Spatial distribution of detrital resources determines the outcome of competition between bacteria and a facultative detritivorous worm

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Abstract

   Macrobenthic deposit feeders and bacteria compete for the same detrital food resources. We hypothesize that the spatial scale at which food is distributed in the sediment is an important factor determining the outcome of this competition. Macrobenthic deposit feeders are better adapted for fast consumption of food in concentrated patches, whereas diluted food can only be exploited by bacteria. This hypothesis was tested in an experiment in which a fixed quantity of isotopically labeled algal detritus was offered to a natural bacterial community and the polychaete worm *Nereis* (=*Hediste*) *diversicolor*, either as a concentrated patch or mixed through the sediment matrix. Worms dominated food uptake in the concentrated treatment, while bacterial uptake was much greater in the diluted treatment. The experiment demonstrated scale-based niche differentiation between these taxonomically distant groups. It also showed that worms spatially redistributed food and made it available to bacteria in that way. Together, these mechanisms may stimulate stable co-existence through a scale-based partitioning of resources.

   Competition between organisms belonging to different kingdoms is an important gap in ecological studies (Hochberg and Lawton 1990). A widespread but understudied instance is the competition for organic matter between bacteria and higher organisms in aquatic sediments. Macrobenthic deposit feeders and bacteria share similar food resources, namely detrital organic matter deposited on, or buried in, sediments. Both bacteria and macrofauna are known to have a wide potential for hydrolysis and assimilation of the available organic detritus in sediments. They thus seem to directly compete for these available resources. Apart from this competition, macrofauna also ingests bacteria, resulting in omnivory (Hille-RisLambers et al. 2006). However, it is unlikely that bacteria are a major food component for macrobenthic deposit feeders, at least quantitatively (Kemp 1987). Despite this potential for overlap in food resources, a detailed study of an intertidal benthic food web showed very different feeding links for macrofauna and bacteria (Van Oevelen et al. 2006). Two mechanisms are thought to influence the division of resources between macrobenthic deposit feeders and bacteria. First, as proposed by Mayer et al. (2001), resource partitioning between bacteria and animals may be explained by differences in digestive systems. Deposit feeders have high-intensity digestion within a digestive tract, whereas bacteria use a low-intensity hydrolysis based on extracellular enzymes. Within an animal digestive tract, organic matter is hydrolyzed at a rate that is two to three orders of magnitude higher than in the ambient sediment under bacterial attack. These authors suggest that the metabolic cost of the high-intensity digestive system of deposit feeders can only be compensated for when they feed on high-quality resources, whereas bacteria can live off low-quality organic matter. In addition, bacteria are also known to possess the widest range in digestive abilities, including the possibility to hydrolyze very recalcitrant substrates such as lignin, cellulose, or even crude oil. However, such compounds are relatively rare in marine sediments. Moreover, marine organic matter is generally of high quality and relatively rich in nitrogen, at least when compared to terrestrial systems (Herman et al. 1999).

   As an alternative hypothesis, we propose that the competitive ability of both groups depends on the spatial distribution of the food sources. The spatial distribution of food sources has been shown in theoretical studies to have a large effect on resource partitioning between large and small organisms with similar feeding requirements but a different 'perceptive scale' (Szabó and Meszéna 2006). The perceptive scale (Holling 1992) is the size of the window through which an organism views the world. Small patches of food are noticeable resources for small consumers but remain unnoticed (or are unexploitable) by large animals. Szábo and Meszéna (2006) show that scale of spatial resource distribution can lead to niche differentiation, even for a single resource type. Ritchie and Olff (1999) use the same principle to derive body size distributions of animals feeding on similar resources distributed spatially over several scales. The hypothesis of scale niches, resulting from resource aggregations at different scales acting as distinct resources, seems particularly applicable to the case of bacteria and macrofauna in sediments.

   At the perceptive scale of bacteria (on the order of micrometers) the sediment forms a very heterogeneous environment. Within this environment, bacteria are, on average, spaced some tens of micrometers apart, although

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actual distributions may be clumped rather than regular (Schmidt et al. 1998; Vetter et al. 1998). Very small (micrometer-sized) parcels of organic matter will appear as distinguishable resource concentrations to which bacteria can react with the excretion of exo-enzymes, locomotory activity, and local growth and development. They thus have the ability to exploit even a very small parcel of food and can develop within a short time on every possible organic source. Macrobenthic deposit feeders possess the advantages of a high digestive rate for material in their guts and motility and sensory abilities that can bring them quickly to rich food sources over distances of decimeters or more. These advantages come with two disadvantages: a minimal amount of digestible organic matter must be present in the material ingested to compensate for the costs of the enzymatic machinery used for digestion, and gut residence time is relatively long and gut volume is small compared to total sediment volume (Mayer et al. 2001). Macrobenthic deposit feeders can only ingest a tiny fraction of the total sediment volume per day. This may force them to concentrate on dense patches of food material. Bacterial metabolism may be too slow for the exploitation of these patches. Moreover, bacteria in sediments have been reported to be strongly regulated by viruses (Middelboe et al. 2003), which may further reduce their exploitation of these patches.

Based on this model, we hypothesize that the share of bacteria and macrobenthic deposit feeders in terms of obtaining freshly added algal detritus to sediments depends on the spatial distribution of this food. We added isotopically labeled algal detritus to sediments, either homogenized (and thus diluted) over the sediment or in concentrated patches, and measured uptake by bacteria and by the macrofaunal polychaete *Nereis* (=*Hediste*) *diversicolor* (Müller 1776). We tested the hypothesis that worms obtained a larger share of the food when it was presented as a concentrated patch, whereas bacteria obtained a larger share in the homogeneous case of a more diluted resource.

Methods

Sediment and worm collection—Sediment and specimens of *Nereis diversicolor* were obtained from the Katsplaat, an intertidal flat in the Oosterschelde estuary situated in the southwestern part of The Netherlands (51°32′89″N, 3°55′78″E). Specimens of *Nereis diversicolor* were hand-picked from the surface layer of the sediment. After transport to the laboratory worms were checked for damage, and intact specimens were stored in a thin layer of sediment covered by Oosterschelde water at 4°C for later use in the experiment. Approximately 15 liters of surface sediment (upper 10 cm) was collected and sieved through a 1-mm mesh to remove macrofauna and larger particles. Meiofauna and microfauna were not removed. Their presence does not interfere with our estimates of organic matter (further abbreviated as OM) incorporation by bacteria or worms but may have slightly influenced total community respiration. Freshly sieved sediment was transferred to a total of 28 Plexiglas cores (52-mm inner

diameter; 15 cm long) to a depth of 5 cm, allowing a water column of approximately 10 cm. The cores were allowed to acclimatize submerged in a darkened, continuously aerated seawater reservoir for 1 week.

Experimental setup—After acclimatization cores were divided into two sets (one that was processed after 1 d and another after 7 d of incubation). Each set consisted of four treatments with three replicates each. Background characteristics (sediment and pore water) were documented by processing four untreated cores, two at the beginning of the incubations and two after 1-d incubations. Axenic, freeze-dried 20% ^{13}C-enriched *Thallassiosira rotula* (cultured and concentrated as described in Moodley et al. [2002]) was used as traceable fresh OM, of which a fixed amount was added to each core (equivalent to an addition of 1 g C m^{-2}). Labeled OM was added in two different ways. In the concentrated treatment, addition was achieved by carefully introducing OM suspended in seawater onto the surface through the overlying water with a long glass pipette (Moodley et al. 2005). Visual control confirmed that the algal material formed a dense layer on top of the sediment surface and was not brought into suspension. In the diluted treatment, after gentle removal of overlying water, the upper 3 cm of the sediment was removed (pushed out with a piston). Labeled OM was gently mixed into this material. The sediment was then replaced and water added without resuspending the sediment by pouring water onto a piece of floating plastic placed on the sediment. To half of the cores of each of these treatments two specimens of *Nereis diversicolor* (152.0 ± 9.7 mg blotted wet weight) were added. This resulted in four treatments: concentrated OM addition plus *Nereis*; concentrated OM addition without *Nereis*; diluted OM addition plus *Nereis*; and diluted OM addition without *Nereis*. Cores remained submerged in the darkened seawater aquarium for a period of 7 d and were provided with continuously aerated, filtered (0.2-μm) Oosterschelde water, and the whole setup was placed in a climate-controlled room (16°C).

Measurements and analysis—We measured use of the labeled OM by bacteria and worms by recording incorporation of ^{13}C label into the biomass of bacteria and worms, as well as by recording sediment community respiration rates. Respiration is a measure for the rate of degradation of the added OM, but no distinction between bacterial and worm respiration can be made. However, the experimental setup does allow testing for the influence of worm feeding on total degradation rate of OM.

Sediment community respiration rates of the added labeled OM were determined by measuring $\Sigma^{13}CO_2$ increase in the overlying water on days 1, 3, and 6 in duplicate cores of each treatment. This was done by randomly picking two of the three cores per treatment, which were then placed in a flow system allowing temporary closure of separate cores for flux measurements. Thorough mixing of the overlying water was achieved with a flow rate of 65 mL min^{-1} (turnover time ~3.5 min). Cores were flushed with fresh aerated and filtered Oosterschelde water for 15 min before the start of the

Table 1. Average bacterial biomass (total sediment column g C m^{-2} ± SE) and range of $\Delta\delta^{13}$C (‰) of the three pools followed under the four treatments after 7 d of incubation with tracer algal carbon containing 20% ^{13}C.*

Treatment	Bacteria biomass	$\Delta\delta^{13}C_{bact}$	$\Delta\delta^{13}C\ \Sigma CO_2$	$\Delta\delta^{13}C_{worm}$
D + N	19.74(0.34)	+8.6 to +240.5	+11.0 to +27.2	+7.3 to +38.0
D − N	15.34(1.18)	+2.7 to +226.6	+6.4 to +15.0	—
C + N	22.06(0.86)	+9.4 to +15.1	+4.1 to +18.8	+281 to +478
C − N	21.40(2.35)	+1.4 to +34.8	+3.1 to +35.0	—

* Treatments: (D) diluted vs. (C) concentrated tracer addition with (+N) or without (−N) *Nereis diversicolor*. $\Delta\delta^{13}$C was computed as the difference between observed δ^{13}C in the experiment and background δ^{13}C for the pool considered. We used the following weighted average background δ^{13}C values: bacteria-specific phospholipid derived fatty acids: −18.36‰; ΣCO_2: −5.12‰; and *Nereis diversicolor*: −13.59‰.

closed incubation. Water samples (~4 mL) were taken after 0 and 60 min from the start of the incubation, transferred to pre-weighed 10-mL helium-filled headspace vials, immediately acidified (10 μL 99% H_3PO_4 per mL sample), and stored upside down until analysis.

Assimilation of the tracer OM in fauna and bacteria was measured after 1 and 7 d; cores were sliced from 0–2 and 2–5 cm and 0–3 and 3–5 cm for the concentrated and diluted treatments, respectively. At each processing event, 100% of the worms were recovered alive, weighed (blotted wet weight), and stored at −20°C. Sediment was gently homogenized, and a subsample of 20–40 mL was stored at −20°C and was later freeze dried. Of this sediment, 3 g was used for extraction of phospholipid derived fatty acids (PLFAs) for analysis of bacterial carbon uptake through bacteria-specific biomarkers. Another 20 mL of the sediment of each section was used to collect pore water through centrifugation, for analysis of ΣCO_2 concentration and carbon isotopic signature. Details of the measurement of δ^{13}-ΣCO_2 and $\delta^{13}C_{org}$ of faunal compartments are given in Moodley et al. (2002).

Flow of the tracer OM was thus followed in three major pools: total sediment community respiration, polychaete, and bacterial uptake calculated through excess ^{13}C. Carbon-isotopic analyses of PLFAs were done according to the method of Middelburg et al. (2000). Bacterial data are based on the concentrations and ^{13}C content of bacteria-specific biomarkers (i14:0, i15:0, a15:0, i16:0), assuming that bacterial biomarkers = 14% of total bacterial PLFAs, as calculated from literature data given in Middelburg et al. (2000), and 0.056 g C PLFA (g C)$^{-1}$ biomass (Brinch-Iversen and King 1990). Carbon isotopes are expressed in the delta notation (δ^{13}C) relative to Vienna Pee Dee Belemnite. Carbon uptake is expressed either as $\Delta\delta^{13}$C (‰) (i.e., specific uptake [$\delta^{13}C_{sample} - \delta^{13}C_{background}$]) or as total uptake. The latter is calculated as the product of excess ^{13}C (E) and carbon concentration of the respective pool (Middelburg et al. 2000). Excess (E) ^{13}C is the difference between the fraction ^{13}C of the background (F$_{background}$) and the samples (F$_{sample}$). For the F$_{background}$ of CO_2, we did not use ambient $\delta^{13}CO_2$ but that of water samples taken from experimental cores at the beginning of the closed incubation to determine respiration rates. Uptake of total ^{12}C + ^{13}C tracer OM was calculated as the quotient of total uptake of ^{13}C and the fractional abundance of ^{13}C in the OM (0.20).

All data are presented as average values of the replicates, and error bars indicate standard errors of the mean.

Statistical significance was tested with one-way ANOVA contrasting the four treatments (for bacteria) or two treatments (for *Nereis*), followed by post-hoc comparison of the treatments with the Least Significant Difference test. Reported *p*-values refer to these post-hoc comparisons, since ANOVA always demonstrated the existence of significant differences. Homogeneity of variances was tested prior to ANOVA analysis using Levene's test; no problems were detected.

Results

The addition of algal OM triggered an immediate response. Even after only 1 d of incubation, significant uptake by both bacteria and worms, as well as significant respiration rates, were recorded (Table 1). Label transfer is indicated by positive $\Delta\delta^{13}$C values that clearly exceed analytical uncertainty. Based on the biomass and $\Delta\delta^{13}$C values summarized in Table 1, the fraction of labeled algal OM recovered in the different pools was calculated. Depending on treatments, up to approximately 25% of the added algal OM was recovered in biomass of worms and bacteria (Fig. 1). In accordance with the original hypothesis, uptake by the worms was much lower when algal OM was mixed into the sediment than when it was concentrated on the surface (Fig. 1). The opposite was observed for bacteria (Fig. 1). Bacterial tracer uptake was approximately 10 times greater when the algal OM was mixed in the upper 3 cm of the sediment, compared with a concentrated addition in the surface layer. Addition of worms to the diluted treatment resulted in low uptake by the worms but enhanced uptake by the bacteria (diluted treatment with worms vs. diluted treatment without worms; ANOVA, $p < 0.01$).

Bacterial uptake of algal OM was almost exclusively limited to the upper layer of the sediment column, except in the treatment with worms, where the worms apparently mixed a substantial fraction of the substrate down into the lower layer and made it available for bacterial uptake (Fig. 2).

As was the case with uptake, respiration of the added algal OM was also immediate, with 6–12% of the added carbon respired within 1 d (60–120 mg C m^{-2}, Fig. 3). Strong temporal and treatment differences were measured in sediment community respiration rates of labeled OM; maximum respiration rates were encountered at day 1, and all incubations further followed exponential decrease with time (data not shown). The exponential regressions with time ($R^2 > 0.9$, $p < 0.01$) calculated for each replicate of
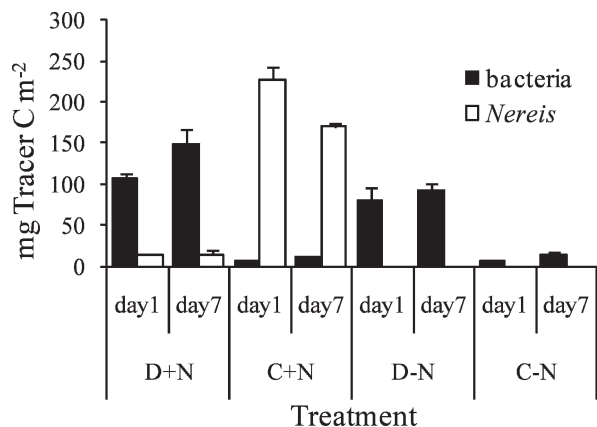
Fig. 1. The amount of tracer carbon recovered in bacteria (black bars) and worm (*Nereis*) tissue (white bars) after 1 and 7 d for the different treatments: (D) diluted vs. (C) concentrated tracer addition with (+N) or without (−N) *Nereis diversicolor*. Each bar represents average ± standard error of the mean, $n = 3$ per treatment and day. Separate cores have been used for the 1-d and 7-d results.

each treatment were used to integrate respiration rates over the entire 7-d incubation period. Together with pore-water concentrations measured at day 7, this yielded the total amount of labeled OM respired. This amount ranged from 188 to 405 mg C m^{-2} after 7 d (Fig. 3) (18.8–40.5% of the total addition of 1 g C m^{-2}). Respiration thus accounted for the major fate of the added OM. However, it was significantly (ANOVA, $p < 0.05$) lower in the concentrated treatment with worms than in all other treatments. In the concentrated treatment with worms the worms had direct access to labeled OM and incorporated a large fraction in their biomass. OM respiration and total carbon processing were highest in diluted additions with worms.

Discussion

The results of our experiment confirmed the assumptions at the basis of our simple conceptual model. Although in
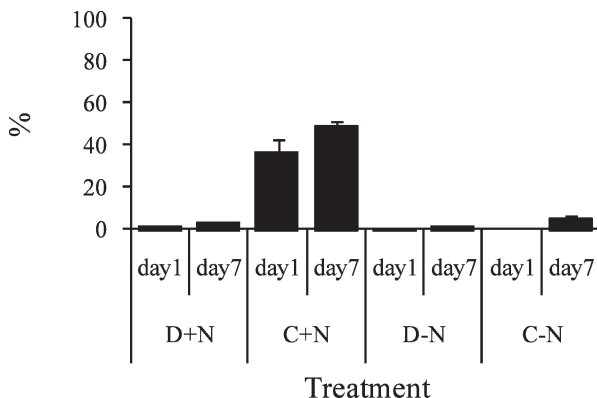

Fig. 2. Percentage (average ± SE, $n = 3$) of tracer carbon retrieved from bacteria in the lower sediment layers after 1 and 7 d of incubation. Percentage is expressed vs. the total tracer carbon retrieved from bacteria in both lower and upper sediment layers in each experiment. Treatments: (D) diluted vs. (C) concentrated tracer addition with (+N) or without (−N) *Nereis diversicolor*.
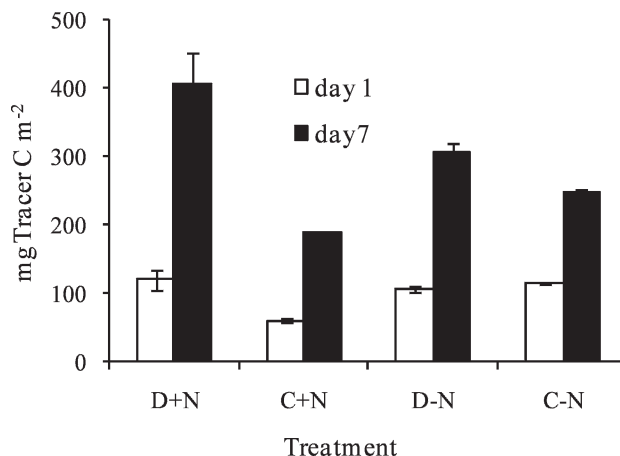

Fig. 3. The total amount of tracer OM respired after 1 and 7 d under the different treatments (average ± SE, $n = 2$): (D) diluted vs. (C) concentrated tracer addition with (+N) or without (−N) *Nereis diversicolor*.

three out of four experimental treatments bacteria incorporated much more material than worms, the reverse was true in the concentrated treatment with worms. We had assumed that digestion by bacteria would be more or less constant per unit of sediment volume. This is based on the observation that bacterial numbers are remarkably constant per unit of sediment volume (Schmidt et al. 1998), a factor probably related to viral lysis as a control mechanism (Middelboe et al. 2003). In fact, the 10-fold difference in bacterial uptake between the diluted and concentrated treatments largely confirms this assumption. Much more OM can be taken up by bacteria when the material is diluted (at the macroscopic scale) than when it is concentrated in space. For worms, the difference in uptake between the diluted and concentrated treatments is even larger. It is likely that they focused on the concentrated layer of OM in the concentrated treatments, while they probably neglected the labeled OM in their feeding strategy in the diluted treatment.

In all treatments, a high proportion of the added OM was processed by the benthic community, either in respiration or incorporation into biomass. This indicates that the OM used was of high quality and degradable for both worms and bacteria. Our experiment thus showed that intrinsic reactivity of OM cannot be the only factor explaining resource partitioning between bacteria and macrobenthic deposit feeders.

A potential source of error in the interpretation of these experimental results is that we failed to provide a proper procedural control, in which the upper sediment layer would be mixed (as in the diluted treatments) and then provided with a concentrated algal layer (as in the concentrated treatments). It is unlikely, however, that the gentle mixing of the top layer has resulted in strong oxidation of the sediment (which would have been visible by color), and, moreover, all treatments were thoroughly mixed shortly before the start of the experiment. We thus believe that the treatment itself is the major cause of the variation.

It is remarkable that all worm uptake seems to have taken place in the first day of the experiment. In part this result can be influenced by the determination of stable isotope ratios in worms including gut contents. Thus, on day 1, part of the tracer measured in the worms could have been gut content. In part it can also be due to variability in the activity of the (few) worms used in the experiment. However, the feeding activity of the worms itself may have destroyed the nice concentrated layer of algae on which they initially fed very intensively. Visual inspection of the cores showed that in the worm treatment, this layer was no longer conspicuous after 1 d. Moreover, the concentrated treatment with worms was the only one in which a substantial bacterial tracer uptake was recorded in the lower layer of sediment (Fig. 2), also indicating possible effects of bioturbation. Mixing down of algal organic matter added on top of sediments has also been reported to be very rapid in other experiments (Blair et al. 1996; Levin et al. 1997).

The stimulatory effects of worms on bacterial metabolism are indicated by the diluted treatment with worms, in which bacterial uptake is significantly higher than in the diluted treatment without worms, and total respiration is the highest of all the treatments. Stimulatory effects of fauna on bacteria have been recorded in many studies (Aller 1994; Kristensen 2000; Marinelli et al. 2002), including studies using *Nereis* as an experimental animal (Kristensen and Mikkelsen 2003). The effect has been attributed to the increased volume of sediment with aerobic respiration and/or removal of diagenetic end products as a consequence of animal bioturbation and ventilation of the sediment. It is likely that these mechanisms have increased bacterial uptake rates also in the diluted treatment with worms, as compared to the diluted treatment without worms. The relatively elevated bacterial uptake in the lower sediment layers of the concentrated treatment with worms, however, indicates an additional stimulatory effect of macrofauna on bacterial metabolism—transfer of organic substrates to the lower layer and consequent dilution into the sediment matrix—which would make the material unavailable for macrofauna but more available for bacteria.

The treatments chosen in our experiment were designed to demonstrate the effect of spatial distribution of food resources on resource partitioning. They focus on the principle of the mechanism rather than on a faithful mimicking of natural conditions. The diluted treatment without worms, in particular, is unlikely to be a realistic scenario. In nature, animal bioturbation is generally the main factor responsible for dilution of resources. It is unlikely to find strongly diluted organic matter in the absence of macrofauna. However, this may be the case when the upper sediment is constantly disturbed by waves and currents, as is common in many estuarine sediments. Highly mobile sediments in deltaic and shelf environments represent the extreme case (Aller 2004). These episodically mixed deposits are dominated by microbial processes and poor in macrofauna biomass.

For the sake of experimentation, we also chose to use exactly the same OM in all treatments, so as to demonstrate independence of the spatial distribution effect from the effect of quality of the OM. In nature, both aspects will seldom be uncorrelated. Material ages while it is diluted by bioturbation, and therefore diluted material will inevitably be more refractory than freshly deposited, concentrated organic material. In addition, the restriction to a single macrobenthic species (*Nereis*) in the experiment may seriously limit the possibility that one can generalize from our experiment to all natural conditions. Macrobenthic species differ in their feeding strategies, and this will influence the type and local concentration of OM that they find. However, the demonstration of the principle that spatial distribution of resources may affect resource partitioning opens the scope for further examination of the importance of this principle in nature.

Whereas our experimental results confirm hypotheses based on the concept of scale niche differentiation (Szabó and Meszéna 2006), the bioturbation effects also add an additional dynamic feedback mechanism to it. Bioturbation by the large animals is an inevitable consequence of their foraging activity. It apparently results in dilution of resources, rendering them unavailable for the animal. At the same time, however, it creates new microscopic patches for the small organism, such as bacteria (this study) and meiofauna (Levin et al. 1997). Thus, the scales at which resources are distributed in space and time are not entirely imposed by the landscape but also result from community composition and the corresponding activities of the community members. The mechanism may be much more general than the bioturbation reported here (e.g., the leaving of grass patches by large grazers around dung heaps, or carcasses left by large carnivores and used as valuable resources by smaller carnivores).

Our study indicates that when OM is added to sediments in experiments aimed at deciphering the benthic food web (Blair et al. 1996; Witte et al. 2003; Buhring et al. 2006), the actual method of administering this OM can have a substantial influence on the outcome, both in terms of preferred pathways (animals vs. bacteria) and in terms of total rates of OM processing.

With respect to the dynamics of competition between bacteria and macrobenthic deposit feeders, we suggest that the details of the interaction can easily lead to stable coexistence of both groups, a fact that is widely observed in nature. Stable coexistence is expected if neither of the two competitors can avoid invasion into the system by the other competitor.

Our study directly illustrates the inability of macrobenthic deposit feeders to exclude bacteria, even when the initial situation favors worms over bacteria. When fresh detrital material is added to sediments in relatively concentrated 'packages,' animals have a definite competitive advantage shortly after deposition (Witte et al. 2003). However, the feeding activity itself, and the bioturbation associated with animal movement, inevitably lead to dispersion of some of the food in the sediment. This dispersed food material can be taken up much more effectively by bacteria than by macrofauna, leading to a reversal of preferred uptake route from animals to bacteria as material ages in the sediment. Aging of organic material also causes

a decline in its chemical quality (the components that are easily degraded disappear first), and this shift may further add to the advantage of bacteria over animals.

The reverse interaction (bacteria being unable to exclude macrobenthic deposit feeders from sharing resources) may often occur but is not the only realistic scenario. As mentioned above, in physically well-mixed sediments resources may almost exclusively occur in the diluted form, and bacteria could outcompete macrofauna. Further, bacteria may exclude higher taxa through chemical interference. Examples are production of sulfide in toxic concentrations under hypertrophic conditions (Pearson and Rosenberg 1978) or bacterial monopolization of rich food-falls (Burkepile et al. 2006). In most field conditions without strong physical mixing and without strong chemical interference, we can expect that the superior ability of macrobenthic deposit feeders to locate and absorb spatially concentrated resources gives them an advantage over bacteria. We then expect coexistence of bacteria and macrofauna, as macrofauna will also dilute some of the resources.

Our experimental study has demonstrated the principle of scale niche differentiation. Further research is needed to investigate whether the theoretical implications discussed above are effectively present in real field situations and to determine how far results using one particular polychaete worm species can be extended to other macrobenthic deposit feeders, or to an even wider spectrum of situations in which animals and bacteria compete.

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