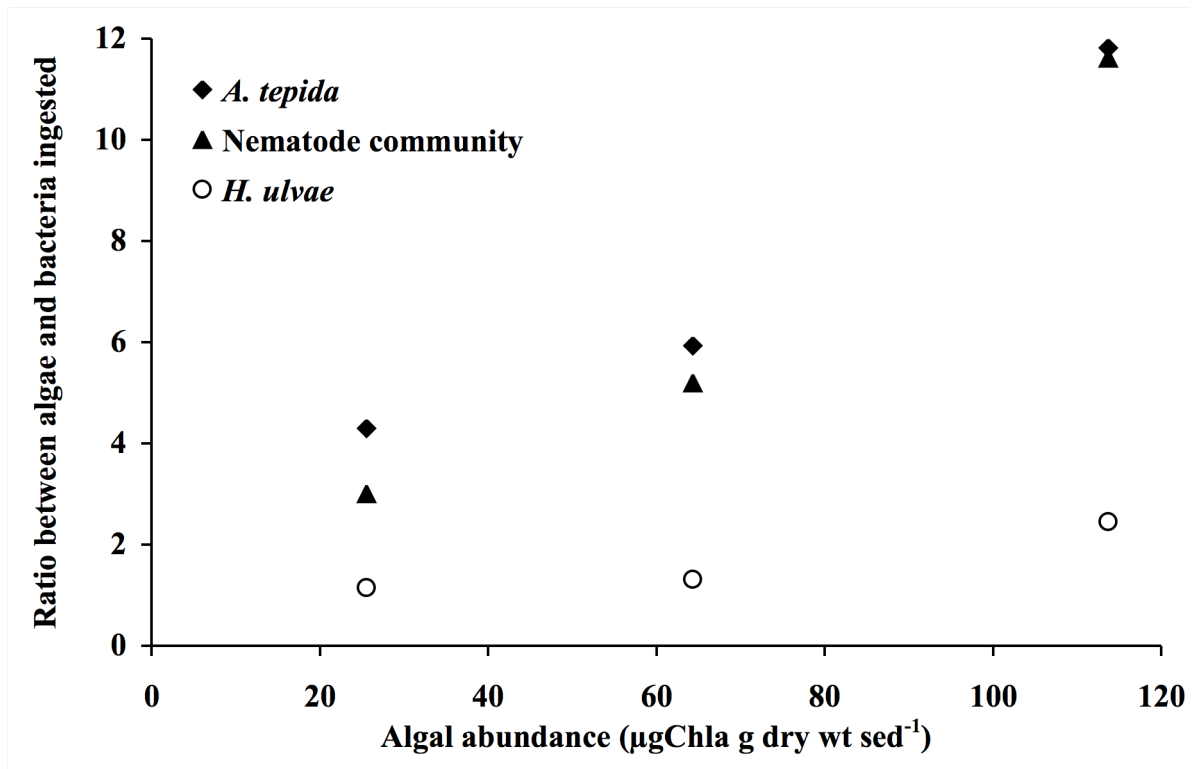


Fig. 5