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1 **Bacterivory in the common foraminifer *Ammonia tepida*:**
2 **isotope tracer experiment and the controlling factors**

3 Pierre-Yves Pascal ^{*1}, Christine Dupuy ¹, Pierre Richard ¹, Nathalie Niquil ¹

4 ¹Littoral, Environnement et Sociétés (LIENSS) UMR 6250 CNRS-Université de La
5 Rochelle, 2 Rue Olympe de Gouges, 17042 La Rochelle *cedex*, France

6 *Corresponding author: pypascal@univ-lr.fr; Tel. 33 (0)5-46-45-83-88

7 **Abstract**

8 The majority of sediment dweller foraminifera are deposit feeders. They use their
9 pseudopodia to gather sediment with associated algae, organic detritus and bacteria. Uptake of
10 bacteria by foraminifera have been observed but rarely quantified. We measured uptake of
11 bacteria by the common foraminifera *Ammonia tepida* using ¹⁵N pre-enriched bacteria as
12 tracers. In intertidal flats, seasonal, tidal and circadian cycles induce strong variations in
13 environmental parameters. Grazing experiments were performed in order to measure effects
14 of abiotic (temperature, salinity and irradiance) and biotic (bacterial and algal abundances)
15 factors on uptake rates of bacteria. In mean conditions, *A. tepida* grazed 78 pgC ind⁻¹ h⁻¹
16 during the first eight hours of incubation, after which this uptake rate decreased. Uptake of
17 bacteria was optimal at 30°C, decreased with salinity and was unaffected by light. Above 7 ×
18 10⁸ bacteria ml wt sed⁻¹, uptake of bacteria remained unchanged when bacterial abundance
19 increased. Algal abundance strongly affected algal uptake but did not affect uptake of
20 bacteria. As uptake of bacteria represented 8 to 19% of microbes (algae plus bacteria) uptake,
21 *Ammonia* seemed to be mainly dependant on algal resource.

22 **Key-Words**

23 Grazing, bacteria, foraminifera, trophoecology, environmental factor, mudflat, prey
24 abundance

25

25 **Introduction**

26 Benthic foraminifera are heterotrophic protozoa that have the morphological characteristics
27 of pseudopodia and a test with one or more chambers. Since the Cambrian era, they have been
28 present in a wide range of environments, from shallow brackish waters to deepest oceans.
29 They are used as proxies for paleoecological studies because they are wide spread, numerous
30 and well preserved. In recent times, foraminifera increasingly appeared as dominant members
31 of benthic communities in both shallow and deep-sea environments (Snider et al. 1984;
32 Alongi 1992; Gooday et al. 1992; Moodley et al. 1998; Moodley et al. 2000), suggesting that
33 they may play an important role in food webs (Altenbach 1992; Linke et al. 1995).

34 Foraminifera exhibit a wide range of trophic behaviours: dissolved organic matter (DOM)
35 uptake, herbivory, carnivory, suspension feeding and most commonly, deposit feeding (Lipps
36 1983). Deposit feeders are omnivorous, using their pseudopodia to gather fine-grained
37 sediment with associated bacteria, organic detritus and, if available, algal cells. As a large part
38 of organic detritus is indigestible, it must be cycled by bacteria before becoming available to
39 deposit feeders (Levinton 1979). Benthic bacteria are highly abundant and productive in
40 benthic sediments. Due to their high nutritional value they are suspected to be an important
41 resource for sediment dwelling fauna.

42 Bacteria could play a major role or be an obligatory item in foraminiferal nutrition. Several
43 littoral benthic foraminifera require bacteria to reproduce (Muller and Lee 1969) and have
44 been shown to selectively ingest bacteria according to strain (Lee et al. 1966; Lee and Muller
45 1973). Some epiphytic foraminifera show a farming strategy. They produce nutrient-rich
46 substrate for bacteria and then ingest cultured bacteria (Langer and Gehring 1993).
47 Foraminifera are also able to feed actively on bacterial biofilms (Bernhard and Bowser 1992).
48 Bacteria may also play a symbiotic role in bathial species of foraminifera (Bernhard 2003).
49 Uptake of bacteria by *Ammonia* has been displayed using direct food vacuole observation

50 (Goldstein and Corliss 1994) and bacteria labelled with fluorescent dyes (Langezaal et al.
51 2005). Nevertheless, those studies do not give access to quantitative data concerning the
52 uptake rate of bacteria, and the precise role that bacteria play in foraminiferal nutrition
53 remains elusive. Assessing grazing rate on bacteria remains a major point that must be
54 documented to determine the role that foraminifera play in benthic food webs.

55 *Ammonia* is one of the most common genera of benthic foraminifera with a worldwide
56 distribution in inner shelf, estuarine, and salt marsh environments (Murray 1991). One
57 remarkable characteristic of this genus is its ability to survive over a broad range of
58 temperatures, salinities, and seasonal regimes (Bradshaw 1961; Walton and Sloan 1990).

59 The aim of this study is to assess experimentally in different controlled conditions uptake
60 rates of bacteria by *Ammonia* from an intertidal mudflat habitat (Marennes-Oléron, France).
61 ¹⁵N enriched bacteria were used as tracers to determine uptake rate of bacteria (Pascal et al.
62 2008). This habitat is subject to large and quick changes in many environmental features.
63 Three relevant time scales drive these environmental variations: long-term (seasonal cycle),
64 medium-term (lunar cycle) and short-term (solar and tidal cycles) (Guarini et al. 1997). Since
65 these variations may influence foraminiferal feeding behaviour, grazing experiments were
66 performed in order to evaluate effects of abiotic (temperature, salinity and irradiance) and
67 biotic (bacterial and algal abundances) factors on uptake rates of bacteria.

68

68 **Experimental procedure**

69 *Study site*

70 The Brouage intertidal mudflat is located in the eastern part of the Marennes-Oléron Bay
71 (Atlantic coast of France). Meteorological conditions exhibit a strong seasonality typical of a
72 temperate climate. Temperature and salinity of emerged sediments are more extreme during
73 summer tidal cycles (Guarini et al. 1997). Minimum and maximum mud temperatures are 5°C
74 and 34°C respectively. The maximum daily range of mud temperature due to emersion and
75 immersion cycle reaches 18°C (Guarini et al. 1997). Salinity of overlaying water is controlled
76 by the river Charente freshwater input, ranging from 25 to 35‰ over the year (Héral et al.
77 1982). Salinity of the upper layers of sediment may also decrease with rainfall. The sediment
78 surface irradiance shifts from dark during submersion and night emersions to high levels of
79 incident light during daytime emersions. This irradiance can reach 2000 μM of photons $\text{m}^{-2} \text{s}^{-1}$
80 (Underwood and Kromkamp 2000). Details of numerous benthic organisms and processes are
81 available concerning this intertidal zone (gathered in Leguerrier et al. 2003; Leguerrier et al.
82 2004; Degré et al. 2006).

83 *Preparation of ^{15}N enriched bacteria*

84 Superficial sediment (1 cm depth) was collected on the Brouage mudflat (45,55,074 N;
85 1,06,086 W). One ml of the collected sediment was added to 20 ml of bacterial liquid culture
86 medium and kept in darkness during 24 hours at 13°C. The composition of this culture
87 medium were previously described in Pascal et al. (2008). This primary culture was then
88 subcultured during 24 hours under the same conditions to get approximately 2×10^9 cells ml^{-1}
89 ¹. Finally, bacteria were collected in 0.2 μm filtered seawater after 3 centrifugations (3500 g,
90 10 mn, 20°C), frozen in liquid nitrogen and kept frozen at -80°C until grazing experiments.

91 *Preparation of ¹³C enriched algae*

92 An axenic clone of the diatom *Navicula phyllepta* (CCY 9804, Netherlands Institute of
93 Ecology NIOO-KNAW, Yerseke, The Netherlands), the most abundant diatom species in the
94 study area (Haubois et al. 2005), was cultured in medium described by Antia and Cheng
95 (1970) and containing NaH¹³CO₃ (4 mM). Diatoms were concentrated by centrifugation
96 (1500 g, 10 mn, 20 °C), washed three times to remove the ¹³C-bicarbonate, and freeze-dried.

97 *Quantification of bacteria and algae abundance*

98 In order to determine the ratio between enriched and non-enriched preys in microcosms,
99 abundances of bacteria and algae were assessed. To separate bacteria from sediment particles,
100 incubation in pyrophosphate (0.01M during at least 30 min) and sonication (60 W) were
101 performed. Bacteria from both sediment and culture were labelled using 4,6-diamidino-2-
102 phenylindole dihydrochloride (DAPI) (2500 µg l⁻¹), filtered onto 0.2 µm Nucleopore black
103 filter (Porter and Feig 1980) and then counted by microscopy. We check the absence of ciliate
104 and flagellate in bacterial culture during this microscope observation step. Abundance of
105 diatom in sediment was assessed using Chl *a* as a proxy, measured using fluorometry
106 (Lorenzen 1966).

107 *Grazing experiments*

108 Incubation of enriched bacteria and algae with foraminifera were performed in Petri dishes
109 (4.5 cm diameter). Experiments were done in standardized condition similar to field ones:
110 temperature (20°C), irradiance (darkness), salinity (31‰), bacterial abundance (10.5 × 10⁸
111 cells ml wt sed⁻¹) and algal abundance (15 µgChl *a* g dry sed⁻¹). For each type of experiment,
112 one environmental incubation factor was modified in order to determine its impact on
113 foraminifera grazing activity. Each experiment was carried out in triplicate, along with
114 triplicate controls. Control samples were frozen (-80°C) in order to kill foraminifera.

115 During the ebb tide of 13th of March 2006, one sample of the first centimetre of sediment
116 was collected from the Brouage intertidal mudflat (France). First, the sediment was sieved on
117 a 500 µm mesh in order to remove macrofauna. Then, it was sieved on a 200 µm mesh to
118 extract large foraminifera. One ml of the sediment remaining on the mesh was put in each
119 microcosm. Sediment that passed through the 200 µm mesh was sieved through a 50 µm
120 mesh. Fraction passing through the mesh was mixed with ¹⁵N enriched bacteria. This slurry
121 contained 10.5×10^8 cells ml of wet sediment⁻¹ with a ratio of total and enriched bacteria of
122 1.5. Four ml of this slurry were put in each microcosm.

123 First, for the calculation of grazing rates, a kinetic study was realised to validate the linear
124 or hyperbolic uptake kinetics. Incubations for this kinetic study were run during variable
125 times (1 to 12 hours). As all other experiments were run for 5 hours, this first step is necessary
126 to check the linear uptake during the first five hours of incubation.

127 For each type of experiment one environmental incubation factor was modified. Light
128 effect was tested with one irradiance ($83 \mu\text{M}$ of photons $\text{m}^{-2} \text{s}^{-1}$). In order to decrease salinity,
129 cultured bacteria were rinsed with 0.2 µm filtered sea-water diluted with 0.2 µm filtered fresh
130 water (final salinity of 18‰). Bacterial abundance was modified adding various quantities of
131 bacteria enriched in ¹⁵N. Bacterial abundances (total enriched and non-enriched) tested were
132 4, 7 and 17 cells ml wt sed⁻¹ with respectively the following ratio between abundance of total
133 and enriched bacteria: 6.1, 2.0 and 1.3. Algal abundance was modified adding various
134 quantities of cultured *N. phyllepta* enriched in ¹³C while bacterial abundances (total enriched
135 and non-enriched) were kept constant at 10×10^8 cell ml⁻¹. Algal abundance (total enriched
136 and non-enriched) were 26, 64 and 114 µgChla g dry sed⁻¹ with respectively the following
137 ratio between abundance of total and enriched algae: 2.4, 1.3 and 1.2.

138 Incubations were stopped by freezing the microcosms at -80°C. Samples were thawed and
139 stained with rose Bengal in order to identify freshly dead foraminifera. For each sample, 150

140 specimens of the species *A. tepida* were picked up individually and cleaned of any adhering
141 particles. Samples from experiments with ¹³C enriched *N. phyllepta* were processed with HCl
142 0.1 M in silver boats to remove any inorganic carbon.

143 *Isotope analysis and calculations*

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

149 Incorporation of ¹⁵N is defined as excess above background ¹⁵N (control experiment) and
150 is expressed in terms of specific uptake (*I*). *I* was calculated as the product of excess ¹⁵N (*E*)
151 and biomass of N per grazer. *I* was converted in bacterial carbon grazed using C/N ratio of
152 bacteria. *E* is the difference between the background ($F_{\text{background}}$) and the sample (F_{sample}) ¹⁵N
153 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
154 isotope ratio. For the $F_{\text{background}}$, we used control values measured with killed grazers (frozen).
155 *R* was derived from the measured $\delta^{15}\text{N}$ values as: $R = ((\delta^{15}\text{N}/1000) + 1) \times \text{RairN}_2$ where RairN_2
156 $= 7.35293 \times 10^{-3}$ (Mariotti 1982). The uptake of bacteria was calculated as $\text{Uptake} = (I \times (\%$
157 $\text{C}_{\text{enriched bacteria}} / \% \text{N}_{\text{enriched bacteria}}) / (F_{\text{enriched bacteria}} \times \text{incubation time})$. This uptake was
158 multiplied by the ratio between the abundance of total and enriched bacteria determined by
159 DAPI counts.

160 Incorporation of ¹³C was calculated analogously, with $F = {}^{13}\text{C} / ({}^{13}\text{C} + {}^{12}\text{C}) = R / (R + 1)$,
161 RairN_2 is replaced by $R_{\text{VPDB}} = 0.0112372$ and $\text{Uptake} = I / (F_{\text{enriched bacteria}} \times \text{incubation time})$.
162 The uptake measured was multiplied by the ratio between the abundance of total and enriched
163 diatom, determined from fluorometrical measurements.

164 Enriched *N. phyllepta* carbon consisted of $22.95 \pm 0.54\%$ ^{13}C . The C/N ratio of enriched
165 bacteria was 3.49 and bacterial nitrogen consisted of $2.88 \pm 0.03\%$ ^{15}N . The average weight of
166 *A. tepida* used was 18.1 ± 3 $\mu\text{g DW}$ ($n = 115$ samples of 150 specimens each). Decalcified
167 specimens of *A. tepida* were composed on average of 1.03 ± 0.23 μg of C and 0.15 ± 0.03 μg
168 of N. Uptake expressed as $\text{gC}_{\text{bacteria}} \text{h}^{-1} \text{gC}_{\text{Ammonia}}^{-1}$ was obtained by dividing uptake of bacteria
169 ($\text{gC ind}^{-1} \text{h}^{-1}$) by *A. tepida* decalcified mean weight (gC ind^{-1}).

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

174 **Results**

175 Foraminiferal isotopic compositions and rates of bacterial and algal uptakes rates are
176 presented in Table 1.

177 During the kinetic experiment, uptake of bacteria by *A. tepida* increased linearly during the
178 first eight hours of incubation and then levelled off (Fig. 1). The linear regression slope for
179 the first eight hours suggested an uptake rate of $78 \text{ pgC ind}^{-1} \text{h}^{-1}$ equivalent to 75×10^{-6}
180 $\text{gC}_{\text{bacteria}} \text{gC}_{\text{Ammonia}}^{-1} \text{h}^{-1}$ ($r^2 = 0.99$). The linear regression slope between eight and twelve hours
181 was more than five times lower than for the first eight hours and suggested an uptake rate of
182 $14 \text{ pgC ind}^{-1} \text{h}^{-1}$.

183 Temperature had a significant effect on *Ammonia* uptake rate of bacteria ($F = 27$;
184 $p < 0.001$). Temperatures tested fluctuated between 5 and 40°C and were in the range of those
185 found in the study area (Guarini et al. 1997). Uptake of bacteria was almost null at 5°C , then
186 increased with temperature. It reached an optimum at around 30°C and then decreased (Fig.
187 2). Uptake rates measured at 10, 20 and 40°C were not significantly different. Maximum

188 uptake rate of bacteria (30°C) reached 113 pgC ind⁻¹ h⁻¹ and was significantly different from
189 others.

190 Uptake rate of bacteria by *Ammonia* decreased significantly from 67 to 32 pgC ind⁻¹ h⁻¹
191 when salinity dropped down from 31 to 18‰ (bilateral t-test; p<0.05) (Fig. 3). In the study
192 area, salinity of overlaying water fluctuates between 25 to 35‰ (Héral et al. 1982) but salinity
193 of sediment can be reduced by rainfall.

194 The sediment surface irradiance shifts from dark during submersion and night emersions to
195 high levels of incident light during daytime emersions. Irradiance tested (83 μM of photons
196 m⁻² s⁻¹) corresponds to a low irradiance. Light did not affect foraminifera feeding activity:
197 uptake rates of bacteria were similar under light and darkness (bilateral t-test; p = 0.71) (Fig.
198 3).

199 Ingestion of bacteria was significantly linked with abundance of bacteria in microcosm (F
200 = 32; p<0.001) (Fig. 4). Four different bacterial concentrations were tested: 4, 7, 10 and 17 ×
201 10⁸ cells ml wt sed⁻¹. There was no uptake when the bacterial abundance was 4 × 10⁸ cells ml
202 wt sed⁻¹ (Fig. 5), uptake rate of bacteria remained constant around 67 pgC ind⁻¹ h⁻¹ when
203 bacterial concentrations increased from 7 to 17 × 10⁸ cells ml wt sed⁻¹ (Fig. 4).

204 When algal concentration increased from 15 to 114 μgChla g dry sed⁻¹ with constant
205 bacterial abundance (10.5 × 10⁸ cell ml⁻¹), the uptake rate of bacteria remained constant (F =
206 1.4; p = 0.29) (Fig. 5). The uptake rate of algae increased from 329 to 971 pgC ind⁻¹ h⁻¹
207 linearly when algal abundance increased ($r^2 = 0.99$; p<0.001) (Fig. 7). When algal abundance
208 increased, the fraction of algae in the diet of foraminifera increased. The fraction of bacteria
209 decreased from 18.8 to 14.4 and 7.8% of microbes (algae plus bacteria) taken up when algal
210 concentration was equal to 25.6, 64.3 and 113.7 μgChla g dry sed⁻¹ respectively.

211 **Discussion**

212 *Experimental procedure*

213 Like all various methods previously developed and applied to measure bacterivory, the
214 method used in the present study presents methodological shortcomings that make
215 interpretation of the resulting problematic. For instance, sieving the sediment changes the
216 bacterial availability for foraminifera, bacteria being not attached to particle as in natural
217 situation. Foraminifera are known to selectively graze different bacterial strains (Lee et al.
218 1966; Bernhard and Bowser 1992). As grazing experiments are based on the hypothesis that
219 grazers take up ^{15}N enriched bacteria and natural sediment bacteria at the same rate, the
220 cultured bacteria community has to present characteristics roughly similar to the natural one.
221 Despite the fact that culture modified the specific composition of the natural bacterial
222 community, characteristics of size, activity and diversity of the cultured bacterial consortium
223 in our experiments would be more representative of the natural community than in most
224 previous grazing experiments (Pascal et al. 2008). As enriched algae (monospecific and
225 freeze-dried) may present characteristics different from natural algal community, bias due to
226 selective ingestion of algae may exist. Control experiments were always performed in similar
227 conditions to assess bias due to bacterial or algal cell adhesion on foraminiferal test. ^{13}C
228 enriched freeze dried algae are potential source of enriched DOM and transfer to bacteria
229 drive to formation of ^{13}C enriched bacteria but as incubations were short-term, we consider as
230 negligible this bias due to recycling.

231 *The kinetics of bacterial uptake*

232 Foraminifera use pseudopodia in order to form a long and extensive network for trapping
233 food particles (Travis and Bowser 1991). Actively feeding specimens are characterized by
234 feeding cysts. Aggregates of particles are firmly attached around the test apertures and they
235 may encompass the entire test. Collected material is partitioned into small fractions before

236 ingestion. The possibility of extracellular digestion (Meyer-Reil and Köster 1991) and
237 reticulopodial digestion (Lee et al. 1991) has been suggested. Food vacuoles contain large
238 amounts of sediment, organic detritus, algal cells and bacteria (Goldstein and Corliss 1994).
239 Those vacuoles are most abundant in the terminal chamber, but occur throughout the last four
240 chambers as well. The digestion of bacteria seems to occur in the terminal chamber of
241 *Ammonia* (Goldstein and Corliss 1994; Langezaal et al. 2005). This genus ingests bacteria and
242 readily digests them, implying that bacteria are more probably used as food source than as
243 symbionts (Langezaal et al. 2005).

244 Langezaal et al. (2005) found that *Ammonia beccarii* grazed 90 bacteria during a 20 h
245 period. Converting their uptake rate into bacterial biomass (Norland et al. 1995), gives a
246 grazing rate of 1.7 pgC ind⁻¹ h⁻¹. This rate is lower than the rate found in the present study (78
247 pgC ind⁻¹ h⁻¹). This may be linked to the bacterial concentration used by Langezaal et al.
248 (2005) in their microcosms (1.4×10^3 cells ml⁻¹), which was substantially lower than benthic
249 bacterial abundance in natural environments (c.a. 10⁹ cells ml⁻¹) and in the present study.

250 In present experiments, uptake of bacteria by *Ammonia* was rapid and detectable after 2
251 hours of incubation (Fig. 1). This is in accordance with Moodley et al. (2000) who observed a
252 detectable uptake of algal carbon by *Ammonia* after three hours of incubation. Uptake of
253 bacteria increased linearly during the first eight hours and then levelled off (Fig. 1). A similar
254 pattern was observed for uptake of algae by *Ammonia* (Moodley et al. 2000). This levelling
255 off may reflect satiation or more likely excretion, effective after eight hours. Foraminifera
256 have been reported to assimilate ingested algal carbon within 12 h (Rivkin and De Laca 1990)
257 and *Ammonia* was found to assimilate carbon from phytodetritus in 12 h (Moodley et al.
258 2000). A simplified energy budget can be calculated with following parameters, $C = A + FU$
259 (C = food uptake, A = assimilation of metabolisable energy, FU = loss by faeces and urinary
260 wastes) (Klekowski et al. 1979; Schiemer 1982). We suggest that during the first eight hours

261 of incubation, *Ammonia* takes up and assimilates bacteria. Then, after eight hours, uptake and
262 assimilation still occur but excretion begins. By assuming, that uptake is constant during all
263 the grazing experiments, assimilation and excretion rates can be assessed. The first slope from
264 the origin to eight hours would correspond to the uptake rate while the second slope would
265 correspond to the assimilation rate. *Ammonia* retains five times more tracer during the first
266 eight hours than after. As a result, 17% of ingested bacteria would be assimilated and 83%
267 would be rejected. This result is disputable because the uptake rate constancy was not
268 determined and the uptake rate after eight hours is determined from only two data points,
269 however, this result fits well with assimilation rate of bacteria by nematodes (25%) (Herman
270 and Vranken 1988) and polychaetes (26%) (Clough and Lopez 1993).

271 *Effects of abiotic factors*

272 Studies on the influence of environmental factors on *Ammonia* are limited. However,
273 Bradshaw (1957; 1961) determined the influence of temperature and salinity on *Ammonia*
274 reproductive activity, growth rate and survival under experimental conditions.

275 In the present experiments, temperature had a similar effect on uptake rate of bacteria to
276 the one shown by Bradshaw on growth and reproductive rates. We found no uptake of
277 bacteria at 5°C (Fig. 2), in accordance with Bradshaw, showing that foraminifera metabolism
278 is very low at low temperatures. Under a temperature less than 10°C, *Ammonia* fail to grow
279 and reproduce and individuals appear to live an indefinitely long period (Bradshaw 1957).
280 The optimal grazing temperature appeared at 30°C (Fig. 2) as in Bradshaw's experiments
281 (Bradshaw 1961). When temperature exceeded 30°C in our microcosms, grazing rate
282 decreased. Similarly, no growth was observed in Bradshaw's experiments, and specimens
283 lived less than one day at 35°C (Bradshaw 1957). Those physiological characteristics have
284 implications for foraminiferal abundances at the seasonal time scale. Limited activity during
285 winter prevents reproduction and limits abundance, while in summer, high temperature can

286 lead to mortality, in particular in the intertidal habitat subject to a wide range of rhythmically
287 and rapidly varying temperature due to tidal cycles.

288 Uptake rate of bacteria declined when salinity was reduced to 18‰ (Fig. 3). This result is
289 also in accordance with those of Bradshaw (1957; 1961). According to this author, normal
290 growth and reproduction of *Ammonia* occur when salinity fluctuates between 20 and 40‰,
291 and *Ammonia* failed to grow below 13‰. *Ammonia* is an euryhaline genus found from
292 brackish (Debenay and Guillou 2002) to hypersaline environments (Almogi-Labin et al.
293 1992). However, conditions of brackish environments would not be optimal for *Ammonia*.
294 Foraminifera use a network of pseudopoda to gather and ingest food particles. Each
295 pseudopoda contains an elongated cytoskeleton primarily composed of microtubules.
296 Modifications of salinity induce a decrease of the number of pseudopodal microtubules
297 (Koury et al. 1985), that may lead to a lower pseudopodal efficiency. This could explain the
298 lower uptake rate observed at low salinity, considering that sediment salinity is under control
299 of tidal cycles and weather conditions, like rainfall, which induces a strong decrease of
300 salinity during low tide.

301 Light did not affect uptake rate of *Ammonia* (Fig. 3). Although foraminifera frequently
302 form symbiosis with algae, *Ammonia* is not known as an algal-bearing foraminifera (Lee and
303 Anderson 1991). Consequently, irradiance would not influence feeding behaviour of
304 *Ammonia*. This is confirmed by our grazing experiment results with a low irradiance rate.
305 Owing to this, *Ammonia* seems not influenced by nycthemeral cycles and seems able to graze
306 in superficial sediment exposed to sun in the temperature range that allows grazing. This
307 suggests that *Ammonia* is able to feed actively in environment affected by irradiance
308 variations.

309 *Effects of biotic factors*

310 Sedimented organic carbon from the photic zone can represent a major food source for
311 deep-sea benthic foraminifera (Gooday 1988). Many studies report that the abundance of
312 benthic foraminifera assemblages is strongly correlated with surface ocean productivity (e. g.
313 Altenbach et al. 1999; Fontanier et al. 2002). Quick uptake of phytodetritus was observed
314 within the deep sea but also within shallow water dwellers (Middelburg et al. 2000; Moodley
315 et al. 2000; Moodley et al. 2002; Moodley et al. 2005; Nomaki et al. 2005a; Nomaki et al.
316 2005b). This high reactivity to food pulses may imply that uptake rates are strongly linked
317 with food abundance and type of food.

318 Theoretically, food uptake by a grazer increases with abundance of food. However, above
319 a threshold value of prey concentration, uptake rate remains constant (Holling's prey-
320 dependent type II functional response (Holling 1959)). Uptake of bacteria is not detectable at
321 the lowest bacterial concentration of 4.2×10^8 cells ml wt sed⁻¹ (Fig. 4). This lack of uptake
322 may occur for different reasons. One possibility could be that foraminifera does not feed at
323 low bacterial concentrations. Most probably, the ratio between enriched and non-enriched
324 bacteria used in our experiments was not high enough to allow uptake detection at low
325 concentration. Above 7×10^8 cells ml wt sed⁻¹, the rate of uptake of bacteria remained
326 constant, despite the increased of bacterial abundance (Fig. 5). The threshold value of prey
327 abundance may have been overshoot, which would mean that uptake by *Ammonia* would
328 seldom be higher than those measured. Bacterial abundance in superficial marine sediment is
329 relatively constant around 10^9 cells ml wt sed⁻¹ and seldom lower than 7×10^8 cells ml wt sed⁻¹
330 (Schmidt et al. 1998). According to these data, bacterial abundance in natural environment
331 would always satisfy the *Ammonia* optimal uptake rate and would never be limiting factor for
332 uptake.

333 Algal uptake rate increased linearly with algal abundance reaching 971 pgC ind⁻¹ h⁻¹
334 without levelling off for the tested values (Fig. 5). Algal abundances used during this
335 experiment (15 to 114 µgChla g dry sed⁻¹) are not high enough to reach the maximum algal
336 uptake rate; indeed *Ammonia* was found to graze at a higher rate on *Chlorella* (2180 pgC ind⁻¹
337 h⁻¹) (Moodley et al. 2000). In natural conditions, chlorophyll *a* content of the first centimetre
338 of sediment varies between 0 and 50 µgChla g dry sed⁻¹ (review in MacIntyre et al. 1996).
339 However, through vertical migration, benthic microalgae concentrate near the surface during
340 diurnal low tides producing a biofilm. In this algal mat, concentration of chlorophyll *a* can
341 reach 150 µgChla g dry sed⁻¹ (Serôdio et al. 1997) and even 300 µgChla g dry sed⁻¹ (Kelly et
342 al. 2001). *Ammonia* feeding on the algal biofilm would then present a higher uptake rate than
343 in the present study.

344 The use of differential labelling of bacterial food (¹⁵N) and algal food (¹³C) allows to
345 access simultaneous uptake rates of bacteria and algae, thus permitting to determine the
346 preferred item according to their availability. While algal uptake increased with algal
347 abundance, uptake of bacteria remained constant (Fig. 5). *Ammonia* still ingested bacteria
348 when other food resources were available. Bacteria might be a source of essential compounds
349 for deposit feeders (Lopez and Levinton 1987). This assumption is in accordance with Muller
350 and Lee (1969) who suggested that some foraminifera reproduce only when bacteria are
351 present as food source. Then, uptake of bacteria would be essential for *Ammonia*.

352 Uptake of bacteria by *Ammonia* never represented more than 19% of microbial biomass
353 (bacteria plus algae) taken up. This low contribution of bacteria to food uptake was also
354 observed with algal concentrations comparable with sediment natural conditions of 25 µg
355 Chla g dry sed⁻¹ (MacIntyre et al. 1996). Muller (1975) suggest that shallow water dwelling
356 species mainly depend on algal resources. In their study, van Oevelen et al. (2006) found that

357 bacterial carbon constitutes only 9% of total needs of hard-shelled foraminifera of an
358 intertidal mudflat community.

359 In intertidal areas, algal abundances vary seasonally (e. g. Haubois et al. 2005). In addition,
360 benthic microalgae of intertidal sediments vertically migrate with rhythms associated with
361 diurnal and tidal cycles (Blanchard et al. 2001). During day time, at low tide, algal cells
362 concentrate near the surface of sediment and form a mat (Herlory et al. 2004). According to
363 our results, *Ammonia* seems to depend principally on algal feeding resource. For this reason,
364 this species may feed on the mat of microphytobenthos when it is formed in order to maximize
365 its rate of energy gain. This feeding behaviour would imply that *Ammonia* dwells at the
366 surface of the sediment during low tide. Thus, *Ammonia* would be subject to all of the fast and
367 large environmental variations that are typical of the intertidal habitat, especially at the air-
368 sediment interface during low tide. Though *Ammonia* is considered as one of the most tolerant
369 genus of foraminifera to temperature and salinity variations (Bradshaw 1961; Walton and
370 Sloan 1990), we showed that variations of these parameters influence uptake of bacteria (Fig.
371 2 and 3). Vertical migration from the food-rich surface into deeper layers is a possible
372 mechanism for foraminifera to avoid unfavourable conditions (Groß 2002). In this deeper
373 layer, bacteria would constitute a large part of the diet of *Ammonia*. When temperature and
374 salinity allow *Ammonia* to migrate to the surface sediment, *Ammonia* would principally graze
375 on the microphytobenthic mat.

376 In conclusion, bacteria appeared to be quantitatively of minor importance in the nutrition
377 of foraminifera compared to algae. The present work demonstrates that, at the tidal scale,
378 grazing rate of bacteria is affected by abiotic (temperature and salinity) whereas it would not
379 be affected by biotic (algal and bacterial abundances) factors. *A. tepida* may further respond
380 to environmental changes at a seasonal scale, by physiological adjustment and shifting of its

381 optimum conditions. However, the present study does not permit to evaluate this acclimation
382 capacity and more efforts need to be made to take it into account.

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552 **Table and figure captions**

553 **Table 1.** Foraminiferal isotopic compositions ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$ means \pm SD, N = 3) and
554 bacterial and algal uptake rates calculated.

555 **Figure 1.** Bacteria uptake (mean \pm SD, N = 3) as function of incubation time (h).

556 **Figure 2.** Bacteria uptake rate (mean \pm SD, N = 3) as function of temperature ($^{\circ}\text{C}$).
557 Different letters above bars indicate significant differences between incubation conditions
558 (ANOVA; Tukey test).

559 **Figure 3a & 3b.** Bacteria uptake rate (mean \pm SD, N = 3) under low versus high salinity
560 (a) and dark versus light incubation (b). * indicate significant difference (t-test).

561 **Figure 4.** Bacteria uptake rate (mean \pm SD, N = 3) as function of bacteria abundance (10^8
562 cell ml wt sed $^{-1}$). Different letters above bars indicate significant differences between
563 incubation conditions (ANOVA; Tukey test).

564 **Figure 5.** Algae uptake rate \circ (mean \pm SD, N = 3) and bacteria uptake rate \bullet (mean \pm
565 SD, N = 3) as function of algal abundance ($\mu\text{gChla g dry wt sed}^{-1}$) under constant bacteria
566 abundance (10.5×10^8 cell ml wt sed $^{-1}$).

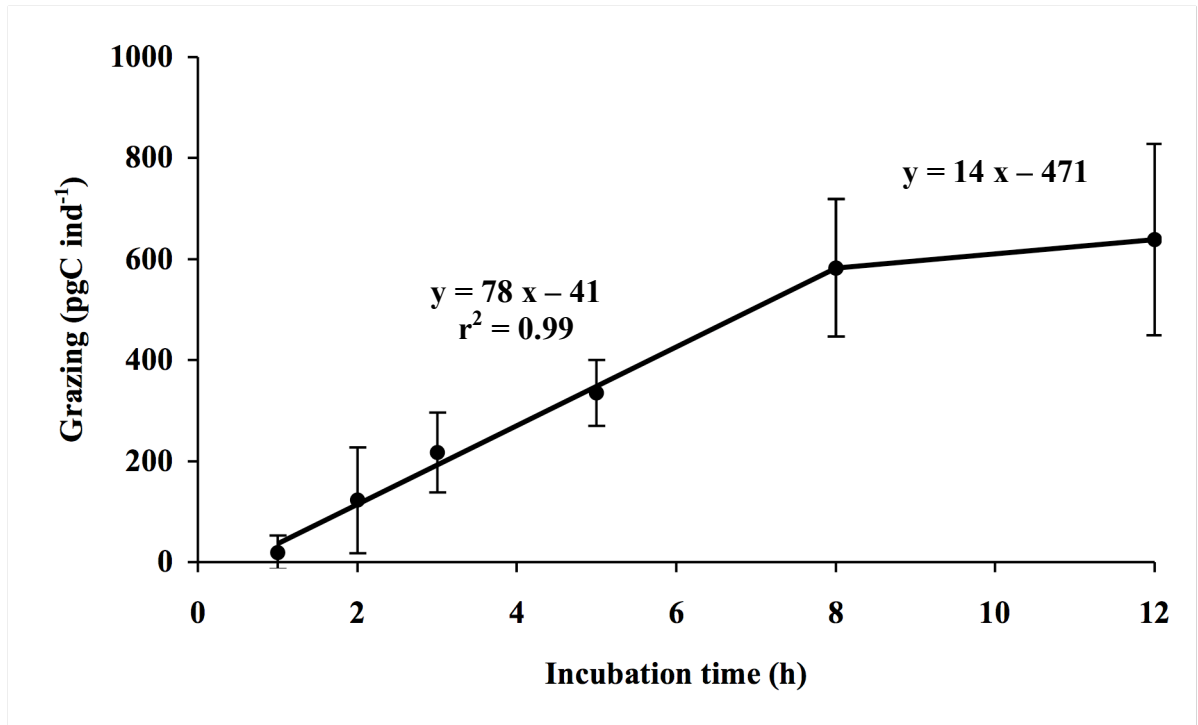


Fig. 1

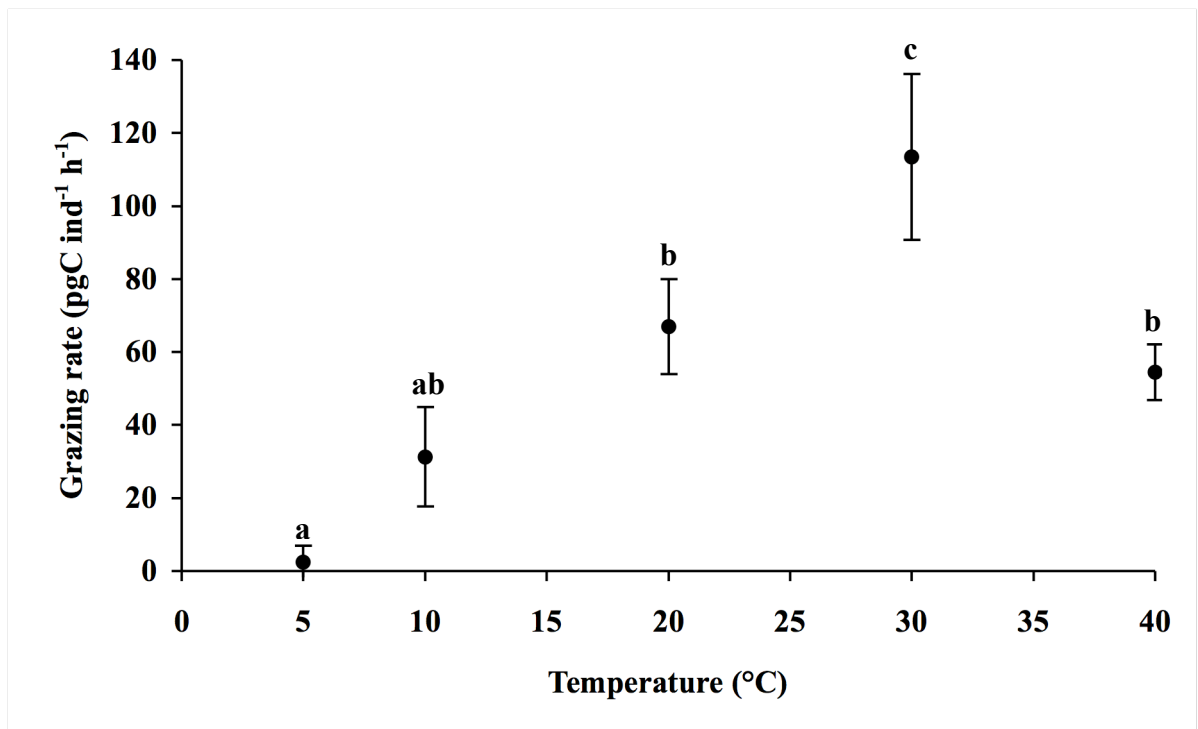


Fig. 2

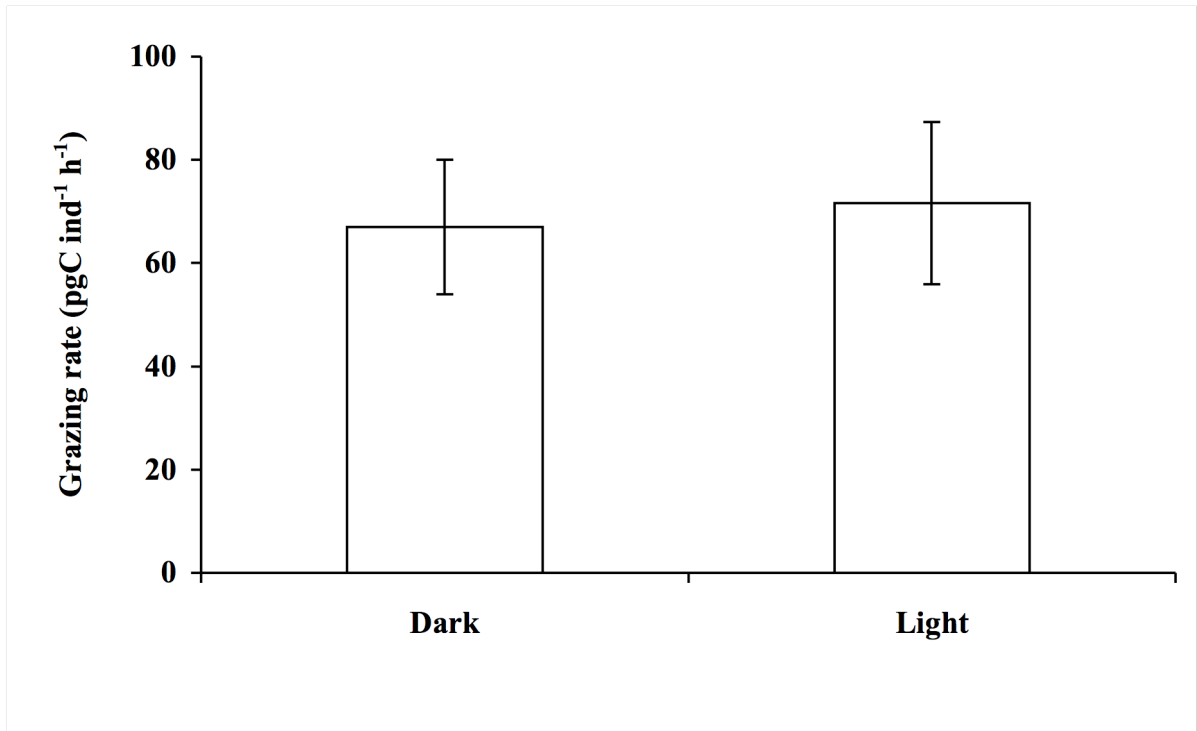
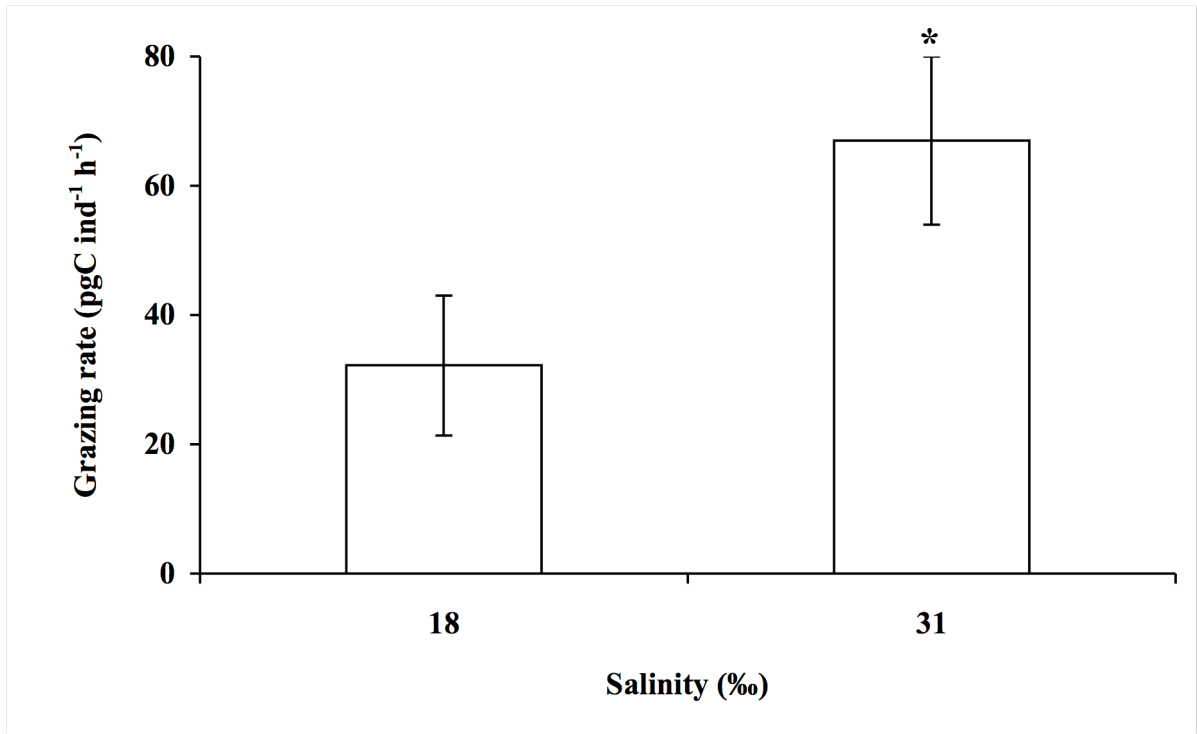


Fig. 3a & 3b

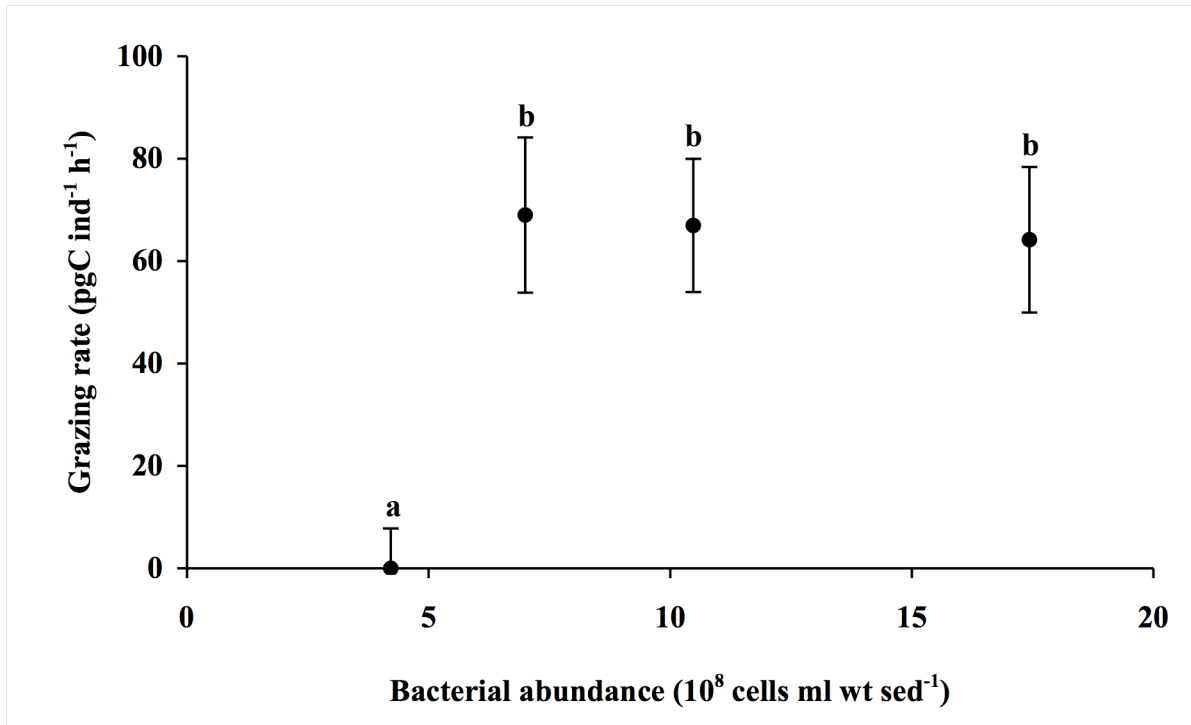


Fig. 4

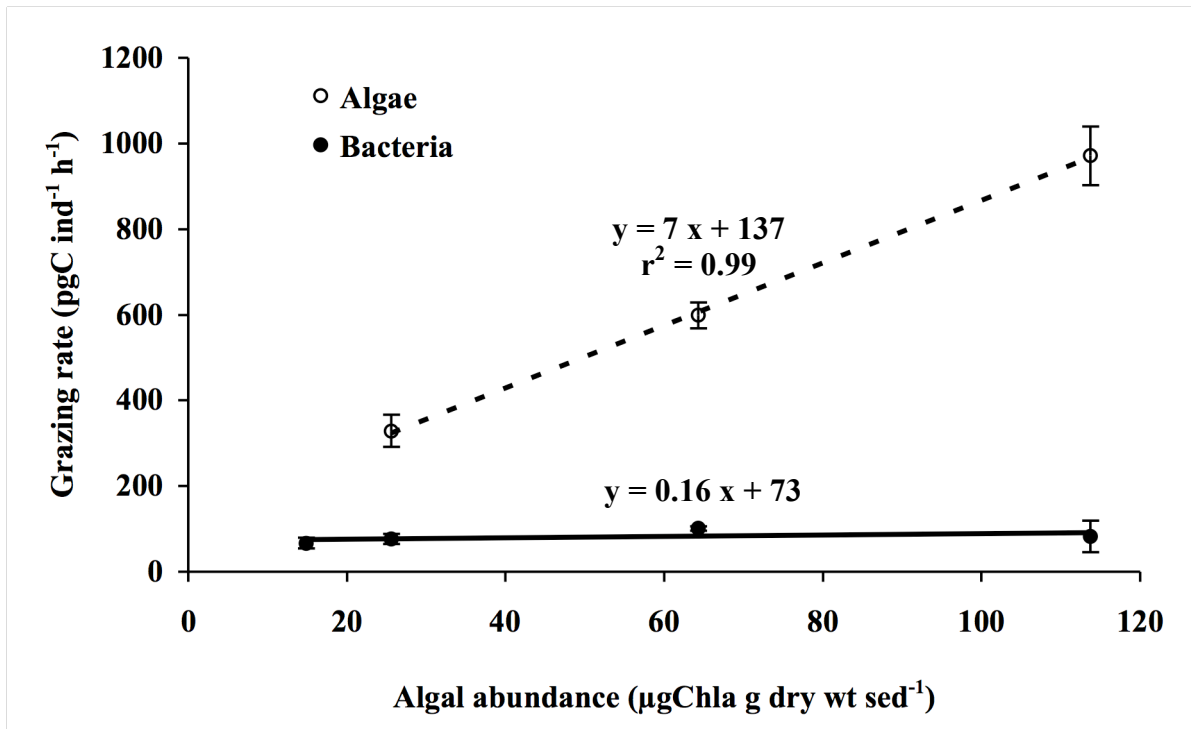


Fig. 5

Table

	$\Delta^{15}\text{N}$		Bacteria uptake (pg C ind ⁻¹ h ⁻¹)	$\Delta^{13}\text{C}$		Algae uptake (pg C ind ⁻¹ h ⁻¹)
	Control	Normal		Control	Normal	
Kinetics (hours)						
1	13.21 ± 0.33	13.40 ± 0.33	19.07 ± 33.03			
2	13.27 ± 0.18	14.50 ± 1.06	61.29 ± 52.57			
3	14.83 ± 0.12	17.02 ± 0.79	72.35 ± 26.24			
5	16.70 ± 0.19	20.08 ± 0.66	66.96 ± 13.00			
8	16.45 ± 0.21	22.33 ± 1.37	72.83 ± 16.97			
12	17.23 ± 0.48	23.67 ± 1.91	53.20 ± 15.80			
Temperature (°C)						
5	15.89 ± 0.45	16.01 ± 0.23	2.44 ± 4.54			
10	15.11 ± 0.34	16.68 ± 0.69	31.24 ± 13.63			
30	16.71 ± 0.63	22.44 ± 1.15	113.44 ± 22.77			
40	18.53 ± 0.24	21.28 ± 0.39	54.42 ± 7.65			
Irradiance						
Light	18.07 ± 0.19	21.69 ± 0.79	71.65 ± 15.73			
Salinity						
18	16.24 ± 0.48	17.87 ± 0.55	32.22 ± 10.82			
Bacterial abundance (10 ⁸ cells ml wt sed ⁻¹)						
4.2	12.83 ± 0.10	12.82 ± 0.11	0.84 ± 7.78			
7.0	14.10 ± 0.10	16.70 ± 0.57	69.00 ± 15.16			
17.4	20.96 ± 1.67	24.86 ± 0.86	64.17 ± 14.20			
Algal abundance (µg Chla g dry sed ⁻¹)						
25.6	16.70 ± 0.19	20.55 ± 0.57	76.29 ± 11.35	-3.63 ± 1.99	9.86 ± 1.55	328,80 ± 37.77
64.3	16.94 ± 0.08	22.03 ± 0.29	100.97 ± 5.73	-11.37 ± 0.27	36.31 ± 2.39	598,90 ± 30.05
113.7	17.48 ± 0.60	21.63 ± 1.84	82.15 ± 36.55	-8.21 ± 0.50	75.73 ± 5.93	971.45 ± 68.58

Tab. 1