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Effects of benthic fauna on organic matter mineralization in fish-farm sediments: importance of size and abundance

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The effects of the polychaetes *Nereis diversicolor* and *Capitella* sp. I on organic matter mineralization in marine sediments collected under a fish farm were studied *in vitro*. The two species differ significantly in size, feeding, and burrowing activity. The presence of benthic fauna stimulated the total benthic metabolism (measured as O_2 uptake, CO_2 release, and SO_4^{2-} reduction) substantially compared to the microbial metabolism in an azoic sediment. *Nereis* and *Capitella* stimulated mineralization over a two-month period by 135% and 87%, respectively. The stimulation was primarily microbial (54%) in *Capitella* sediments. Sulphate reduction remained similar to azoic sediments, indicating that in particular the aerobic activity was enhanced. Microbial stimulation was less (23%) for *Nereis* sediments, while sulphate reduction was reduced (42%), indicating enhanced oxidation compared to azoic sediments. The fauna-mediated oxidation of the sediment probably causes increased removal of nitrogen through increased nitrification and denitrification and enhanced binding of phosphorus, thereby reducing nutrient fluxes to the water column.

Key words: bioturbation, fish farms, organic matter mineralization, sediment.

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Introduction

An important environmental impact of marine fish farming is organic enrichment of the sediment under the net cages, and benthic metabolism is usually stimulated significantly (Hall *et al*., 1990; Holmer and Kristensen, 1992). This organic matter is labile with a low C:N ratio and with a high content of nutrients compared to organic matter usually found in marine sediments (Kristensen, 1990; Holmer and Kristensen, 1994). Waste products (food pellets and faeces) originate from animal and terrestrial sources, while marine organic matter usually consists of refractory plant material (Dauwe and Middelburg, 1998).

Accumulation of waste products in farm sediments usually results in dramatic changes in sediment chemistry, and also the macro- and meiobenthic communities are affected (Brown *et al*., 1987; Karakassis *et al*., 1999). The changes in benthic community structure follow an organic enrichment gradient (Pearson and Rosenberg, 1978). A zone dominated by a few opportunistic species (e.g. *Capitella capitata*) in high densities has often been found in the immediate vicinity of the cages (Tsusumi *et al*., 1991; Ye *et al*., 1991; Karakassis *et al*., 1999). In some cases, for example if the farm is placed in a natural deposition area or if the sedimentation rate of waste products is high, the fauna may disappear completely (azoic zone). The community becomes more diverse with increasing distance from the farm. The number of species increases and species that are more sensitive to pollution can be found. Some studies have shown fauna changes in agreement with the Pearson–Rosenberg model (Brown *et al*., 1987), while others have identified only parts of the sequence.

The benthic fauna plays an important role in the supply as well as mineralization of organic matter. Suspension-feeders link the pelagic and the benthic environment, while benthic deposit-feeders redistribute organic matter deposited on the sediment surface by sediment reworking, and oxidize the sediment by ventilation (Aller, 1982). Mineralization is often enhanced significantly (Kristensen and Blackburn, 1987; Banta *et al*., 1999). In particular, decomposition of refractory organic matter is stimulated (Andersen and Kristensen,

1992; Kristensen *et al.*, 1992), probably because this material has been buried in anoxic sediment layers. When refractory organic matter is exposed to oxygen during bioturbation, decomposition may increase by one order of magnitude (Kristensen *et al.*, 1995; Kristensen and Holmer, 2001). Benthic fauna also affects nutrient cycling in the sediment. N-cycling is faster, and both nitrification and denitrification are enhanced in comparison to azoic sediments, because of a ventilation-mediated increase in transport of dissolved oxygen and N-compounds (Kristensen *et al.*, 1991; Pelegri and Blackburn, 1995; Hansen and Kristensen, 1998). Few studies have addressed the effects of benthic fauna on phosphorus cycling, but in general an increased retention of phosphorus can be expected because phosphorus binds to oxidized iron (Clavero *et al.*, 1994).

We examine the effect of benthic fauna on the mineralization of organic matter originating from marine fish farms by quantifying the aerobic and anaerobic microbial processes. Two polychaete species were selected: the small (1–2 cm long) opportunistic *Capitella* sp. I and the larger (5–7 cm long) *Nereis diversicolor*, which inhabits enriched as well as uncontaminated sediments. The species differ also in feeding habits and burrowing activity. *N. diversicolor* is a surface deposit-feeder which burrows to 10–15 cm depth (Andersen and Kristensen, 1992). *Capitella* sp. I is an abundant, head-down deposit-feeder restricted to the upper 2–3 cm of the sediment (Madsen *et al.*, 1997). The polychaetes were added to fish farm sediment in natural densities. Decomposition of organic matter was measured as sediment metabolism (O_2 uptake and CO_2 production) and the effects of benthic fauna on anaerobic processes and redox conditions in the sediment were examined by measurement of sulphate reduction and pore-water sulphide concentration.

Materials and methods

Sampling

Sediment was sampled at a marine fish farm situated in Horsens fjord, Denmark (55°50′208 N 10°03′875 E). The farm contained 12 rectangular net cages with rainbow trout (*Oncorhynchus mykiss*), each with a dimension of 15 × 11 × 3 m. The annual net production was around 130 t. Fish were fed manually and the effective conversion coefficient (ratio between food input and net fish production) in 1997 was 1.3.

Water depth was ca. 4–5 m and the distance between the bottom of the net cages and the sediment was ca. 0.5 m. Tidal action in the area is low, the intertidal range generally being <0.5 m. The current is driven by run-off during winter and by wind during summer. Annual variations in temperature and salinity cover the range 4–22°C and 19–29 psu, respectively. The sediment was silty with an organic carbon content (POC) of 1.2–2.2% dry weight and organic nitrogen (PON) content of 0.14–0.2% dry weight. The average C:N ratio was 10.4–12.6. The benthic fauna in the area is sparse (ca. 500 individuals m^{-2}) and is dominated by Polychaeta and Mollusca.

Sediment cores were collected in 30-cm long acrylic core liners (8-cm internal diameter) in February, 1998. Cores were taken directly below one of the net cages by scuba diving, and adjusted to a sediment depth of ca. 20 cm. After returning to the laboratory, the overlying water of all cores was purged with N_2 and sealed. The induced anoxia forced the macrofauna to the surface to escape from the increasing sulphide concentration in the pore water. After 36 h, all visible macrofauna were removed and the anoxic water was replaced by oxygenated water. Five *N. diversicolor* of similar size (200–400 mg wet weight) collected from Odense Fjord, Denmark, were added to each of three sediment cores (equivalent to 1000 individuals m^{-2}). Similarly, 50 *Capitella* sp. I were added to three cores (equivalent to 10 000 individuals m^{-2}). The remaining three cores were kept without fauna and served as controls. *Capitella* were obtained from a culture in organic-rich sediment, to which periodically a mixture (equal parts by weight) of dried spinach, whole meal baby cereal, and commercial fish food was added. The cores were kept in darkness in an open circulation incubation system at 15°C and 20 psu for 64 d and continuously aerated by air pump.

Measurements

The exchange of O_2 and total CO_2 ($TCO_2 = H_2CO_3 + HCO_3^- + CO_3^{2-}$) across the sediment-water interface of individual cores was determined every 6–7 d during the experimental period. During each flux measurement, initial samples were taken from the overlying water. The cores were closed with lids, leaving no air in the head-space, and incubated for 3–6 h before final samples were taken. Concentration changes in the supernatant during incubation were assumed to be linear and O_2 concentration never decreased below 60% of full saturation (Anderson *et al.*, 1986). Samples were analysed within 12 h. Oxygen was measured by standard Winkler technique, and TCO_2 was measured by the flow injection analysis of Hall and Aller (1992).

Immediately before and after the 64-d experimental period, porosity, sediment density, particulate organic carbon (POC), and nitrogen (PON) and pore-water solute concentrations (TCO_2, SO_4^{2-} and sulphide) were determined. *Nereis* and control cores were sectioned into depth intervals of 0–1, 1–2, 2–3, 3–4, 4–6 and 6–8 cm. *Capitella* cores were sectioned into depth intervals of 0–0.5, 0.5–1, 1–1.5, 1.5–2, 2–3, 3–4, 4–6, and 6–8 cm.

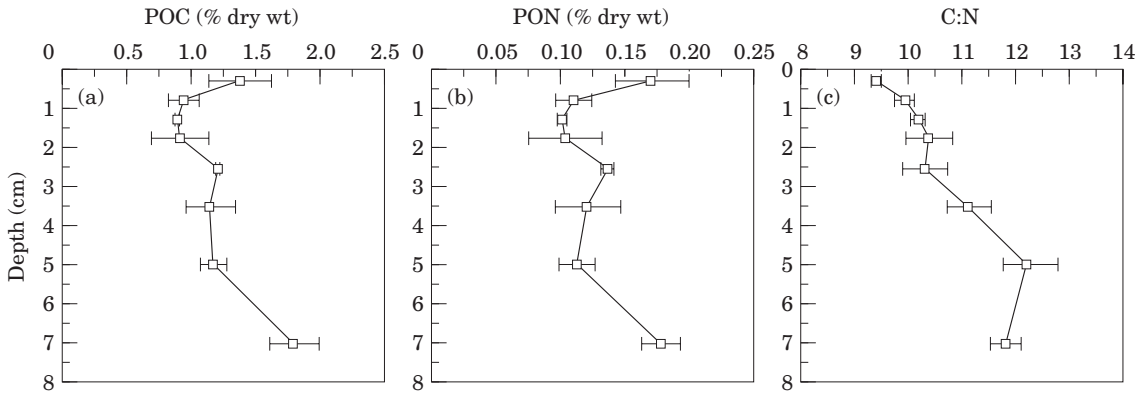

Figure 1. Initial profiles (means and ranges) of (a) particulate organic carbon (POC) in % dry weight, (b) particulate organic nitrogen (PON) in % dry weight and (c) C:N ratio (mol/mol).

Sediment density was obtained by measuring the weight of a known volume, and water content was measured as the weight difference after drying overnight at 105°C. POC and PON were determined in pre-dried (105°C) sediment. Inorganic carbon and nitrogen were measured in ashed (520°C) sediment according to Kristensen and Andersen (1987) using a Carlo Erba elemental analyser.

Pore water was obtained from a subsample of each sediment slice by centrifugation (3000 rpm; 10 min) in double centrifuging tubes with pre-combusted GF/F filters. Samples for TCO_2 were analysed within 12 h as described above, and those for SO_4^{2-} and sulphide were fixed in 100 mM zinc acetate and kept frozen until analysis. SO_4^{2-} was measured by ion-chromatography with a Dionex autosuppressed anion-system (IonPac AS4S-SC column and AMMS supressor) and sulphide was analysed by the methylene blue technique of Cline (1969).

Sulphate reduction was measured (in triplicate) immediately before and after the 64-d experimental period. The experimental cores (internal diameter 80 mm) were carefully sub-cored (internal diameter 26 mm). The sub-cores were injected with 1 µl $^{35}S\text{-}SO_4^{2-}$ through holes (with silicone stoppers) at 0.5 cm intervals down to 8 cm and incubated for 6 h at 15°C. Incubation was terminated by sectioning the cores according to the same intervals as for sediment characteristics. These sections were immediately fixed in 1 M zinc acetate and frozen. Reduced sulphur compounds were separated by the one-step distillation procedure of Fossing and Jørgensen (1989). Briefly, 2 g of centrifuged sediment (10 min, 2000 rpm) was transferred to a reaction flask and 10 ml of 50% (v/v) ethanol was added. After degassing with N_2 for 10 min, 8 ml 12 M HCl and 16 ml Cr^{2+} solution were added to the slurry, and the mixture was boiled for 30 min. The reducible sulphur compounds were released as H_2S and trapped as ZnS in 10 ml 250 mM zinc acetate. Subsamples from supernatants and suspended ZnS from the traps were mixed with Ultima Gold scintillation cocktail, and radioactivity was counted on a scintillation counter (Packard 2200CA Tricarb).

One way ANOVA was used to test the different macrofauna treatments (three groups: control, *Nereis, Capitella*). Significant effects were further investigated using Tukey *post hoc* multiple comparisons between treatment means (Zar, 1984).

Results

A light-grey oxidized sediment layer of approximately 6–8 mm overlying a black sulphidic layer could be identified visually in the defaunated control sediment, while oxidized conditions were clearly enhanced in bioturbated sediment cores. *Nereis* sediment had an irregular oxidized zone of 1–2 cm. Burrow structures extended the oxidized zone ca. 8 cm into the otherwise reduced sediment in the form of 1–3-mm thick oxidized wall linings around the burrows. In cores with *Capitella*, burrowing and feeding activity was seen as fresh faecal pellets on the sediment surface, and an irregular oxidized zone to 3-cm depth.

The initial sediment characteristics showed a peak of POC and PON in the surface layer. POC content decreased from 1.4% dry weight in the surface layer to 0.9% dry weight at 1.5 cm depth. Below this, the profile stabilized except for an increase at 6–8 cm depth [Figure 1(a)]. PON content showed a similar pattern, with 0.17% dry weight in the surface, followed by a decrease to 0.11% dry weight at 1.5-cm depth [Figure 1(b)]. C:N ratios were low (9.4) in the surface layer and increased with depth to 11.4 at 8-cm depth [Figure 1(c)]. The pattern did not change significantly during the experimental period, except for a decrease in POC and PON in the top layer and an increase in C:N ratio in *Nereis* sediment (data not shown).

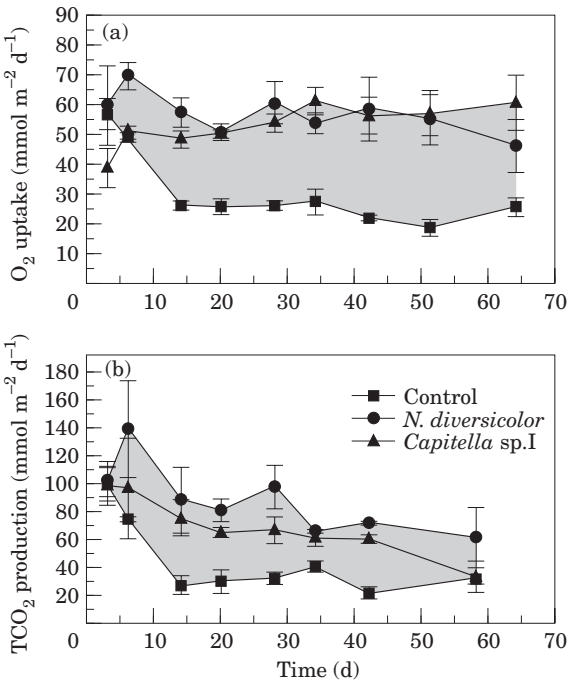

Figure 2. Time-dependent changes (means ± s.e.) in oxygen uptake (a) and TCO_2 release (b) in three replicate cores by treatment.

The O_2 uptake and TCO_2 release (Figure 2) in control sediment decreased gradually from high initial fluxes of 57 mmol m^{-2} d^{-1} and 100 mmol m^{-2} d^{-1}, respectively towards a constant level after 14 d of incubation (TCO_2: 30 mmol m^{-2} d^{-1}; O_2: 25 mmol m^{-2} d^{-1}). The addition of macrofauna resulted in a considerable increase in both parameters. After day 6, the presence of *Capitella* increased the O_2 uptake and TCO_2 release by 88–207% and 4–178%, respectively, relative to the control, while the presence of *Nereis* led to an increase of 61–228% and 81–136%, respectively. TCO_2 pore-water concentrations decreased during the experimental period in all cores, but more so in bioturbated sediments [Table 1(a)]. Total CO_2 production (CO_2 release plus change in pore-water concentration) was markedly enhanced by the addition of benthic macrofauna. *Nereis* stimulated the TCO_2 production by 135% ($p<0.0001$), while stimulation by *Capitella* was lower (87%; $p<0.0001$). Thus, *Nereis* had a significantly larger influence on mineralization than *Capitella* ($p<0.001$).

Sulphide was not detected in the water column and surface sediment (Figure 3) and the concentration was constant in control sediment (ca. 10 µM) over the 1–6 cm depth interval followed by a slight increase. The effect of benthic fauna on pore-water sulphide did not differ between *Nereis* and *Capitella*. Both species reduced the concentration by 70–95% in the upper 5 cm, whereas the concentration increased to values approximately similar to control (15 µM) at 6–8 cm depth.

In the control sediments, the maximum sulphate reduction rates (SRR) (ca. 800 nmol SO_4^{2-} cm^{-3} d^{-1}) were detected at 1–3 cm depth, followed by a decrease to ca. 30 nmol SO_4^{2-} cm^{-3} d^{-1} at 6–8 cm depth. The addition of fauna changed the depth profile. In *Capitella* sediment, SRR increased gradually with depth from 90 to 430 nmol SO_4^{2-} cm^{-3} d^{-1}. Compared to the control, SRR was reduced by 80–90% in the upper 3 cm, while SRR increased by a factor of 3–10 below this depth. In *Nereis* sediment, SRR reached its highest value at 1–2 cm depth and its lowest at 4–6 cm. Compared to the control, SRR was reduced by 21–66% in the upper 4 cm and increased by a factor of 4 at 6–8 cm depth.

We did not measure respiration of the fauna, but Chareonpanich *et al.* (1994) and Banta *et al.* (1999) have measured respiration rates of 31 mmol m^{-2} d^{-1} and 12 mmol m^{-2} d^{-1} for *Capitella* and *N. diversicolor*, respectively, at temperatures corresponding to those used for core incubation [15°C; Table 1(b)]. The direct contribution of *Nereis* accounted for 77% of the bioturbation-induced excess mineralization, while *Capitella* respiration accounted for 46% of the excess mineralization.

Discussion

The marked increase in TCO_2 release and O_2 uptake caused by the addition of macrofauna to the sediment indicates that organic matter mineralization was enhanced. Fauna-induced stimulation of mineralization of organic matter is well known and caused by enhanced microbial activities (Kristensen, 1988). Microbial activity increases owing to enhanced oxidation of the sediment, increased surface area of the organic substrates and presence of organic-rich faecal pellets. In addition, animals contribute to organic matter turnover by direct ingestion and assimilation of detritus and associated microorganisms (Cammen, 1980; Hansen and Blackburn, 1992).

While the two species have almost the same effect on fluxes of TCO_2 release and O_2 uptake, *Nereis* had a larger effect on total metabolism, when including the change in TCO_2 concentration in pore water. During the experiment, the TCO_2 concentration in pore water decreased more in bioturbated sediment than in the defaunated control sediment. A decrease in pore-water solutes is commonly observed in bioturbated sediment and is due to ventilatory pore-water flushing (Hansen and Kristensen, 1997; Banta *et al.*, 1999). The decrease was largest in *Capitella* sediment. Total metabolism was enhanced by 135% by *Nereis*, while *Capitella* caused a stimulation of 87% compared to the control. Earlier investigations (Holmer *et al.*, 1997) have shown

Table 1. Metabolism budgets (± s.e.; n=3) estimated for sediment cores without fauna (control) and with *Nereis* and *Capitella*: (a) TCO_2 budgets during 64 d of incubation (TCO_2 release: integration of curves in Figure 2; ΔTCO_2: change in pore-water concentration in the top 8 cm by subtracting final profiles from initial profiles; total metabolism: sum; values in parentheses: changes relative to the control). (b) Average daily rate of total metabolism, macrofauna metabolism (calculated on the basis of respiration data for *Nereis* given by Banta *et al.* (1999) and for *Capitella* by Chareonpanich *et al.* (1994) and converted to 15°C by assuming Q_{10}=2 and RQ=1) and microbial metabolism, calculated as the difference between the two (values in parentheses; percentage of the increase that is accounted for by each component. (c) Anaerobic metabolism (I_{SRR}: integrated sulphate reduction rates over the top 8 cm at day 64; SRR: fraction of TCO_2 release accounted for by I_{SRR} assuming that 2 moles of CO_2 are produced per mole of SO_4^{2-} reduced; TCO_2 release: on day 64; values in parentheses represent changes in SRR relative to control).

Treatment	Control	*Nereis*	*Capitella*
(a) TCO_2 budgets (mmol m^{-2})			
TCO_2 release	1919 ± 93	4365 ± 95 (+127%)	3560 ± 92 (+86%)
ΔTCO_2	− 171 ± 30	− 264 ± 34	− 283 ± 8
Total	1748 ± 59	4101 ± 85 (+145%)	3277 ± 101 (+87%)
(b) Metabolism (mmol C m^{-2} d^{-1})			
Total	32 ± 2	72 ± 2	58 ± 2
Macrofauna	0	31 (77%)	12 (46%)
Microbial	32	41 (23%)	46 (54%)
(c) Anaerobic metabolism (mmol m^{-2} d^{-1})			
I_{SRR}	26 ± 10	15 ± 2 (− 42%)	25 ± 2 (− 4%)
SRR	81%	24%	73%
TCO_2 release	32 ± 4	62 ± 22	34 ± 11

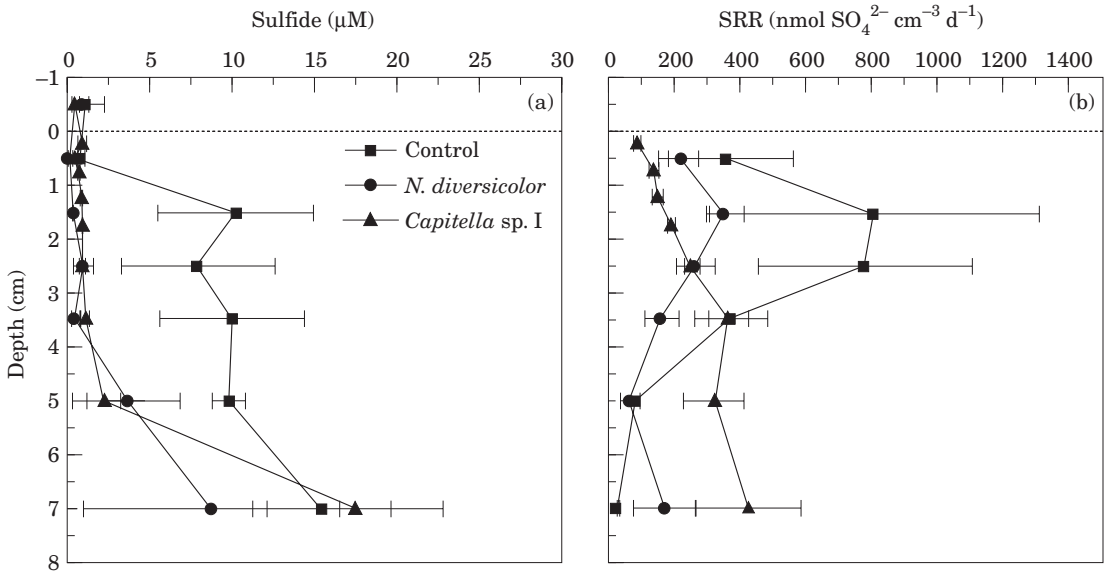

Figure 3. Profiles (means ± s.e.) of pore-water dissolved sulphide (a) and sulphate reduction rates (b) at day 64 in three replicate cores by treatment.

stimulation of TCO_2 release and O_2 uptake by factors of 2.3 and 1.7, respectively, when *Capitella* is added to sediment in the same densities as used here. Hansen and Kristensen (1998) found that *N. diversicolor* stimulated the metabolism by 154% in a muddy sediment and by 64% in a sandy sediment, indicating that the effects depend on sediment composition. The stimulating effect is possibly controlled by the lability of the organic matter and by differences in degradability under aerobic and anaerobic conditions. Andersen and Kristensen (1992) and Kristensen *et al.* (1992) have shown that macrofauna stimulates the degradation of old and relatively refractory compounds, while the effect on fresh and relatively labile detritus is low. This difference is

most likely caused by differences in degradability under aerobic and anaerobic conditions. Relatively refractory compounds are mineralized up to 10 times faster under aerobic than anaerobic conditions, while the degradation of more labile compounds is unaffected by redox condition in the sediment (Kristensen *et al*., 1995; Kristensen and Holmer, 2001). Therefore, the influence of benthic fauna might be expected to be smaller in fish-farm sediments, where the contribution of labile organic matter is relatively higher (indicated by the lower C:N ratio in surface sediment). However, this appears not to be the case because the observed stimulation is in accordance with results obtained from muddy sediment with a large content of refractory organic matter (Hansen and Kristensen, 1998). Thus, our results indicate that the stimulating effect of bioturbation is also significant in fish-farm sediments. Furthermore, van Duyl *et al*. (1992) suggest that the supply of labile organic matter acts as a catalyst for decomposition of the refractory organic pool. Thus, fauna-induced downward transport of organic matter might be a contributory factor to increased mineralization.

Despite its smaller size, *Capitella* caused a relatively high stimulation of the total metabolism. Aller and Aller (1998) have shown that decreased diffusion length (e.g. diminished distance between burrow structures) and efficient transport of toxic metabolites enhance decomposition of organic matter. Although *Capitella* irrigate the burrows to a lesser extent than *N. diversicolor*, the transport of reduced metabolites is probably efficient because of the high abundance.

The observed stimulation of total sediment metabolism by benthic fauna combines the direct contribution from fauna respiration and an indirect contribution from enhanced microbial activity. While *Nereis* had a larger effect on total mineralization, this was largely due to faunal respiration and microbial mineralization was less stimulated than for *Capitella* [Table 1(b)]. In accordance with our results, Alongi (1985) found enhanced bacterial production and protozoan density in burrow structures of *Capitella*. The differences between the two species may be due to differences in bioturbational activity. Head-down deposit-feeders may rework the sediment more intensely than surface deposit-feeders. By sediment reworking, labile organic matter from the surface is redistributed and becomes available for microbial populations in the deeper parts of the sediment (Aller, 1982; Kristensen, 1988). Banta *et al.* (1999) also observed a larger effect on microbial metabolism for the head-down deposit-feeder *Arenicola marina* compared to *N. diversicolor*. The stimulating effect of *Nereis* on microbial activity might be largely related to a ventilatory supply of electron acceptors and the removal of reduced metabolites.

Benthos also affects anaerobic metabolism, because sulphate reduction rates are reduced in the upper part of the sediment and enhanced in the deeper parts. Similar effects on the zonation of sulphate reduction have been shown for *Capitella* (Holmer *et al.*, 1997) and *N. diversicolor* (Banta *et al*., 1999). Burrowing and ventilation cause increased oxidation, thereby hampering anaerobic metabolism in the upper layers. Labile organic material is transported down in the sediment, and is mineralized under anaerobic conditions if ventilation is insufficient.

Sulphate reduction is the dominant anaerobic decomposition pathway in marine sediments, while other anaerobic processes are less important (Mackin and Swider, 1989). The fraction of total metabolism accounted for by sulphate reduction is estimated from the following C/S stoichiometry: $2\,CH_2O + SO_4^{2-} \rightarrow H_2S + 2\,HCO_3$ [Table 1(c)]. Berner and Westrich (1985) have shown that this approach is valid for coastal marine sediments. The high proportion of anaerobic metabolism (80%) in the control is in accordance with earlier investigations of fish-farm sediments (Holmer and Kristensen, 1992), and reflects organic enrichment causing high metabolism and reduced sediment conditions. The effect of the two species on sulphate reduction differed. While *Capitella* had only a minor influence (4%) and sulphate reduction accounted for 73% of the total metabolism [Table 1(c)], the anaerobic fraction tended to be smaller in *Nereis* sediment (24%), although the difference was not significant owing to the large heterogeneity among samples ($p = 0.52$). Bioturbation has been found to stimulate sulphate reduction in some investigations (Aller and Yingst, 1978; Kristensen and Blackburn, 1987; Hansen and Blackburn, 1992), while others, in accordance with our results, have seen a reduction. Thus, Holmer *et al.* (1997) observed a reduction by 20–26% for a similar abundance of *Capitella* and Banta *et al.* (1999) found an inhibition of sulphate reduction by 66% in sediments with *N. diversicolor*. Whether macrofauna stimulates or inhibits anaerobic decomposition processes may depend on the balance between counteracting effects, e.g. stimulation caused by an increased supply of electron acceptors and labile organic material to anaerobic layers, and inhibition caused by more oxidized conditions.

The reduction of anaerobic metabolism and the simultaneous stimulation of total sediment metabolism by *Nereis* indicate the increased importance of aerobic processes. Enhanced oxidized conditions probably also affect N-cycling. Both nitrification and denitrification may be stimulated in the sediment surrounding ventilated burrow structures of the genus *Nereis* (Kristensen, 1985; Kristensen *et al.*, 1991; Pelegri and Blackburn, 1995). Ventilation with oxygen-rich surface water stimulates nitrification, while increased nitrate availability, partly by ventilation-mediated transport from the water column and partly by enhanced nitrification activity, enhances denitrification. Moreover, an exhaustion of the ammonium pool was found in the sediment at this farm.

Stimulation of N-cycling results in a larger net-removal of biological accessible nitrogen from the ecosystem compared to azoic sediments.

The oxidized conditions may also affect phosphorus retention in the sediment. Pools of oxidized iron increase with oxidation and this enhances the retention of phosphorus, as shown for *N. diversicolor* by Clavero *et al.* (1994). *Capitella* had only a minor influence on anaerobic metabolism, but caused an increase in microbial metabolism compared to the control, indicating enhanced aerobic activity. Therefore, an increase in N-removal and P-retention can be expected, but to a lesser extent than for *Nereis*, because the oxidizing capacity is smaller. Stimulation of both nitrification and denitrification has been demonstrated for the small amphipod *Corophium volutator*, indicating that other small infauna species also have effects on the N-cycling (Pelegri *et al.*, 1994).

Overall, it is clear that the presence of benthic fauna and bioturbation enhances sediment metabolism compared to azoic sediments. The results clearly indicate the importance of maintaining macrofaunal populations in fish-farm sediments to enhance decomposition of organic matter and to prevent accumulation of organic wastes below the net cages.

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