

Bacterivory of a mudflat nematode community under different environmental conditions

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Abstract The fate of the benthic bacterial biomass is a topic of major importance in understanding how soft-bottom environments function. Because of their high abundance, production and nutritional value, benthic bacteria may constitute an important food resource for benthic fauna. The trophic role of bacteria for a nematode community on the Brouage mudflat (Marennes-Oléron-France), dominated by three species: *Chromadora macrolaima* (64% of the abundance), *Daptonema oxycerca* (15%) and *Ptycholaimellus jacobi* (8%), was determined in grazing experiments using ^{15}N pre-enriched bacteria. On intertidal flats, seasonal, tidal and circadian cycles induce strong variations in environmental conditions. Grazing experiments were performed in order to measure the effects of abiotic (temperature, salinity and luminosity) and biotic (bacterial and algal abundances) factors on assimilation rates of bacteria by nematodes. In order to assess simultaneously bacteria and algal assimilation rates, algal abundances were modified adding ^{13}C pre-enriched *Navicula phyllepta*. Assimilation rate was significantly lower at 5°C; moreover, general trend shows a prominent temperature effect with an optimum around 30°C. Assimilation at salinity 18 was not significantly different from the assimilation at salinity 31. Assimilation

was higher under light conditions than in the dark. Above 10^9 bacteria ml^{-1} , assimilation of bacteria remained unaffected by bacterial abundance. However, assimilation of algae increased with the algal concentration. Nematode kept feeding under conditions of stress, which are typical of the surficial sediment habitat and they appeared to be principally dependent on the algal resource.

Introduction

Bacteria play a major role in cycling organic matter in marine sediments through the remineralization of nutrients and organic matter and production of particulate and dissolved carbon (e.g. Legendre and Rassoulzadegan 1996; Rivkin et al. 1996). Although bacterial abundance remains stable, around 10^9 cells ml^{-1} (review in Schmidt et al. 1998), bacterial production rates vary greatly (Sander and Kalf 1993). This discrepancy between abundance and production may be induced by bottom-up, biochemical and top-down control (van Oevelen et al. 2006a). In the top-down control situation, bacterial carbon is assumed to be regulated by higher trophic levels of benthic food webs.

The majority of animals feeding on sedimentary deposits are more dependent on attached bacteria than on nonliving organic debris (e.g. Fenchel 1972). Models of benthic ecosystems emphasize the role of bacteria and their immediate grazers as a major route through, which organic material is processed (e.g. Kuipers et al. 1981). Consequently, quantitative data dealing with the link between bacteria and benthic fauna are essential for understanding the extent to which this trophic link structures energy and material fluxes in the communities.

Results concerning the impact of meiofaunal grazing on bacteria are conflicting (Kemp 1990). Montagna (1984b)

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suggested that meiofaunal grazing pressure (principally through polychaetes) represents a significant stimulatory effect on the microbial community and may be important in sandy sediments (Montagna and Bauer 1988). However, quantitative studies on meiobenthos bacterivory are sparse.

Although they are small and inconspicuous, nematodes are consistently the most abundant meiobenthic taxon in mudflat sediments. Their average density of 10^6 ind m^{-2} represent a biomass of roughly $0.2\text{--}2$ gC m^{-2} and some authors have suggested that their ecological significance is great in terms of food-web relationships (review in Platt and Warwick 1980; Heip et al. 1985).

Benthic bacteria can constitute a significant food source for nematodes (Lopez et al. 1979; Tietjen 1980; Montagna 1984b; 1995; Moens et al. 1999b). According to Wieser (1960), there are four different feeding groups of nematodes: selective deposit feeders (1A), non-selective deposit feeders (1B), epigrowth feeders (2A) and omnivore-predators (2B). Nematodes of each feeding group are potentially bacterivores, even predacious ones may benefit directly of bacterial carbon (Moens et al. 1999b). Deposit and epigrowth feeders feed on bacteria and unicellular eukaryotes in different ways. Deposit-feeding species have no teeth and generally swallow the food whole and undamaged. They feed predominantly on bacteria associated with detritus. The epigrowth-feeding species puncture the cell membrane with their teeth and ingest only the cell contents (juice feeders). Diatoms and other benthic microalgae are known to be important trophic sources for many epigrowth feeders but the importance of bacteria as a food source remains poorly documented (Moens and Vincx 1997). The aim of this study was to experimentally assess rates of bacteria uptake by a nematode community from an intertidal mudflat using ^{15}N -enriched bacteria as tracers. The intertidal habitat studied is subject to a wide range of environmental varying factors. Three relevant time scales drive these environmental variations: long-term (seasonal cycle), medium-term (lunar cycle) and short-term (solar and tidal cycles) (Guarini et al. 1997). Variations concern both biotic (i.e., temperature, salinity, and luminosity) and abiotic factors (i.e., bacterial and algal abundances). As those variations may influence the feeding behavior of nematodes, one aim of the present study is to determine if nematodes bacterivory is constant in the mudflat or influenced by environmental factors. The other aim is to describe feeding behavior of nematodes when an alternative algal resource is available.

For this purpose, a mudflat nematode community from surficial sediment was put in microcosms, in contact with labeled preys: a bacterial community and one algal species. Grazing experiments were performed in order to evaluate the effects of abiotic (temperature, salinity, and luminosity) and biotic (bacterial and algal abundances) factors on rates

of prey uptake. We focused on the surficial mudflat sediment nematode community because the surficial sediment (1) has high bacterial production, (2) contains the highest nematode densities and (3) undergoes faster and more wide-ranging changes in environmental factors than do the deeper layers.

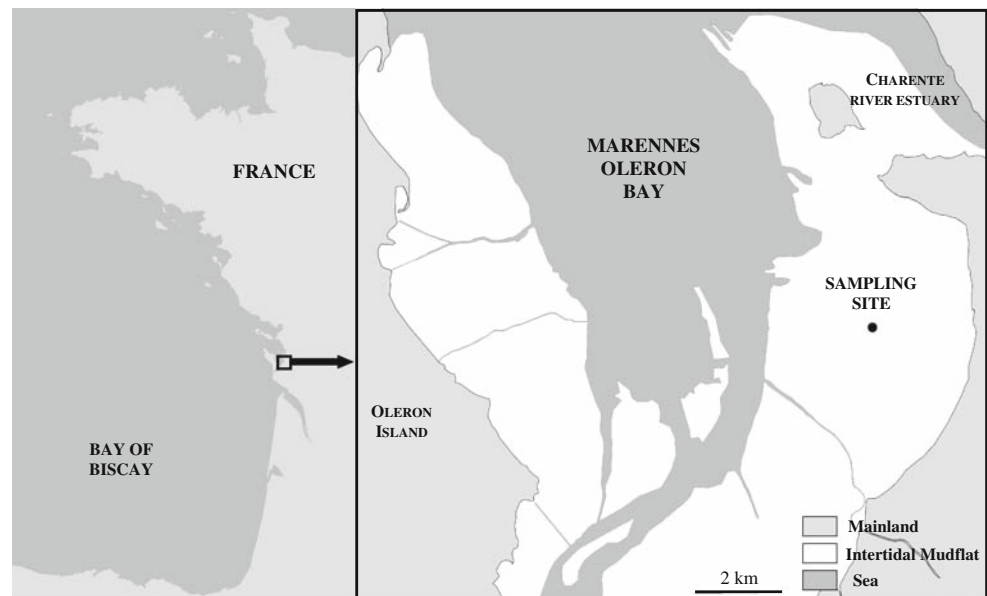
Material and methods

Study site

The Brouage intertidal mudflat is located in the eastern part of the Marennes-Oléron Bay (Atlantic coast of France). Meteorological conditions exhibit a strong seasonality typical of a temperate climate. Temperature and salinity of emerged sediments are more extreme during summer tidal cycles (Guarini et al. 1997). Minimum and maximum mud temperatures are 5 and 34°C, respectively. The maximum daily range of mud temperature due to emersion and immersion cycle reaches 18°C (Guarini et al. 1997). Salinity of overlaying water is controlled by the river Charente freshwater input, ranging from 25 to 35 over the year (Héral et al. 1982). Salinity of the upper layers of sediment may also decrease with rainfall. The sediment surface irradiance shifts from dark during submersion and night emersions to high levels of incident light during daytime emersions. This irradiance can reach $2,000$ μM of photons $m^{-2} s^{-1}$ (Underwood and Kromkamp 2000). Details of numerous benthic organisms and processes are available concerning this intertidal zone (gathered in Leguerrier et al. 2003, 2004; Degré et al. 2006).

^{15}N -enriched bacteria and ^{13}C -enriched algae as tracer

The method used was as described in Pascal et al. (2008). This method is based on the assumption that grazers ingest unselectively enriched and natural bacteria. Briefly, 1 cm-depth of surficial sediment was sampled during ebb tide in the Brouage mudflat (45°55N, 1°06W) (Fig. 1). Bacteria from surficial sediment were cultured in a liquid bacterial culture medium containing $^{15}\text{NH}_4\text{Cl}$ 1 g l^{-1} (99% ^{15}N -enriched NH_4Cl CortecNet), rinsed by centrifugation and frozen until the grazing experiments. An axenic clone of the *Navicula phyllepta* diatom (CCY 9804, Netherlands Institute of Ecology NIOO-KNAW, Yerseke, The Netherlands) was cultured in a liquid medium containing $\text{NaH}^{13}\text{CO}_3$, then rinsed and freeze-dried until the grazing experiments. Isotopic composition of enriched prey was assessed using mass spectrometry. For these experiments, labeled preys were mixed with sediment from the Brouage mudflat that had been previously sieved through a 50- μm mesh. The abundance of bacteria and algae in the slurry

Fig. 1 Map of the study site

was estimated in order to determine the ratio between enriched and unenriched prey.

Grazing experiments

The top centimeter of sediment was collected on 13 March 2006. At the time of sampling, the sediment presented a temperature of 7°C and a salinity of 29. The sediment sampled was first sieved through a 500- μm mesh to remove macrofauna, then through a 50- μm mesh to extract meiofauna. One milliliter of the sediment remaining in the mesh was put into each microcosm (Pyrex beakers, $\phi = 4.5$ cm) and the fraction which passed through the mesh was mixed with ^{15}N -enriched bacteria. This slurry contained 10.5×10^8 bacteria ml^{-1} , with the ^{15}N -enriched bacteria being twice as abundant as unenriched ones. Four ml of this slurry were put into each microcosm. Each experiment was carried out in triplicate. Control samples were frozen (-80°C) in order to kill any nematodes.

A kinetic study was performed to validate its linear or hyperbolic shape in order to calculate the grazing rate. Incubations for this kinetic study were run for 1–12 h, including the 3-h run that was used for all other experiments. Incubations were made under the following standardized conditions that were close to the year-round mean values recorded on the study site: temperature (20°C), salinity (31), luminosity (darkness), bacterial abundance (10.5×10^8 bacterial cell ml^{-1}) and algal abundance ($15 \mu\text{gChla g}^{-1}$).

For each other experiment one environmental incubation factor was modified. In order to decrease salinity, cultured bacteria were rinsed with 0.2 μm filtered-sea-water diluted

with 0.2 μm filtered water (final salinity of 18). The light effect was tested with a light intensity of 83 μM photons $\text{m}^{-2} \text{s}^{-1}$. Bacterial abundances (total enriched and non-enriched) tested were 4, 7 and 17 cells ml wt sed^{-1} with, respectively, the following ratio between abundance of total and enriched bacteria: 6.1, 2.0 and 1.3. Algal abundance was modified by adding various quantities of cultured *N. phyllepta* enriched in ^{13}C , while bacterial abundances (total enriched and non-enriched) were kept constant at 10×10^8 cells ml^{-1} . Using two isotopes for labeling bacterial (^{15}N) and algal food (^{13}C) offers the opportunity to assess bacterial and algal ingestion rates simultaneously. Algal abundance (total enriched and non-enriched) were 26, 64 and 114 $\mu\text{gChla g dry sed}^{-1}$ with, respectively, the following ratio between abundance of total and enriched algae: 2.4, 1.3 and 1.2.

Incubations were halted by freezing the microcosms at -80°C . Samples were thawed and nematodes were extracted from the sediment using Ludox TM (Heip et al. 1985). For each sample, at least 700 nematode specimens were picked up randomly and individually with Pasteur pipette, rinsed twice in Milli-Q water to remove adhering particle, and transferred to aluminium cup.

Isotope analysis and calculations

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of prey (bacteria and algae) and grazers (nematodes) were measured using an EA-IRMS (Isoprime, Micromass, UK). Nitrogen isotope composition is expressed in the delta 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 isotope composition is expressed in the delta notation

($\delta^{13}\text{C}$) relative to Vienna Pee Dee Belemnite (VPDB): $\delta^{13}\text{C} = [(^{13}\text{C}/^{12}\text{C})_{\text{sample}} / (^{13}\text{C}/^{12}\text{C})_{\text{reference}} - 1] \times 1000$.

The ^{15}N incorporated was defined as excess (above the background level) ^{15}N and is expressed in terms of specific uptake (I). I was calculated as the product of excess ^{15}N (E) and the biomass of N per grazer. E is the difference between the background ($F_{\text{background}}$) and the sample (F_{sample}) ^{15}N 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 isotope ratio. For the $F_{\text{background}}$, we used highest control values ($\Delta^{15}\text{N} = 11.78$ and $\Delta^{13}\text{C} = -16.34$) measured using killed (frozen) grazers. R was derived from the measured $\delta^{15}\text{N}$ values as: $R = [(\delta^{15}\text{N}/1000) + 1] \times R_{\text{air-N}_2}$ where $R_{\text{air-N}_2} = 7.35293 \times 10^{-3}$ (Mariotti 1982). The uptake of bacterial carbon was calculated as

$$\text{Uptake} = (I \times (\%C_{\text{enrichedbacteria}} / \%N_{\text{enrichedbacteria}}) / (F_{\text{enrichedbacteria}} \times \text{incubationtime}))$$

This uptake was multiplied by the ratio between the abundance of total and enriched bacteria determined by DAPI counts.

Incorporation of ^{13}C was calculated analogously, with $F = ^{13}\text{C} / (^{13}\text{C} + ^{12}\text{C}) = R / (R + 1)$, $R_{\text{air-N}_2}$ is replaced by $R_{\text{VPDB}} = 0.0112372$ and $\text{Uptake} = I / (F_{\text{enriched bacteria}} \times \text{incubation time})$. The uptake measured was multiplied by the ratio between the abundance of total and enriched diatom, determined from fluorometrical measurements.

Enriched *N. phyllepta*-produced carbon consisted of $22.95 \pm 0.54\%$ ^{13}C . The C/N ratio of enriched bacteria was 3.49 and bacterial nitrogen consisted of $2.88 \pm 0.03\%$ ^{15}N . The average weight of nematodes was $0.33 \pm 0.18 \mu\text{g}$ DW and each nematode was composed on average of $0.11 \pm 0.05 \mu\text{gC}$ and $22.28 \pm 5.82 \text{ ngN}$ ($N = 72$ samples of at least 700 specimens each). Uptake expressed as $\text{gC}_{\text{bacteria}} \text{ gC}_{\text{nematode}}^{-1} \text{ h}^{-1}$ was obtained by dividing the uptake of bacteria ($\text{gC ind}^{-1} \text{ h}^{-1}$) by the mean nematode weight (gC ind^{-1}).

Variations of assimilation rates with respect to the salinity and luminosity were tested using two-tailed test. One-way analysis of variance (ANOVA) was used in order to test the impact of temperature and algal and bacterial abundance on the uptake rates of bacteria and algae. The Tukey test was used for post hoc comparisons.

Nematode community composition

Nematode communities used in the grazing experiments were extracted from sediment with Ludox TM (Heip et al. 1985). In order to determine the taxonomic composition of the community studied, 303 nematodes were collected at random, determined to species or generic level under the microscope and sorted by feeding group as indicated by Wieser (1953, 1960).

Table 1 List of species ranked by dominance [feeding types according to Wieser (1953, 1960)]

Genera species	Feeding type	Relative abundance (%)
<i>Chromadora macrolaima</i>	2A	64.2
<i>Daptonema oxycerca</i>	1B	15.2
<i>Ptycholaimellus jacobi</i>	2A	7.9
<i>Sabatieria pulchra</i>	1B	2.6
<i>Axonolaimus paraspinosus</i>	1B	1.7
<i>Praeacanthonchus punctatus</i>	2A	1.7
<i>Halalaimus</i> sp.	1A	1.0
<i>Aegialoalaimus</i> sp.	1A	1.0
<i>Sphaerolaimus gracilis</i>	2B	0.7
<i>Spilophorella</i> sp.	2A	0.7
<i>Metachromadora</i> sp.	2A	0.7
<i>Theristus</i> sp.	1B	0.3
<i>Parodontophora marina</i>	1B	0.3
<i>Tripyloides marinus</i>	1B	0.3
<i>Eleutherolaimus</i> sp.	1B	0.3
<i>Desmolaimus zeelandicus</i>	1B	0.3
<i>Daptonema hirsutum</i>	1B	0.3
<i>Terschellingia</i> sp.	1A	0.3
<i>Viscosia</i> sp.	2B	0.3

1A: selective deposit feeders; 1B: non-selective deposit feeders; 2A: epigrowth feeders; 2B: omnivores/predators

Results

Composition of the nematode community

In the sample collected for the taxonomy of the nematode community, 19 species belonging to 18 genera were observed (Table 1). Three species made up more than 87% of the community: *Chromadora macrolaima* (64%), *Daptonema oxycerca* (15%) and *Ptycholaimellus jacobi* (8%). The other species were much less abundant, 11 species representing less than 1%.

The community was dominated by epigrowth feeders 2A (75%) due to high abundances of *C. macrolaima* and *P. jacobi*. Non-selective deposit feeders 1B (21%) were the second most abundant trophic group due to high abundance of *D. oxycerca*. Selective deposit feeders 1A (2%) and omnivores/predators 2B (1%) exhibited marginal abundances in the community studied.

Uptake of microbes by nematodes

Nematodes isotopic compositions and rates of bacterial and algal uptakes are presented in Table 2.

The kinetic experiment showed that bacterial uptake by the nematode community increased linearly during the 12-h of incubation (Fig. 2). The linear regression slope

Table 2 Nematodes isotopic composition ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ mean \pm SD, $N = 3$) and bacterial and algal uptake rates calculated

	$\delta^{15}\text{N}$		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 (h)						
1		12.01 \pm 0.25	3.67 \pm 4.06			
2		14.24 \pm 0.86	20.00 \pm 7.03			
3	11.78 \pm 0.23	15.20 \pm 0.38	18.51 \pm 2.05	-15.4 \pm 1.32		
5		20.63 \pm 1.49	28.80 \pm 4.84			
8		27.72 \pm 1.55	32.41 \pm 3.15			
12	11.56 \pm 0.87	32.66 \pm 4.91	28.31 \pm 6.65	-15.8 \pm 0.77		
Temperature ($^{\circ}\text{C}$)						
5		12.41 \pm 0.53	3.38 \pm 2.87			
10		14.60 \pm 0.50	15.26 \pm 2.70			
30		16.38 \pm 0.79	24.92 \pm 4.27			
40		15.18 \pm 1.73	18.42 \pm 9.38			
Irradiance Light		19.42 \pm 2.01	41.43 \pm 10.88			
Salinity 18		15.03 \pm 0.66	17.62 \pm 3.57			
Bacterial abundance (10 ⁸ cells ml wt sed ⁻¹)						
4.2		11.75 \pm 0.20	-0.65 \pm 4.39			
7.0		12.25 \pm 0.40	3.34 \pm 2.93			
17.4		15.86 \pm 0.10	18.34 \pm 0.45			
Algal abundance (μg Chla g dry sed ⁻¹)						
25.6		15.39 \pm 0.59	19.58 \pm 3.19	-4.44 \pm 6.53		58.94 \pm 32.35
64.3		15.58 \pm 0.51	20.59 \pm 2.78	25.60 \pm 4.79		107.11 \pm 12.24
113.7	11.50 \pm 0.17	14.34 \pm 0.61	13.87 \pm 3.33	-16.34 \pm 0.53	52.14 \pm 33.29	161.20 \pm 78.30

suggested an assimilation rate of bacteria of 32 pgC ind⁻¹ h⁻¹ equivalent to 25×10^{-5} gC_{bacteria} gC_{nematode}⁻¹ h⁻¹ ($r^2 = 0.98$).

Temperature had a significant effect on the assimilation rate of bacteria ($F = 7.5$, $P < 0.005$). Temperature tested fluctuated between 5 and 40 $^{\circ}\text{C}$, and was in the range of those found in the study area (Guarini et al. 1997). Uptake of bacteria was reduced at 5 $^{\circ}\text{C}$, then increased with temperature to reach an optimum at around 30 $^{\circ}\text{C}$ and then decreased (Fig. 3). This rate increased from 3 to

25 pgC ind⁻¹ h⁻¹ when the temperature rose from 5 to 30 $^{\circ}\text{C}$ and then decreased, reaching 18 pgC ind⁻¹ h⁻¹ at 40 $^{\circ}\text{C}$. The overall trend is showed a prominent temperature effect but assimilation rates observed at 10, 20, 30 and 40 $^{\circ}\text{C}$ were nevertheless not significantly different from each other, but were significantly different from those observed at 5 $^{\circ}\text{C}$.

The assimilation rate at a salinity of 31 (19 ± 2 pgC ind⁻¹ h⁻¹) was similar (two-tailed test, $P = 0.72$) to that found for a salinity of 18 (18 ± 4 pgC ind⁻¹ h⁻¹) (data not shown).

Light significantly affects the feeding activity of nematodes (two-tailed test, $P < 0.05$). Assimilation rates were more than twice as high (41 ± 11 pgC ind⁻¹ h⁻¹) under light ($83 \mu\text{M}$ of photons m⁻² s⁻¹) than in darkness (19 ± 2 pgC ind⁻¹ h⁻¹) (data not shown).

Assimilation rates were significantly linked with bacterial abundance ($F = 52$, $P < 0.001$) (Fig. 4). Its value was null for the lowest tested abundance (4×10^8 cells ml⁻¹), was amplified more than fourfold when abundance increased from 7×10^8 cells ml⁻¹ to 10×10^8 cells ml⁻¹ and remained stable between this last value and 17×10^8 cells ml⁻¹.

Using two isotopes to label bacterial (¹⁵N) and algal food (¹³C) offers the opportunity to assess bacterial and

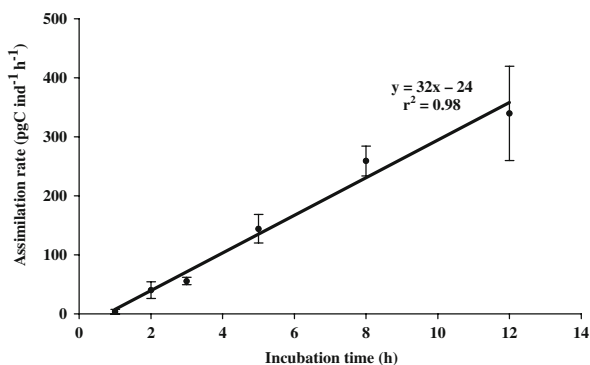


Fig. 2 Assimilation of bacterial carbon (mean \pm SD, $N = 3$) as function of incubation time (h)

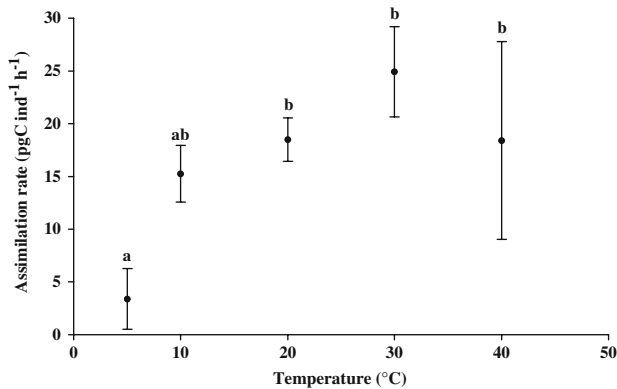


Fig. 3 Assimilation rate of bacterial carbon (mean \pm SD, $N = 3$) as function of temperature ($^{\circ}\text{C}$). Different letters above bars indicate significant differences between incubation conditions (ANOVA; Tukey test)

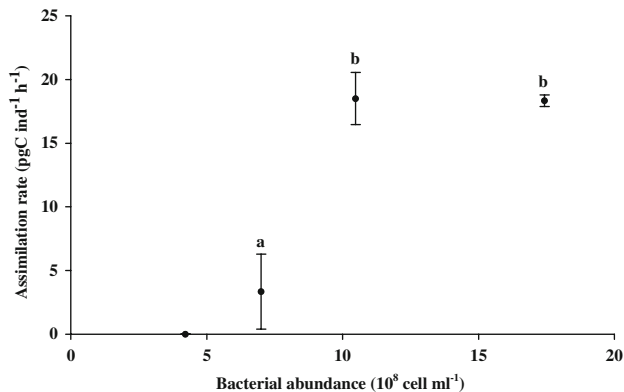


Fig. 4 Assimilation rate of bacterial carbon (mean \pm SD) as function of bacterial abundance (10^8 cell.ml⁻¹). Different letters above bars indicate significant differences between incubation conditions (ANOVA; Tukey test)

algal uptake rates simultaneously. Assimilation of algae increased linearly when algal abundance increased ($r^2 = 0.99$, $P < 0.05$). Bacteria represented 25, 16 and 8% of algal plus bacterial intake when algal concentrations were, respectively, 26, 64 and 114 $\mu\text{gChla g}^{-1}$, with bacterial abundance remaining constant (Fig. 5). Plotted data indicated that assimilation of bacteria declines when the algal concentration is high (114 $\mu\text{gChla g}^{-1}$) and the bacterial concentration remains constant (Fig. 6). Nevertheless, these differences were not significant and assimilation of bacteria was unaffected by algal abundance ($F = 3.24$, $P = 0.11$).

Discussion

Nematode community

Rzeznik-Orignac et al. (2003) studied the Brouage mudflat nematode community and showed that in the lower part of

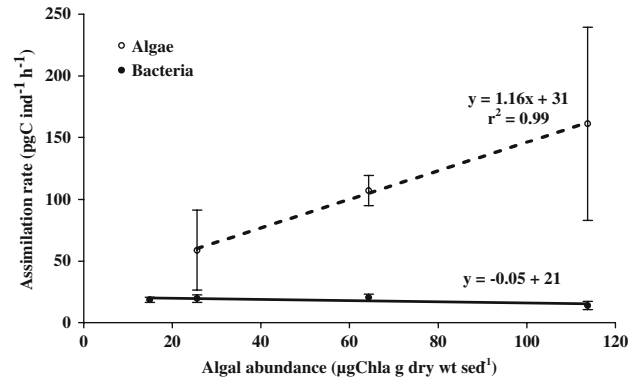


Fig. 5 Uptake rate of algal carbon (open circle) (mean \pm SD) and bacterial carbon (filled circle) (mean \pm SD) as function of algal abundance ($\mu\text{gChla g}^{-1}$). Bacterial abundance was constant (10.5×10^8 cells ml⁻¹)

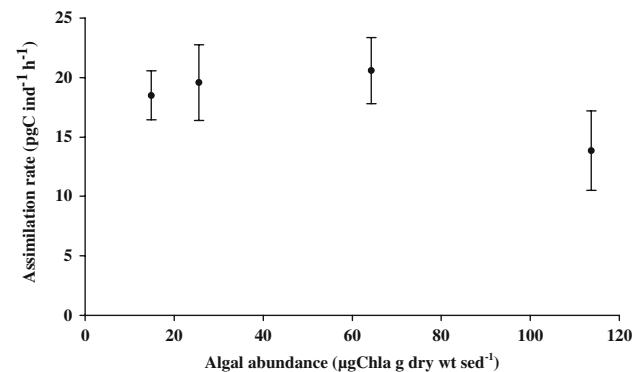


Fig. 6 Assimilation rate of bacterial carbon (mean \pm SD) as function of algal abundance ($\mu\text{gChla g}^{-1}$)

the mudflat and over four seasons (2000–2001), six dominant species represented 45% of the community: *Metachromadoroides remanei* (11.5%), *Terschellingia longicaudata* (11.2%), *P. jacobii* (8.6%), *C. macrolaima* (8.6%), *Sabatiera pulchra* (5.2%) and *D. oxycerca* (0.7%). In our study, performed in March 2006, only three species, although all mentioned in the Rzeznik-Orignac et al. study, represented 87% of the community (Table 1). As the sampling site was the same, difference in nematode community composition may be due to inter-seasons or inter-years fluctuations. More probably, major difference has to be put into relation with the sampling method used in each of these studies. In the present one, only the top centimeter of sediment was sampled, whereas the top 5 cm was sampled in Rzeznik-Orignac et al. (2003) study. As nematodes exhibit a strong vertical distribution of species in sediment (e.g. Platt 1977; Steyaert et al. 2001), the community in the present study is not representative of the total Brouage mudflat nematode community. Moreover, the three major species of the community under study belong

to the *Daptonema* and *Ptycholaimellus* genera that were mainly found in the 5-mm surficial layer of sediment (Steyaert et al. 2003) and the third one, belonging to the family Chromadoridae is a typical surface-dwelling epigrowth feeder (Platt 1977).

Feeding habits on diatoms of some genera close to *Chromadara* are known from culture experiments: *Chromadorita tenuis* (Jensen 1987) and *Chromadora macrolaimoides* (Tietjen and Lee 1973). *Chromadora macrolaima* and *Ptycholaimellus jacobii* break or pierce the frustule of diatoms to suck out their contents, whereas *Daptonema oxycerca* swallow the whole diatom cell (Wieser 1953, 1960). Our nematode community is mainly composed of three dominant species known or suspected to feed predominantly on diatoms. The entire nematode community presents, however, higher abundances of bacterial grazers (Rzeznik-Orignac et al. 2003). As a result, extrapolation of the present grazing results to the rest of the community or to other communities must be realized with caution.

Grazing experiments

Like all various methods previously developed and applied to measure bacterivory, the method used in the present study presents methodological shortcomings that make interpretation of the resulting problematic. For instance, sieving the sediment changes the bacterial availability, bacteria being not attached to particle as in natural situation. Indeed, disruption of microbial-meiofaunal spatial relationships is known to affect grazing rate with slurry method (Carman et al. 1989). Nematode grazing can be highly dependent on their bacterial prey's activity, size and species (Tietjen et al. 1970; Tietjen and Lee 1973; Romeyn and Bouwman 1983; Grewal and Wright 1992; Moens 1999; Moens et al. 1999a). One major hypothesis in grazing experiments is that grazers did not select for or against the added labeled bacteria over the bacteria present in the sediments. Consequently, the cultured bacteria community must present characteristics that are roughly similar to the natural one. Despite the fact that our culturing process modified the specific composition of the natural bacterial community, the size, activity and diversity of the bacterial consortium used in the present study would be more representative of the natural community than in most previous grazing experiments (Pascal et al. 2008).

Bacterial and algal uptake

^{15}N accumulation in nematodes was linear over the 12-h incubation period (Fig. 2). The constant accumulation of labeled food in nematodes had already been observed with comparable incubation times (Herman and Vranken 1988;

Moens et al. 1999c). Since the nematode defecation intervals are very short (e.g. Thomas 1989) and since the gut is emptied completely with each defecation (Duncan et al. 1974), the gut contents would thus be renewed every few minutes. For these reasons, it has been suggested that during long incubation times, the linear accumulation of the label indicates assimilation rather than ingestion (Schiemer 1987; Moens et al. 1999c). The slope of this linear curve gives an assimilation rate of $32 \text{ pgC ind}^{-1} \text{ h}^{-1}$. Assuming an assimilation rate of 25% (Herman and Vranken 1988; Somerfield et al. 2005), the ingestion rate would be four times higher, at $128 \text{ pgC ind}^{-1} \text{ h}^{-1}$. As all other grazing experiments were run for 3 h, they provided the assimilation rate of food.

Abiotic factors

Behavioral responses of plant-parasites and terrestrial nematodes to several stimuli such as electrical, mechanical and chemical stimuli and physical factors such as temperature and light have been well described (review in Croll 1970). However, similar studies concerning the effect of environmental conditions on the feeding behavior of marine or brackish-water nematodes are scarce and limited in scope.

Temperature has received attention as a factor influencing the growth and reproduction of estuarine and marine nematodes (review in Heip et al. 1985). The influence of temperature on feeding has only been studied in the predacious nematode *Enoploides* (Moens et al. 2000), the epigrowth feeder *Chromadora macrolaimoides* (Tietjen and Lee 1973) and in two brackish-water bacterivorous species: *Pellioiditis marina* and *Diplolaimelloides meyli* (Moens et al. 1996; Moens and Vincx 2000). In the present study, nematodes exhibited a classical response which was more or less related to a bell-shaped function as also observed by Moens and Vincx (2000). The assimilation rate of bacteria rose when the temperature increased and reached its upper value of 30°C before declining. As assimilation rates recorded for the tested temperatures were statistically different at 5°C , it may be suggested that the nematode grazing rate is lower in winter when the temperature drops below 5°C . However, nematodes may adjust their optimum temperature conditions along seasons (Gee 1985). Studied nematodes were probably adapted to low temperature as sediment temperature was 7°C at the time of the sampling. Montagna (1984b) did not observe different grazing rates between winter and summer, but the temperature range in his study area was small ($18\text{--}23^\circ\text{C}$).

Salinity plays a major role in determining the spatial structure of the nematode community along permanent gradients (Soetaert et al. 1995) or in its seasonal variations (Chatterji et al. 1995). However, nematodes can also be

affected by short-term variations in salinity (Forster 1998) and intertidal habitats are subject to major changes in interstitial salinity over short time periods. During low tide, raindrops implode into fine sediments, disturbing and mixing the surface sediment of mudflats. Moreover, freshwater run-off passively diffuses into the interstitial pores of the sediment. In their review of marine nematode ecology, Heip et al. (1985) compiled an extensive list of marine and estuarine species with their salinity tolerances. *C. macrolaima*, the most abundant species in the present study, is found in areas with salinities ranging from 35 to 24, whereas *D. oxycerca*, the second most abundant species, is found in area ranging from 35 to 0.9. This species seemed to be able to tolerate gradual changes in salinity, but not rapid ones. After exposure to salinity of 3.33 for 10 min and 48 h, Forster (1998) recorded adult mortalities of 10–35 and 70%, respectively. This species from the lower level of the intertidal zone is able to osmoregulate, but unable to sustain water regulation over long periods (Forster 1998). In the present study, assimilation at salinity 18 was not significantly different from the assimilation at salinity 31. Since the nematodes were not acclimated until the grazing experiment, they seemed to be able to cope with rapid, but limited, osmotic stress. Our conclusions concerning the minor role of salinity in bacterial assimilation by nematodes are in accordance with Moens and Vincx's (2000) results. Among the three factors they investigated (temperature, salinity and food abundance) affecting *P. marina* and *D. meyli* food intake, salinity played a minor role in bacterial assimilation by nematodes.

When exposed to air at low tide, benthic organisms at the sediment's surface are subject to the highest solar and UVB radiation that can be experienced by marine organisms. There are few investigations assessing the effects of luminosity on nematodes. The predacious nematode *Enoploides* caught approximately twice as many prey nematodes in the dark as in light (Moens et al. 2000). On the other hand, Sundbäck et al. (1996a) concluded that ambient UVBs did not exert any strong selective pressure on the meiofaunal community of a muddy microtidal area. Nozais et al. (1999) observed a deleterious effect of UVBs on the nauplia stages of harpacticoid copepods from a tidal mudflat. However, they did not observe any effect on nematode abundance. In our study, light may not present damaging effect as nematodes fed actively; moreover bacterial assimilation was enhanced when light increased. Uptake rates of bacteria by foraminifera (Pascal et al. 2008) and the gastropoda *Hydrobia ulvae* (P. Y. Pascal et al., in preparation) that were obtained by grazing experiments performed under the same conditions as in present study did not demonstrate any effect of light. Consequently, the response we observed should not be due to experimental bias and seems to be specific to nematodes.

Montagna et al. (1995) observed a significant correlation between algal production and the grazing rate of a nematode community from the Brouage mudflat. In their experience, algal production was increased by increasing the light intensity above microcosms. They concluded that nematode's ingestion rate increases with algal production. In intertidal mudflats, benthic diatoms migrate to the surface sediment along the diurnal cycle (e.g. Serôdio et al. 1997). The nematode community under study was dominated by epigrowth feeders (Table 1), with a diet mainly composed of benthic diatoms. Those nematodes may graze when luminosity is high, during low tide, in order to graze in algal biofilm and maximize their algal intake. This feeding behavior has not been documented for nematodes, but harpacticoid copepods were shown to graze at a higher rate just after the mudflat became exposed (Decho 1988). Buffan-Dubau and Carman (2000) also observed a midday feeding peak by ostracods and harpacticoid copepods. This result suggests that nematodes would have a feeding behavior principally controlled by algae and that bacteria might be taken up accidentally with algae.

Biotic factors

For nematodes, the effects of bacterial concentration on growth, fecundity, population development and feeding rates have been studied (Nicholas et al. 1973; Schiemer et al. 1980; Schiemer 1982a, 1982b, 1983; Vranken et al. 1988; Moens and Vincx 2000). Nematode ingestion rates are generally proportional to food availability (Nicholas et al. 1973; Schiemer et al. 1980; Moens et al. 1996). However, the relationship between assimilation rate and food concentration is not linear and has been described by a Michaelis–Menten function (Schiemer 1982b). This function is consistent with Holling's prey-dependent type II functional response (Holling 1959). Assimilation rates depend on the amount of ingested food and efficiency with which the material is assimilated. The assimilation efficiency has been found to decrease when food concentration increases: at a high food concentration *Plectus palustris* presented a low assimilation efficiency (12%) (Duncan et al. 1974), whereas at a food concentration one order of magnitude lower, the assimilation efficiency reached 57% (Schiemer et al. 1980). A similar conclusion was drawn by Moens et al. (2006) on the marine bacterivore *Pellioiditis marina*. Low efficiencies at high concentrations appear to result from short gut retention times, with the gut transit being too fast for effective digestion (Taghon et al. 1978). In the present study, it is not possible to determine if assimilation rates fluctuations are due to variations of ingestion rates or assimilation efficiencies. The number of bacterial concentrations tested was limited; however, the response observed could be described by a sigmoid

function. This function is consistent with Holling's prey-dependent type III functional response (Holling 1959). The threshold value for significant assimilation appeared to fall between 4 and 7×10^8 cells ml^{-1} and the threshold value for constant assimilation appeared to be between 7 and 10×10^8 cells ml^{-1} . Those values are within the range of data provided by literature for fast-growing opportunistic bacterivore nematodes typical of plant material or root systems: an optimal grazing rate was obtained for *Caenorhabditis briggsae* (Nicholas et al. 1973) and *P. marina* and *D. meyli* (Moens and Vincx 2000) at a bacterial concentration of 5 , 25 , and 5×10^8 cells ml^{-1} , respectively. Our study, dealing with tidal flat microalgal grazer community, suggests that the optimal level of bacterial foraging is also reached at high bacterial densities, when bacterial concentrations attain 1×10^9 cells ml^{-1} . As bacterial concentrations are rarely lower in marine sediments, (Hondeveld et al. 1992; Schmidt et al. 1998; Hamels et al. 2004), bacterial assimilation rate would seldom be lower than $18 \text{ pgC ind}^{-1} \text{ h}^{-1}$.

The relationship between the assimilation rate of algae and the algal concentration is poorly documented. Montagna et al. (1995) observed a proportional rise in the algal grazing rate with increasing algal concentration. In the present study, algal assimilation increased linearly without reaching a plateau. This function may be consistent with Holling's prey-dependent type I functional response (Holling 1959). Thus, the algal concentration threshold was not reached and maximal algal assimilation may be higher than those we obtained. Under natural conditions, the chlorophyll *a* content of the first centimeter of sediment varies between 0 and $50 \text{ } \mu\text{gChla g}^{-1}$ (review in MacIntyre et al. 1996). However, through vertical migration, benthic microalgae were concentrated near the surface during diurnal low tides and produced a biofilm with an average thickness of $50 \text{ } \mu\text{m}$ (Herlory et al. 2004). In this thin layer of algal mat, the concentration of chlorophyll *a* can reach $150 \text{ } \mu\text{gChla g}^{-1}$ (Serôdio et al. 1997) and even $300 \text{ } \mu\text{gChla g}^{-1}$ (Kelly et al. 2001). Thus, the higher algae abundance used in the present study ($114 \text{ } \mu\text{gChla g}^{-1}$) is not representative of conditions occurring in the natural environment and the nematode community feeding on the algal biofilm could thus present a higher assimilation rate of algae.

In our experiment, algal assimilation by nematodes always represented more than three times the bacterial assimilation. Nematodes are able to select potential food items. *Chromadora macrolaimoides* have a preference for diatoms and chlorophytes whereas they assimilate fewer bacteria (Tietjen and Lee 1973). *D. oxycerca* is able to swallow particles of different sizes and large frustules of diatoms (Boucher 1974). The three dominant species of the community studied, i.e., *C. macrolaima*, *D. oxycerca* and *P. jacobi*, were found to dominate the Brouage nematode

community during spring diatom blooms (Rzeznik-Orignac et al. 2003) indicating that they are highly dependent on algal resources. The use of natural stable isotopic analyses led to a similar conclusion elsewhere that the microphytobenthos constitutes the main food source for the nematode community dwelling in the surficial centimeter of mud in the study area (Riera et al. 1996). Montagna et al. (1984b), looking at the grazing rates of a nematode community from a saltmarsh, found that diatoms are selected 14 more times than bacteria. Algal carbon accounted on average for more than 90% of carbon grazed by a nematode community from a microtidal sandy sediment (Sundbäck et al. 1996b). In the present study, nematodes also ingested algae at a higher rate than bacteria. Depending on the algal concentration, the nematode community assimilates 3–11 times more diatoms than bacteria.

Nematode production can be estimated on the basis of the *P/B* ratio, bearing in mind that the choice of this ratio may be inaccurate (Heip et al. 1982). With an individual biomass of $0.11 \text{ } \mu\text{gC ind}^{-1}$, the estimation of production yielded $0.11 \text{ ngC ind}^{-1} \text{ h}^{-1}$, given a *P/B* ratio of 9 as often advocated (Gerlach 1971; Warwick and Price 1979; Bouvy 1988). Using a 10% factor for energy conversion efficiency (Bouvy 1988), a nematode carbon demand of $1.13 \text{ ngC ind}^{-1} \text{ h}^{-1}$ can be calculated. In the present study, the maximum ingestion rate of bacteria measured would represent 4% of this energy demand. On the other hand, the maximum algal ingestion measured would correspond to 15% of this demand. To fulfill 100% of their energy needs, nematodes may graze at a higher rate on the algal compartment, as discussed above. Nematodes may also be dependent on other food sources such as detritus, protozoa, oligochaetes or nematodes (Moens and Vincx 1997). The role of Dissolved Organic Matter in nematode nutrition also remains elusive, although it is likely to be highly relevant (Lopez et al. 1979; Meyer-Reil and Faubel 1980; Montagna 1984a; Jensen 1987). Bacterial carbon was found to constitute 6% of the total carbon requirement of a mudflat nematode community (van Oevelen et al. 2006b). On the other hand, using inverse modeling, Van Oevelen et al. (2006c) suggested that mudflat community of nematodes relied for 50% on algae and 39% on bacteria. Variations between studies can be due to differences in methodology and to nematode community composition.

In the Brouage mudflat, nematode present a mean density of $2,112 \text{ ind } 10 \text{ cm}^{-2}$ (Rzeznik-Orignac et al. 2003) whereas biomasses of benthic bacteria represent 0.846 gC m^{-2} (Degré et al. 2006). If nematode's grazing rates measured in the present study are representative of those of total community, it would imply that 0.02% of bacterial biomass is assimilated by nematodes each day. This extrapolation is debatable, as studied nematodes feed predominantly on diatoms whereas total community may

be more dependent on bacterial resource, and consequently, grazing of bacteria is probably underestimated.

Conclusion

Caution must be taken in interpreting our results, since the impact of each environmental factor on the feeding behavior of the nematode community was studied separately, whereas in natural environment all these factors covary greatly. The combination of temperature and salinity factors was found to have a higher impact than each factor taken alone (Tietjen and Lee 1972, 1977). Moreover, nematodes may respond to environmental changes at a seasonal scale, by physiological adjustment and shifting of their optimum conditions (Gee 1985). However, the nematode community studied appeared to have adapted to the highly variable environment constituted by the surficial sediment of intertidal mudflats, except at low temperatures (5°C), and their feeding activity is only slightly decreased by temperature, salinity or light stress. Due to high abundance of bacteria in the marine sediment, nematodes may never be food-limited with bacteria. Nematodes kept feeding under conditions of stress which were typical of the surficial sediment habitat; moreover they appeared to be principally dependent on the algal resource. Consequently, the community of nematodes dwelling in the top centimeter of the Brouage mudflat may also have a feeding strategy which is strongly linked to the formation of algal biofilm during the diurnal ebb.

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