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Contrasting effects of the polychaetes *Marenzelleria viridis* and *Nereis diversicolor* on benthic metabolism and solute transport in sandy coastal sediment

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ABSTRACT: The contrasting effects of the invasive *Marenzelleria viridis* and the native *Nereis diversicolor* on benthic metabolism, partitioning of reaction pathways and distribution of inorganic porewater (C and N) solutes in homogenized sandy sediment were investigated experimentally over a period of 1 mo. The 2 species were studied separately and in combination to observe possible effects and interactions. Benthic O_2 uptake and total CO_2 (TCO_2) release were affected similarly by *M. viridis, N. diversicolor* and the two in combination, with roughly a doubling after 1 to 2 wk compared to defaunated sediment. Sulfate reduction after 1 mo, on the other hand, was more than twice as high in sediment inhabited by *M. viridis* alone than in any other treatment, even when combined with *N. diversicolor*. Denitrification estimated from benthic TCO_2 release, porewater reaction stoichiometry and nutrient fluxes was largely unaffected by the presence of fauna. Accordingly, the partitioning of reaction pathways after 1 mo revealed that *M. viridis* stimulated sulfate reduction at the expense of aerobic respiration. Most of the oxygen uptake in *M. viridis* sediment was apparently due to enhanced oxidation resulting from an upward drifting front of sulfide as indicated by low redox and the appearance of *Beggiatoa* sp. near the surface. Porewater solute profiles showed that *M. viridis* was capable of stronger and deeper irrigation than *N. diversicolor* despite ~10 times higher burrow ventilation by the latter species. This effect was caused by percolation of return water in the deep (>20 cm) I- or J-shaped burrows of *M. viridis* compared to the flushing of the more shallow (6 to 8 cm) U- shaped burrows of *N. diversicolor*. A replacement of the native *N. diversicolor* with the invasive *M. viridis* as the dominant burrow-dwelling polychaete in shallow coastal sediments will probably affect the biogeochemical functioning and ecological stability of the ecosystem. Among other things, organisms tolerant to sulfide are likely to be favored at the expense of more sensitive species.

KEY WORDS: Invasive species · Porewater irrigation · C and N solutes · Reaction pathways · Sulfate reduction

INTRODUCTION

Benthic metabolism and distribution of porewater solutes in soft bottom sediment are controlled by the balance between reaction processes associated with organic matter decay and transport conditions (Jørgensen & Boudreau 2001, Jahnke et al. 2005). This balance can be changed dramatically by the presence of bioturbating infauna (Aller 1982, Kristensen 2001). It is known that burrow-dwelling infauna may enhance the capacity for bulk benthic metabolism up to 300% (Kristensen 2000). Mechanisms responsible for this faunal induced enhancement of microbial metabolism and capacity for organic matter degradation in sediments

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include particle reworking and burrow ventilation (Aller 1982, Aller & Aller 1998, Papaspyrou et al. 2007). Model considerations have shown that exposure of anoxic sediment to oxygen in ventilated burrows enhances carbon oxidation significantly and to a higher extent than particle reworking (Kristensen & Holmer 2001).

Ventilation by burrowing macrofauna disrupts the diffusional gradients and strongly affects the transport conditions within sediments. The associated porewater irrigation facilitates the exchange of solutes across the sediment–water interface and influences the distribution of dissolved reactants and products of early diagenetic reactions (Meile & Van Cappellen 2003, Meysman et al. 2006). Faunal enhancement of solute transport can exceed molecular diffusion by as much as an order of magnitude (Kristensen & Kostka 2005). The actual extent of the enhancement is, however, strongly dependent on the species composition and functional structure of the infaunal community present (Kristensen 2000, Aller 2001).

The 2 burrow-dwelling polychaetes *Marenzelleria viridis* (Spionidae) and *Nereis diversicolor* (Nereididae) are common inhabitants of Danish coastal sediments with a high potential for affecting sediment biogeochemistry. *M. viridis* is an invasive species that originates from North America and was first reported in Europe around 1980 in the Forth Estuary, Scotland (McLusky et al. 1993). It rapidly spread along the mainland coasts of the North Sea (Essink & Kleef 1988, 1993) and reached the western Baltic Sea in 2004 (Bastrop & Blank 2006). An almost simultaneous spread of the sibling species *Marenzelleria neglecta* occurred in the southern and central Baltic Sea (Sikorski & Bick 2004). A salinity of ~10 seems to delimit the distribution of these 2 species in the Baltic Sea, with *M. viridis* restricted to salinities above and *M. neglecta* to salinities below this level. The transition zone is located around the Island of Rügen, Germany (Blank et al. 2008).

Marenzelleria viridis is a surface deposit-feeder that ventilates its 30 to 40 cm deep vertical I- or J-shaped burrows in sandy sediment by ciliary (George 1966, Essink & Kleef 1988) and possibly muscular (Quintana et al. 2011) action. Strong evidence indicates that *M. viridis* has the capacity to outcompete the native *Nereis diversicolor* in certain shallow areas (Essink & Kleef 1993, Kotta et al. 2006). *N. diversicolor* is a common native species along marine and brackish coasts all over Europe (Maltagliati et al. 2006). It is a surface deposit-feeder or suspension-feeder that builds 6 to 10 cm deep U- or Y-shaped burrows in sand and muddy-sand (Esselink & Zwarts 1989, Riisgård 1991). The burrows are ventilated vigorously by undulatory body movements (Kristensen & Kostka 2005).

Effects of *Marenzelleria viridis* on sediment biogeochemistry are poorly known and the only studies available on *Marenzelleria* effects are from the central and northern Baltic Sea (Karlson et al. 2005, Hietanen et al. 2007, Viitasalo-Frösén et al. 2009), where primarily the sibling species *M. neglecta* or *M. arctia* occur in fine-grained muddy sediments. However, Quintana et al. (2007) found that *M. viridis* in Danish waters prefers shallow sandy sediment. These authors also found that *M. viridis* has low particle reworking and considerable irrigation capacity. Nevertheless, its ventilation activity is not very intense as indicated from the lack of an oxidized halo around burrows. Thus, adult individuals are reported to ventilate their blind-ended burrows at an average rate of <4 ml h^{-1} (Quintana et al. 2011). Much of the return water apparently percolates slowly through the sediment back to the surface and increases the exchange of solutes across the sediment–water interface (Quintana et al. 2007). The lack of studies on *Marenzelleria viridis* in relation to sediment biogeochemistry is surprising considering its rapid spread in recent years and current high abundance in European coastal areas. Even more so when its potential for outcompeting the native *Nereis diversicolor* is taken into account. The impact of the latter species on sediment biogeochemistry is well investigated (e.g. Hansen & Kristensen 1998, Kristensen & Mikkelsen 2003, Papaspyrou et al. 2006). *N. diversicolor* ventilates its burrows actively at rates of 80 to 190 ml h^{-1} (Kristensen & Kostka 2005). The burrow walls are surrounded by a several mm thick oxidized halo with intense microbial activity affecting C, N and S biogeochemistry (Nielsen et al. 2004).

The aim of this study was to highlight contrasting effects of the invasive *Marenzelleria viridis* and the native *Nereis diversicolor* on benthic fluxes of O_2, total CO_2 (TCO_2) and dissolved inorganic nitrogen (DIN), as well as sulfate reduction and solute transport in sandy sediment from Odense Fjord, Denmark. We hypothesize that replacement of *N. diversicolor* by the deep burrowing *M. viridis* in sandy coastal areas (1) modifies solute profiles by enhanced transport deep in sediments, and (2) alters the balance of biogeochemical pathways responsible for organic carbon oxidation.

MATERIALS AND METHODS

Sampling site and sample handling. Sandy sediment and specimens of *Marenzelleria viridis* and *Nereis diversicolor* were sampled in the shallow (mean depth of 2.2 m) Odense Fjord estuary on the island of Fyn, Denmark. Historical data from Odense Fjord has shown a rapidly increasing abundance of *M. viridis*

from its first scattered occurrence in 2002 to its presence along 60% of the coastline at densities up to 3000 m^{-2} in 2010 (M. Delefosse et al. unpubl. data). Sampling was conducted during March 2008 at Bregnør Bay (55.48118°N, 10.61002°E) in the outer part of the fjord. The sampling site is normally covered by 20 to 50 cm water, but periods of air exposure can occur depending on the strength and direction of the winds. Freshwater discharge from streams causes the salinity to vary from 15 to 25 (Fyns Amt 2003). Water temperature was 10°C during sampling.

The sediment was wet-sieved through a 1 mm mesh on location to remove larger particles and macrofauna. Specimens of *Nereis diversicolor* and *Marenzelleria viridis* were carefully collected during the sieving procedure. Intact and healthy individuals selected for the experiments were kept in darkened Petri dishes containing seawater at a salinity of 20 and a temperature of 15°C until use in the experiment.

Experimental set up. The sieved sediment was homogenized in the laboratory and transferred to 27 Plexiglas core liners (33 cm long and 8 cm diameter) leaving 10 cm of overlying water. The cores were placed with open tops in two 90 l tanks containing a common reservoir with seawater from the sampling site at 15°C (salinity of 20) and maintained in 12 h light/12 h dark cycles. The cores were illuminated vertically by a greenhouse lamp (Philips, Son-T Agro 400W) at an incident intensity of 250 µmol m^{-2} s^{-1} on the sediment surface to stimulate microphytobenthic growth as a food source for sediment organisms during the experiment. All cores were wrapped in aluminum foil covering the sediment phase to avoid photosynthesis along the walls of the cores. Water circulation inside the cores was assured by an external rotating magnet (60 rpm) driving internal magnetic stirring bars placed in the overlying water phase of each core. Worms were transferred to the sediment cores after a 2 d stabilization period at a natural Odense Fjord density of 1200 individuals (ind.) m^{-2} (M. Delefosse et al. unpubl. data) as follows: (1) 6 *Marenzelleria viridis* ind. (total of 0.7 to 1.0 g wet wt) to each of 6 replicate cores (M-cores); (2) 6 *Nereis diversicolor* ind. (1.1 to 1.5 g wet wt) to each of 6 replicate cores (N-cores); and (3) 3 ind. of *M. viridis* (0.4 to 0.9 g wet wt) and 3 ind. of *N. diversicolor* (0.4 to 0.8 g wet wt) to each of 6 replicate cores (MN-cores). The remaining 9 cores were kept as defaunated controls (C-cores). Triplicates of C-cores were sliced for determination of the initial sediment conditions and sulfate reduction on the day of worm addition (Day 0). Initial fluxes were measured 4 d later (Day 4) and subsequently once every week for 3 wk (Day 11, 18 and 25). From each treatment, 3 cores were sacrificed on Day 16 and the remaining cores on Day 31 for determination of sediment characteristics, sulfate reduction, redox (only Day 31) and porewater solutes.

Benthic fluxes. Fluxes of O_2, TCO_2 ($CO_2 + HCO_3^- + CO_3^{2-}$), NH_4^+ and $NO_2^- + NO_3^-$ (here denoted NO_3^-) across the sediment–water interface were determined from 3.5 h dark incubations initiated at the end of the dark period. The cores were sealed gas tight with rubber stoppers during flux incubations while maintaining water stirring. Fluxes were calculated from the concentration difference between start and end water samples. O_2 was analyzed immediately after sampling by the standard Winkler technique (Parsons et al. 1984) and never decreased <60% of air saturation. TCO_2 samples were preserved with saturated $HgCl_2$ in 5 ml glass Exetainers and stored at 5°C until analysis by the flow injection/diffusion cell technique (Hall & Aller 1992). Subsamples for NH_4^+ and NO_3^- were stored frozen (–20°C) in 20 ml plastic vials. Samples were prefiltered through GF/F-filters before analysis on a Lachat Quickchem 8500 Flow Injection Analyzer according to the protocols of Bower & Holm-Hansen (1980) for NH_4^+ and Armstrong et al. (1967) for NO_3^-.

Sulfate reduction. Sulfate reduction (SR) was measured on Day 0, 16 and 31. One subcore (internal diameter: 2.6 cm) was taken from each of 3 experimental cores before slicing for porewater solutes. The subcores were injected with 5 µl $^{35}S\text{-}SO_4^{2-}$ (60 kBq) through silicone-filled ports at 1 cm intervals down to 19 cm (only 11 cm on Day 0) and left for incubation in darkness at 15°C for ~6 h. The cores were subsequently sectioned into 1-cm depth intervals to 2 cm, and 2 cm intervals to 18 cm (the sections 10–12 and 14–16 cm were discarded). The sediment slices were fixed in 0.5 M zinc acetate and stored frozen until analysis by the one-step distillation procedure of Fossing & Jørgensen (1989). The total reduced inorganic sulfur pool (TRIS) was determined spectrophotometrically (Cline 1969) as part of the same procedure.

Sediment characteristics. Experimental cores were sectioned into the same intervals as for SR. Subsamples were taken from each sediment slice for porosity (i.e. water content × wet density) and organic matter content, while samples for grain size analysis were only taken from the upper 1 cm. All worms observed during slicing were recovered and counted. Subsamples for grain size analysis were wet sieved through a Wentworth series of sieves (1000, 500, 250, 125, 63 µm mesh). The fractions that were retained by sieves and passed through the 63 µm sieve were dried before weighing and grain size analysis was conducted according to Bale & Kenny (2005). Wet density (g cm^{-3}) was determined as the weight of a known volume of sediment. Water content was determined as weight

loss after drying for 20 h at 105°C, and organic content was determined as weight loss of dried sediment after combustion for 6 h at 520°C according to Kristensen & Andersen (1987).

Porewater analysis. Porewater from sediment subsamples of each slice was extracted by centrifugation at 1500 rpm for 10 min in double centrifuge tubes containing GF/F filters. Subsamples from the porewater were taken for TCO_2, SO_4^- and NH_4^+ analysis. TCO_2 was preserved with 20 µl saturated $HgCl_2$ in 1.5 ml glass vials and stored at 5°C until analysis as mentioned above. SO_4^- was analyzed by ion chromatography (Dionex ICS-2000) and normalized to chloride concentrations according to Martin & Banta (1992). Samples for NH_4^+ and NO_3^- were stored frozen until analysis as mentioned above.

Redox. Vertical redox (Eh) profiles were determined on intact cores before the final slicing with a needle Redox electrode (RD-N) (Unisense A/S) connected to a Calomel reference electrode and monitored on an Impo Electronic type 1510 pH/mV-meter. The electrode was inserted into the sediment in steps of 2.5 mm in the upper 1.5 cm, and thereafter every 5 mm down to 5 cm. The Eh signal was allowed to stabilize for 1 min at each depth before the reading was noted. Five profiles were measured from C- and N-cores, while 6 profiles were obtained from M-cores (3 within visible *Beggiatoa* sp. mats and 3 outside mats). No profiles were made in MN-cores.

Statistical analysis. Flux data were analyzed using a 2-way ANOVA to test for effects of treatment and time. Sediment profiles were analyzed using depth integrated values. Significant differences were further investigated using a Tukey's post hoc multiple comparison between means or Dunnet's test for comparison with control means. Data were tested for normality (Kolmogorov-Smirnov test) and homogeneity of variance (Levene's test). The significance level is 0.05 unless otherwise stated.

RESULTS

Sediment appearance during final slicing

The sediment consisted of well-sorted sand with a mean grain size of 265 ± 17 µm (n = 3) and a silt + clay fraction of 2.48 ± 0.02% (n = 3). Porosity and organic content were almost constant with depth and similar among cores. Porosity ranged from 0.28 to 0.30 and organic content varied from 0.55 to 0.72% dry wt among cores.

Visually, C- and M-cores had <0.5 cm thick, brownish, oxidized surface layer, whereas this layer in N- and MN-cores was up to 1 cm thick with patches associated to *Nereis diversicolor* burrow openings extending to depths of 3 to 4 cm. The sediment appeared grayish-black in color underneath the oxidized layer. Up to 2 mm thick microalgal mats were observed on the sediment surface of C-cores at the end. Microalgae were only observed occasionally on the surface of the sediment in M- and N-cores. The surface of M-cores was visually characterized by *Marenzelleria viridis* faeces and burrow openings, and the occurrence of several white *Beggiatoa* sp. patches (maximum area of ~2 cm^2). *M. viridis* burrows had a diameter of ~2 mm and extended all the way to the bottom of the cores (~20 cm), and the worms were always recovered deeper than 8 cm. The openings of *N. diversicolor* burrows protruded a few mm above the surface in N-cores. *N. diversicolor* individuals were always found in the lower part of the U-shaped burrows at a depth of 4 to 6 cm. Burrows of *N. diversicolor* were surrounded by a mm thick oxidized halo. No such oxidized zone was evident around *M. viridis* burrows at any time. The MN-cores shared the characteristics of M- and N-cores with surface deposited faeces of *M. viridis*, protruded *N. diversicolor* burrow openings, occasional microalgae, and *Beggiatoa* sp. patches.

The survival of *Marenzelleria viridis* at Day 16 was 56 ± 10 and 89 ± 38% in M- and MN-cores, respectively, while 78 ± 10 and 100 ± 33% of the introduced *Nereis diversicolor* was recovered in N- and MN-cores, respectively, at that time. Survival at Day 31 decreased slightly, reaching 56 ± 10 and 44 ± 19% for *M. viridis* and 61 ± 10 and 89 ± 19% for *N. diversicolor* in the respective treatments.

Benthic solute fluxes

O_2 was taken up and TCO_2 released by the sediment throughout the experiment (Table 1). There were no significant interactions among treatments and time for O_2 and TCO_2. O_2 uptake was constant with time and always lowest in C-cores (15 to 17 mmol m^{-2} d^{-1}). M- and N-cores had significantly 20 to 40% higher O_2 uptake than C-cores on Day 4, increasing to ~100 to 120% on Day 11, with no further change to the end (Fig. 1A). No such temporal trend was evident for MN-cores that always had significantly ~100% higher rates than C-cores. TCO_2 release from the sediment showed the same pattern as O_2 uptake, but the changes reaching 50 to 70% higher rates in faunated than in C-cores after Day 4 were not significant (Fig. 1B). The respiratory quotient (RQ = TCO_2/O_2 flux ratio) ranged between 3 and 6, and showed a marginally significant decreasing trend with time ($p = 0.07$, data not shown).

There was an apparent uptake of NH_4^+ in C-cores and release in the faunated cores (Table 1), particu-

Table 1. Sediment-water flux of O_2, total carbon oxidation (TCO_2), NH_4^+ and NO_3^- in treatments C, M, N and MN. Fluxes were measured weekly over a 25 d period. Negative flux: uptake by sediment. Values are means ± SE (n = 3). Cores without fauna (C), with *Marenzelleria viridis* (M), with *Nereis diversicolor* (N), and mixture of *M. viridis* and *N. diversicolor* (MN)

Core	Day 4	Day 11	Day 18	Day 25
O_2 (mmol m^{-2} d^{-1})				
C	−16.7 ± 3.6	−14.9 ± 1.0	−17.6 ± 0.1	−16.8 ± 0.8
M	−23.8 ± 2.0	−32.2 ± 1.2	−36.6 ± 4.0	−39.1 ± 2.6
N	−20.5 ± 3.1	−28.6 ± 0.1	−33.1 ± 3.2	−33.9 ± 1.7
MN	−32.0 ± 1.8	−32.4 ± 3.5	−32.3 ± 3.5	−36.9 ± 2.0
TCO_2 (mmol m^{-2} d^{-1})				
C	95.9 ± 3.7	76.0 ± 15.1	64.5 ± 4.4	64.2 ± 6.0
M	99.4 ± 4.5	125.1 ± 17.9	100.9 ± 24.1	110.9 ± 18.6
N	83.1 ± 19.5	99.9 ± 13.9	98.8 ± 29.0	100.9 ± 30.8
MN	100.0 ± 28.0	131.4 ± 24.9	89.5 ± 9.7	109.6 ± 14.5
NH_4^+ (mmol m^{-2} d^{-1})				
C	−7.0 ± 0.9	−8.7 ± 1.2	−3.2 ± 1.3	−3.5 ± 4.4
M	8.3 ± 2.5	6.5 ± 0.9	6.9 ± 1.0	8.7 ± 3.2
N	4.9 ± 1.8	2.4 ± 2.7	2.1 ± 0.5	5.9 ± 0.3
MN	4.6 ± 3.0	13.2 ± 3.1	8.3 ± 0.8	8.4 ± 4.1
NO_3^- (mmol m^{-2} d^{-1})				
C	4.8 ± 0.5	0.7 ± 0.2	0.9 ± 0.2	0.6 ± 0.5
M	−0.3 ± 0.7	−0.8 ± 0.2	−0.3 ± 0.1	−1.0 ± 1.3
N	−0.3 ± 0.3	−0.6 ± 0.3	0.4 ± 0.6	0.3 ± 0.3
MN	−1.5 ± 1.5	0.3 ± 0.2	0.6 ± 0.2	0.4 ± 0.5

larly those containing *Marenzelleria viridis*, but with no significant difference through time. NO_3^- was released from C-cores at a rate corresponding to 69% of the NH_4^+ uptake on Day 1, and 8 to 27% subsequently (Table 1). The faunated cores showed no specific pattern in NO_3^- flux, and rates were rarely significantly different from 0.

Sulfate reduction

SR at Day 0 increased from ~90 nmol cm^{-3} d^{-1} in the upper 2 cm of the sediment to a constant level of ~150 nmol cm^{-3} d^{-1} in the sediment below (Fig. 2). C-cores showed an SR pattern in the upper 6 cm that was similar on both Day 16 and 31: a relatively high level of ~200 nmol cm^{-3} d^{-1} in the top cm followed by a decrease to ~100 nmol cm^{-3} d^{-1} below this depth. While SR remained at ~100 nmol cm^{-3} d^{-1} down to at least 16–18 cm in these cores on Day 16 (Fig. 2A), a progressive decrease occurred below 6 cm depth on Day 31, reaching zero at 16–18 cm (Fig. 2B). M-, N- and MN-cores down to 12–14 cm showed SR profiles at a level of 100 to 150 nmol cm^{-3} d^{-1} at Day 16 that were constant with depth and not significantly different from each other and C-cores. Below this depth, SR in M-cores increased significantly to 240 nmol cm^{-3} d^{-1} at 16–18 cm (Fig. 2A). N- and MN-cores maintained roughly the same profiles on Day 31, while the entire profile in M-cores reached a significantly higher level of 200 to 270 nmol cm^{-3} d^{-1} throughout the sediment column (Fig. 2B).

The concentration of TRIS was low in all treatments and ranged between 5 and 11 nmol S cm^3 in an unpredictable pattern (Fig. 3A,B). There was an increasing trend with time in all treatments, indicating an accumulation of reducing equivalents in the form of precipitated sulfide. The sulfide accumulation ranged from 10 to 40 mmol S m^{-2} d^{-1} among treatments, with highest rates during the first 16 d.

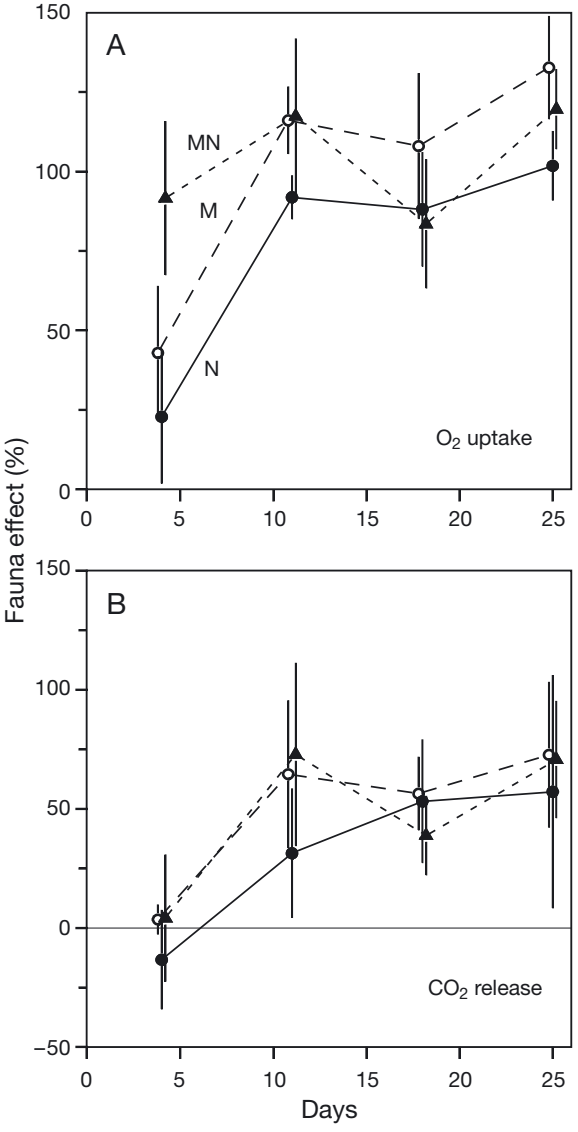

Fig. 1. Enhancement of (A) O_2 and (B) total CO_2 flux across the sediment–water interface over time in M-, N- and MN-sediment relative to C-sediment. Values: mean ± SE (n = 3). Cores: without fauna (C), with *Marenzelleria viridis* (M), with *Nereis diversicolor* (N), and mixture of *M. viridis* and *N. diversicolor* (MN)

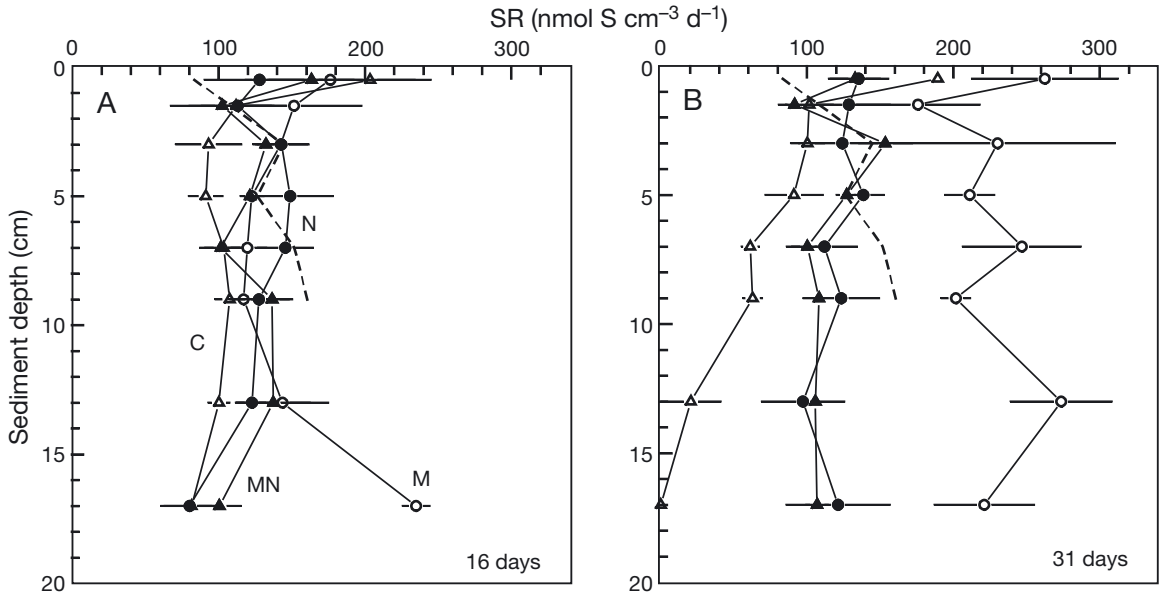

Fig. 2. Vertical profiles of sulfate reduction (SR) in C-, M-, N- and MN-sediment at (A) Day 16 and (B) Day 31. Values: mean ± SE (n = 3). Broken lines: initial (Day 0) SR. See Fig. 1 for core definitions

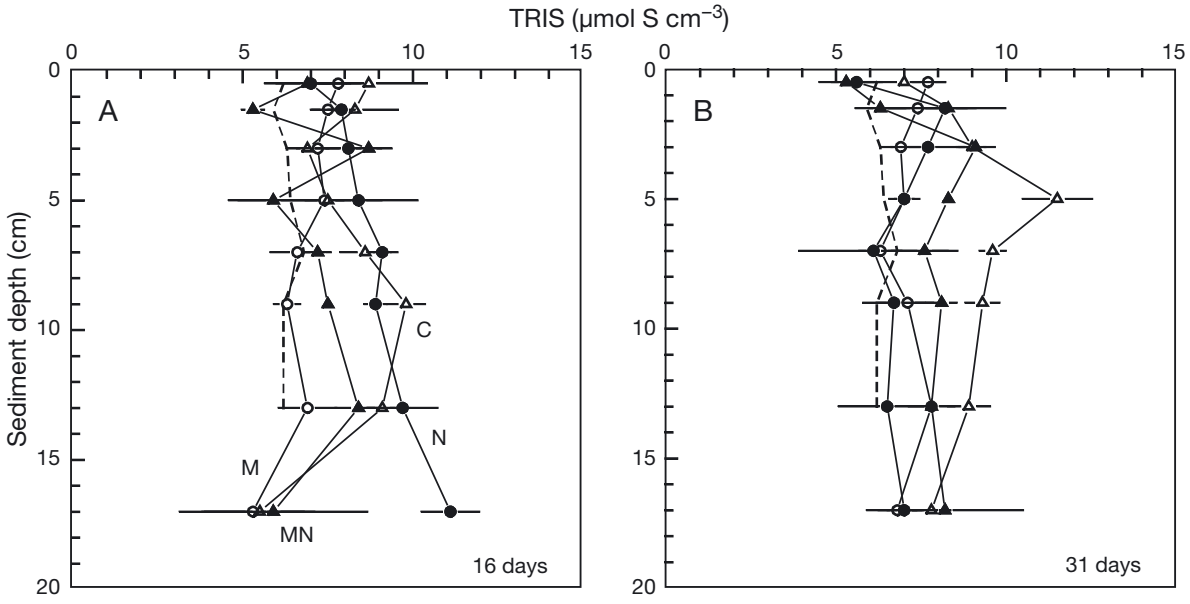

Fig. 3. Vertical profiles of total reduced inorganic sulfur (TRIS) in C-, M-, N- and MN-sediment at (A) Day 16 and (B) Day 31. Values: mean ± SE (n = 3). Broken lines: initial (Day 0) TRIS. See Fig. 1 for core definitions

Porewater solutes

Initial porewater TCO_2 increased rapidly from ~2.5 mM in the overlying water to a constant level of ~10 mM at 1 to 2 cm depth and below. A similar increase was observed near the surface to 6 cm depth in sandy C-cores on Days 16 and 31, followed by a less steep increase below that depth, reaching 21 and 26 mM at 16–18 cm depth, respectively (Fig. 4A,B). C-cores were significantly different from the faunated cores throughout the examined depth interval. TCO_2 in M-cores barely increased beyond the overlying water level in the upper 10 cm (<5 mM) and only increased slightly below this depth, reaching 8 and 9 mM at 16–18 cm depth on Day 16 and 31, respectively. N-cores also exhibited low TCO_2 near the surface, but only to 2–4 cm depth. Below this depth, TCO_2 increased steadily to 16 and 20 mM at 16–18 cm on

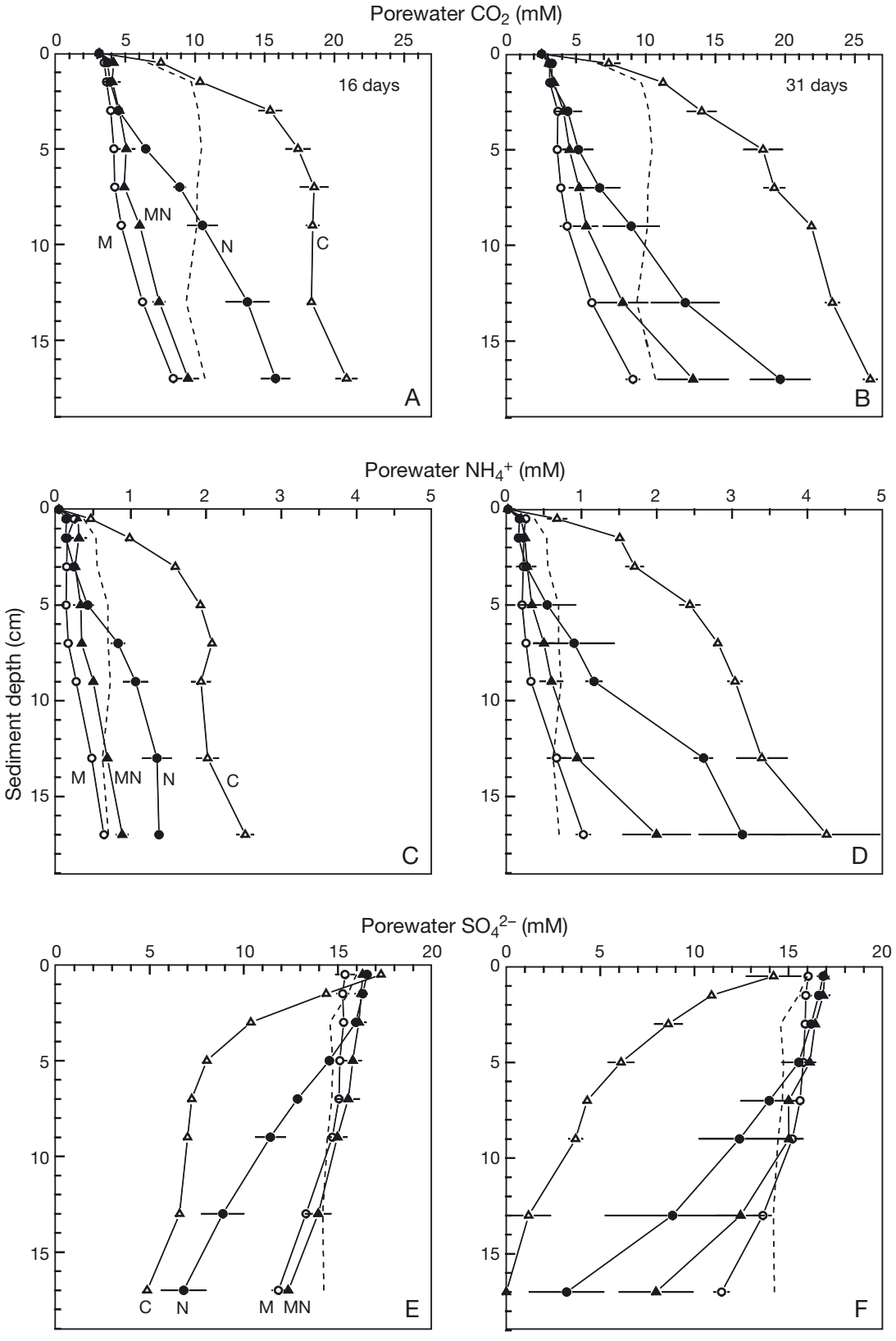

Fig. 4. Vertical profiles of porewater solutes in C-, M-, N- and MN-sediment. Total CO_2, NH_4^+ and SO_4^{2-} at (A,C,E) Day 16, and (B,D,F) Day 31, respectively. Values: mean ± SE (n = 3). Broken lines: initial (Day 0) profiles. See Fig. 1 for core definitions

Day 16 and 31, respectively. The differences between N- and M-cores below 4 cm depth were only significant on Day 16. MN-cores had TCO_2 profiles that were intermediate to those of M- and N-cores, but with profiles and concentrations most similar to and not significantly different from those of M-cores.

Profiles of NH_4^+ showed patterns almost identical to those of TCO_2 among treatments and with time (Fig. 4C,D). Concentrations were considerably lower, and C-cores only reached 2.5 and 4.3 mM in the deepest layer on Day 16 and 31, respectively.

Porewater SO_4^{2-} profiles were almost perfect mirror images of the TCO_2 profiles (Fig. 4E,F), indicating the importance of sulfate reduction and transport processes for carbon dynamics. The low SO_4^{2-} level observed at the bottom of C-cores on Day 31 corresponds to the low SR and indicates SO_4^{2-} limitation (Fig. 4F).

Redox

Redox conditions were clearly affected by *Marenzelleria viridis* and *Nereis diversicolor* (Fig. 5). M-cores showed no or only a thin oxidized zone as Eh < 0 mV was apparent within the upper 0.25 cm. Eh < –150 mV in these cores was observed at 0.5 cm depth and reached almost –200 mV at 5 cm depth. There was only a slight and insignificant trend for lower Eh in patches with, than in those without, visible *Beggiatoa* sp. For N-cores, on the other hand, Eh < 0 mV was first recorded at 0.75 mm depth. These cores had significantly higher Eh than M-cores throughout the measured depth interval and never exhibited values below –150 mV. C-cores showed an intermediate pattern to those of M- and N-cores, with Eh ~ 0 mV between 0.25 and 0.5 cm depth, and approached the level of M-cores below 3 cm depth.

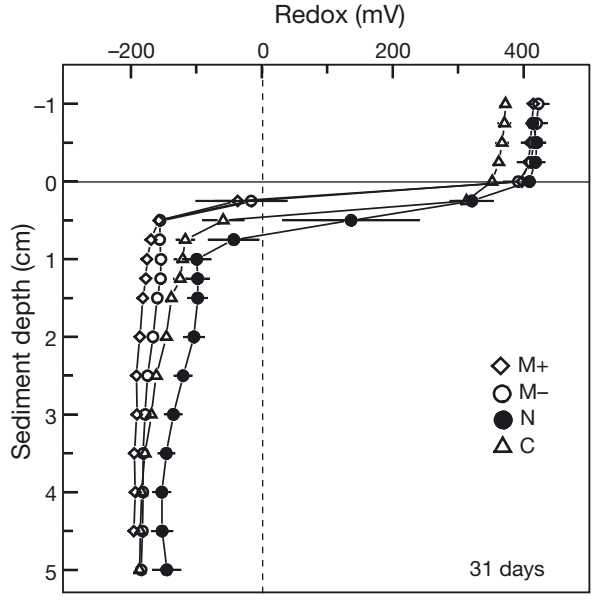

Fig. 5. Vertical redox profiles of upper 5 cm of C-, M-, and N-sediment at Day 31. M+ and M–: profiles within and outside *Beggiatoa* sp. patches, respectively. Values: mean ± SE (n = 5, except M+ and M– where n = 3). See Fig. 1 for core definitions

DISCUSSION

Benthic metabolism and reaction pathways

The presence of *Marenzelleria viridis* and *Nereis diversicolor* clearly affects the flux of solutes across the sediment–water interface. It is noteworthy that the absolute rates and enhancement of O_2 uptake and TCO_2 release were almost similar for the 2 species despite their widely different life habits. The roughly doubling of O_2 uptake and ~50% increased TCO_2 release at Day 11 and onwards in faunated compared to control sediment (Fig. 1) is within the range of 45 and 174% observed previously for homogenized sediment inhabited by *N. diversicolor* (see review by Kristensen 2001). It is important to stress here, though, that the effects of bioturbation on benthic metabolism from our manipulated and transient state laboratory experiment cannot be directly extrapolated to *in situ* conditions. The enhancement of fluxes we found is higher than generally observed *in situ* and should instead be considered an increased decomposition capacity caused by the fauna (Kristensen 2001).

The substantially higher TCO_2 release than O_2 uptake (RQ of 3 to 6) observed in all treatments (Table 1) indicates storage of reducing equivalents and/or dissolution of carbonates within the sediment. Storage of reducing equivalents in the form of sulfide precipitation with, for example, iron can be important, particularly in transient state or manipulated sediments (Ferguson et al. 2003, Gribsholt & Kristensen 2003, Valdemarsen et al. 2009). Accordingly, the present excess TCO_2 efflux relative to a RQ of 1 ranging from 50 to 100 mmol m^{-2} d^{-1} corresponds well with the reducing equivalents of sulfide (TRIS, Fig. 3) accumulated within the sediment during the experiment (20 to 80 mmol m^{-2} d^{-1}). The role of carbonate dissolution can therefore be considered of limited importance in our quartz dominated sandy sediment.

Modification of benthic metabolism by burrow dwelling and irrigating infauna is generally considered a consequence of enhanced microbial activity, altered degradation pathways and the animals own respiration (Aller & Aller 1998, Glud 2008). Unfortunately, we have no direct measure of the partitioning between enhanced microbial activity and the animals'

own respiration in the present study. However, several studies have found that the direct contribution of infauna respiration (including *Nereis diversicolor*) to the total benthic metabolism of bioturbated sediments in general range from 10 to 30% (Kristensen et al. 1992, Banta et al. 1999, Quintana et al. 2007). The presently observed higher enhancement of benthic metabolism therefore indicates substantial stimulation of microbial activity in the presence of fauna. However, partitioning of degradation pathways estimated from the contribution of SR and denitrification (DENIT) to total benthic metabolism reveals marked differences induced by the 2 polychaete species, particularly at Day 31.

While SR measured in N- and MN-sediments is similar to rates found by Banta et al. (1999) for sediment with *Nereis diversicolor* (150 nmol cm^{-3} d^{-1}), SR in M-sediment was ultimately much higher (Fig. 2). It appears that the positive effect of *Marenzelleria viridis* on SR initiated from below as indicated by a high rate in the 16–18 cm layer at Day 16, and the displacement of the entire profile at Day 31 suggests that the transition was fully implemented within a month. For estimating the contribution of SR to total sediment metabolism in the various treatments, the measured profiles were depth-integrated to 18 cm depth. These estimates show only slightly higher rates in M-sediment at Day 16 (27 mmol S m^{-2} d^{-1}) than in the other treatments (19 to 22 mmol S m^{-2} d^{-1}). Depth-integrated SR increased considerably in M-sediment at Day 31, reaching 42 mmol S m^{-2} d^{-1}, which is twice as high as in N- and MN-sediment that remained unchanged with time. The decrease in SR over time and depth in the diffusion controlled C-sediment was probably caused by gradual depletion of sulfate in deeper layers (Fig. 4E,F). Sulfate reduction is generally limited by SO_4^{2-} availability at concentrations <3 mM (Boudreau & Westrich 1984). Accordingly, C-sediment at Day 31 exhibited low depth integrated rates (~11 mmol m^{-2} d^{-1}).

The role of DENIT can be deduced from simple stoichiometric considerations. If decomposition follows first-order kinetics, the C:N ratio of the mineralized organic matter may be ascertained from the vertical steady state porewater profiles of TCO_2 and NH_4^+ from anoxic sediments according to Kristensen & Hansen (1999). Since the solute profiles in the present non-steady state control cores were affected by diffusion down to 4–6 cm depth, only this part of the sediment can be considered an open, diffusion dominated zone approaching steady state (Aller & Mackin 1989). As no sedimentation and compaction occurred, and reaction rates are assumed constant with depth in the upper 6 cm (Fig. 2), the reaction stoichiometry in this diffusion dominated zone of the sediment can be deduced from a linear regression of a porewater TCO_2 versus NH_4^+ plot (Fig. 6). The slope of the regression line is then a proxy for the ratio of CO_2 and NH_4^+ production rate or the C:N ratio of organic matter being mineralized. Total NH_4^+ production within the sediment is then equal to the measured TCO_2 flux divided by the C:N ratio (i.e. the regression slopes given in Fig. 6). Due to the limited change in fluxes after Day 11, we assume that the rates measured on Day 18 and 25 are

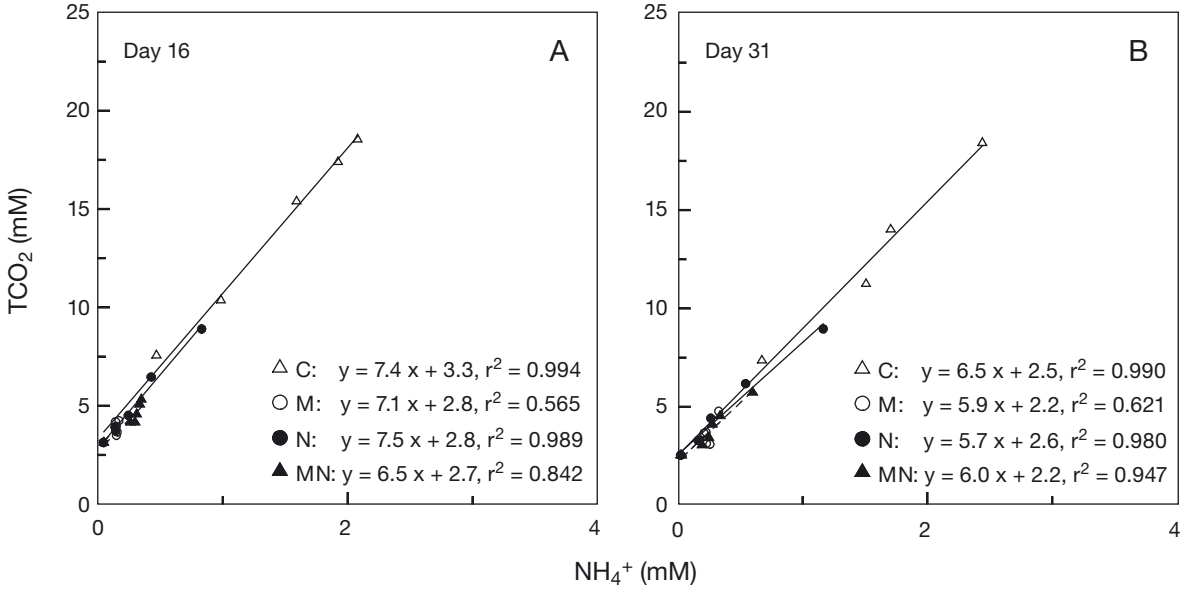

Fig. 6. Relationships between porewater profiles of NH_4^+ and total CO_2 (TCO_2) in C-, M-, N- and MN-sediment at (A) Day 16 and (B) Day 31. Relationships are limited to data from the diffusion controlled upper 6 cm of the sediment. Lines drawn according to least-squares linear regression and the obtained equations are shown. See Fig. 1 for core definitions

representative for the sediment conditions on Day 16 and 31, respectively, and vice versa. The slopes or C:N ratios of organic matter mineralization obtained here (5.7 to 7.5) are comparable to those found for other coastal sediments (Kristensen & Hansen 1999, Weston et al. 2006). DENIT can then be roughly estimated from the missing N calculated as total NH_4^+ production minus DIN (NH_4^+ + NO_3^-) efflux from the sediment. The obtained rates are comparable for C- and N-sediments on Day 16 (11 mmol N m^{-2} d^{-1}) and for all treatments on Day 31 (10 to 13 mmol N m^{-2} d^{-1}), while somewhat lower rates were evident for MN- and M-sediments on Day 16 (5 to 7 mmol N m^{-2} d^{-1}). These indirect estimates of DENIT are in the high range of rates found previously for near-coastal sediments (Herbert 1999, Bartoli et al. 2000, Rivera-Monroy et al. 2010). It must be emphasized that C:N ratios of organic matter decomposition estimated from porewater regressions are crude and rely on steady state assumptions that may not hold. Another source of error is loss of DIN through assimilation by growing microorganisms (microalgae and bacteria) within the sediment. Accordingly, the estimated rates of DENIT are probably too high and should only be considered a rough measure for comparative purposes in the present artificial sediment system.

Uptake of NH_4^+ by C-sediment kept in darkness for at least 8 h prior to incubations suggests consumption by e.g. nitrification. The supply of produced NH_4^+ in the deeper sediment layers was not sufficient to meet the nitrification demand in the upper oxic surface sediment, resulting in an uptake from the overlying water. A lack of a corresponding efflux of NO_3^- was probably caused by DENIT coupled to near-surface nitrification processes (Risgaard-Petersen 2003). The release of NH_4^+ from the sediment in the bioturbated sediment (Table 1) was partly due to increased microbial production of NH_4^+, and partly excretion by the worms. Thus, several studies have found that various infauna generally are responsible for 20 to 60% of faunal enhanced efflux of NH_4^+ (Henriksen et al. 1983, Kristensen 1985, Hansen & Kristensen 1997, Jordan et al. 2009). Furthermore, the measured fluxes of NH_4^+ are similar to those 4 and 9 mmol m^{-2} d^{-1} reported earlier for sandy sediment inhabited by *Nereis diversicolor* (Kristensen 1985, Kristensen & Hansen 1999, Christensen et al. 2000). Fluxes of NH_4^+ for sediment inhabited by *Marenzelleria* spp. are known to range from 1.6 to 13 mmol m^{-2} d^{-1} (Karlson et al. 2005, Viitasalo-Frösén et al. 2009).

Partitioning of reaction pathways based on the above estimates shows that SR (converted to C-units by multiplying by 2) was always the most important anaerobic carbon mineralization process accounting for at least 33 to 75%. This is a minimum estimate because the deepest 5 cm of the sediment, where SR was not measured, is unaccounted for. Accordingly, DENIT (converted to C-units by multiplying by 1.25) was responsible for no more than 7 to 25% of TCO_2 release. The group 'OTHER' in Table 2 accounted mostly for 12 to 52%, which primarily represents aerobic respiration because Fe and Mn concentrations are relatively low in sandy sediments from Odense Fjord (Kristiansen et al. 2002). Aerobic respiration that includes the fauna contribution corresponds roughly to or is lower than the measured rates of O_2 uptake, and the low value for particularly M-sediment at Day 31 leaves room for sulfide oxidation by *Beggiatoa* sp. The estimated partitioning is comparable to those reported from other coastal sediments (Jørgensen & Sørensen 1985, Canfield et al. 1993, Fennel et al. 2009) although considerable variation occurs among environments (Rysgaard et al. 2001)

The pronounced stimulation of sulfate reduction by *Marenzelleria viridis* has wider biogeochemical implications. The low redox and presence of *Beggiatoa* sp. at the sediment surface of M-sediment, indicates that a fraction of the produced sulfide escaped the iron trap in the sediment and moved upward towards the sediment–water interface by diffusion (Kristiansen et al. 2002) and *M. viridis* irrigation (see below). Consequently, the escaped sulfide in M-sediment was, to a larger extent than in the other treatments, oxidized or

Table 2. *Marenzelleria viridis* and *Nereis diversicolor*. Partitioning of reaction pathways in C-, M-, N-, and MN-cores at Day 16 and 31. TCO_2 flux: total carbon oxidation in 23 cm deep sediment column. Since no TCO_2 flux was measured on Day 16 and 31, results from Day 18 and 25 are used instead, assuming limited change over few days late in the experiment. SR: sulfate reduction (only to 18 cm depth); DENIT: denitrification; OTHER: combined aerobic, Fe and Mn respiration. Rates given as mmol C m^{-2} d^{-1} and values in parentheses are percent of total. See text for explanation of calculations. See Table 1 for core abbreviations

Reaction	C	M	N	MN
Day 16				
TCO_2 flux	64.5	100.9	98.8	89.5
SR	37.2 (58)	54.6 (54)	44.6 (45)	44.8 (50)
DENIT	13.8 (21)	8.8 (9)	13.3 (14)	6.3 (7)
OTHER	13.5 (21)	37.5 (37)	40.9 (41)	38.4 (43)
Day 31				
TCO_2 flux	64.2	110.9	100.9	109.6
SR	21.4 (33)	83.6 (75)	42.8 (42)	41.0 (37)
DENIT	16.0 (25)	13.9 (13)	14.4 (14)	12.0 (11)
OTHER	26.8 (42)	13.4 (12)	43.7 (43)	56.6 (52)

released to the overlying water column (Kristensen et al. 2000). It is also remarkable that MN-sediment containing a mixture of *Nereis diversicolor* and *M. viridis* had a partitioning of reaction pathways similar to the N-sediment (Table 2). Higher ventilation activities by *N. diversicolor* than *M. viridis* (Quintana et al. 2011) were apparently responsible for more oxidized conditions in the MN-sediment, which may have hampered sulfate reduction as also noted by Banta et al. (1999). The higher redox in *N. diversicolor* than *M. viridis* sediment (Fig. 5) was visually evident by a thicker oxidized halo around burrows of the former.

The enhancement of SR by the presence of *Marenzelleria viridis* is, however, puzzling. There is no doubt that this polychaete irrigates its burrow, and as such must introduce O_2 and SO_4^{2-} into the sediment (Quintana et al. 2011), which may either hamper or stimulate SR. Nevertheless, redox was lowered and SR was more than doubled in M-sediment compared with the other treatments. Besides the elevated redox in the presence of *Nereis diversicolor* and sulfate depletion in C-sediment, the relatively high SR in M-sediment may be explained by translocation of labile organic matter from the surface to deeper layers through *M.viridis*' feeding activities. This species is known to be a surface deposit-feeder that collects detritus by its palps (Dauer 1997). If some of this detritus enters the burrow, it may, together with faeces deposited inside burrows and mucus secretions along burrow walls (Dauer et al. 1981, Zettler et al. 1994), provide sulfate reducers with reactive organic carbon. Furthermore, deep irrigation by *M. viridis* ensures that SO_4^{2-} is available to all anoxic sediment layers. However, there is at present no clear evidence for the cause of the surprising microbial response in M-sediment and further studies are required to elucidate this enigma.

Solute distribution and irrigation

The considerably lower concentrations of porewater TCO_2 and NH_4^+ in faunated than defaunated sediment was caused by enhanced transport due to irrigation (Shull et al. 2009). The effect appeared most pronounced in the presence of *Marenzelleria viridis*. Despite the higher production of TCO_2 and NH_4^+ in faunated sediment due to stimulated microbial activity and worm respiration/excretion, the enhanced irrigation transport caused by faunal ventilation maintained concentrations lower than in the diffusion controlled C-sediment (Fig. 4). The opposite arguments are valid for SO_4^{2-}, which was consumed by sulfate reduction in the anoxic sediment and supplied from the overlying water by diffusion and irrigation transport. Both *Nereis diversicolor* and *M. viridis* have the capacity to prevent SO_4^{2-} depletion throughout the experimental period, as observed in the deeper part of the C-sediment.

The deep burrowing *Marenzelleria viridis* always maintained porewater solutes close to the overlying water level in the entire sediment column, whereas *Nereis diversicolor* only managed an increased transport within its burrowing depth of ~8 cm. MN-sediment did not appear as a true mixture of M- and N-sediments, but was more affected by *M. viridis* than *N. diversicolor* in terms of porewater profiles. This phenomenon is a consequence of their different life habits. *M. viridis* normally digs burrows down to depths of 30 cm or more, whereas *N. diversicolor* is most commonly restricted to depths >10 cm (Zettler et al. 1994), which is consistent with our observations. Although the ventilation of *N. diversicolor* is ~10 times faster than that of a similar sized *M. viridis* (Christensen et al. 2000, Quintana et al. 2011), the effects of deep irrigation by *M. viridis* on porewater transport appear to be much stronger. Similarly, Mermillod-Blondin et al. (2005) found that *N. diversicolor* hides the effect of shallow burying bivalves and crustaceans on porewater profiles due to its stronger and deeper irrigation.

The irrigation effect of *Marenzelleria viridis* is demonstrated clearly from the empirical ventilation–porewater relationships observed by Christensen et al. (2000). They measured ventilation of various species of *Nereis* under different conditions and found that the irrigation-induced depletion of porewater TCO_2 in the upper diffusion-dominated zone of the sediment related logarithmically to area-specific ventilation (l m^{-2} d^{-1}) according to: Relative TCO_2 depletion = -0.122 ln(ventilation) + 0.99, with $r^2 = 0.99$.

The relative depletion of porewater TCO_2 is defined as the slope of a linear relationship between porewater profiles in faunated and defaunated sediment (Fig. 7). Slopes <1 indicate a faster removal of TCO_2 due to irrigation transport than by molecular diffusion.

The predicted area-specific ventilation based on the TCO_2 depletion relationships in the present N-sediment (Fig. 7), normalized to a *Nereis diversicolor* density of 600 m^{-2}, is 870 and 590 l m^{-2} d^{-1} at Day 16 and 31, respectively, which is remarkably similar to the 754 l m^{-2} d^{-1} measured for the same density of non-suspension feeding *N. diversicolor* by Christensen et al. (2000). However, the predicted area-specific ventilation of 1900 to 2000 l m^{-2} d^{-1} by a population of *Marenzelleria viridis* (600 m^{-2}) exceeds by more than one order of magnitude the 50 to 100 l m^{-2} d^{-1} estimated from directly measured ventilation by this species (Quintana et al. 2011). The discrepancy must be caused by different irrigation efficiency of the 2 species. The high ventilation of *N. diversicolor* creates a

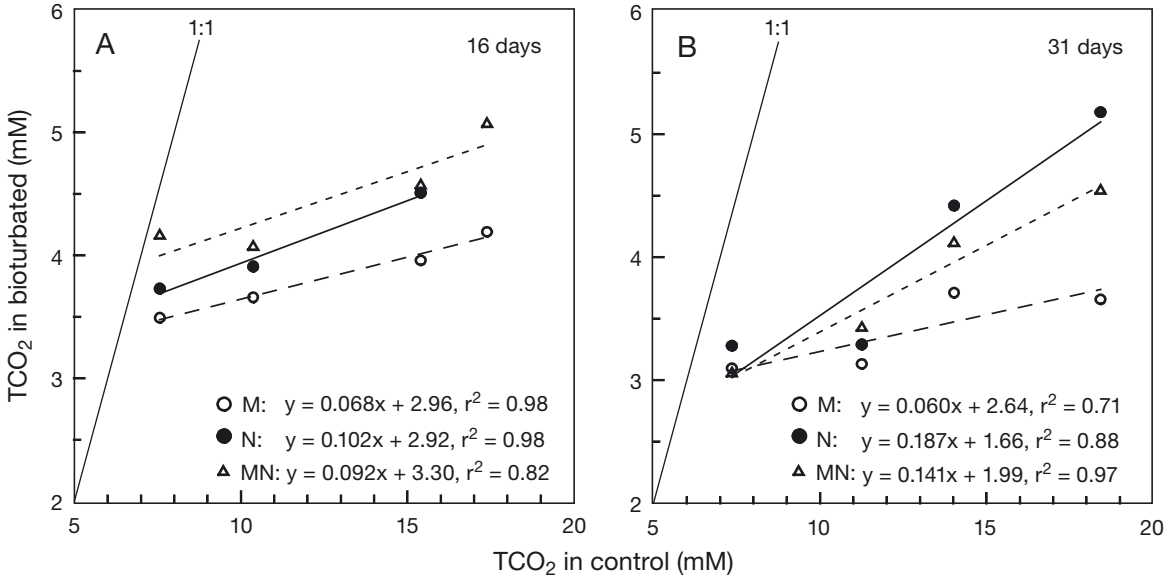

Fig. 7. Relationship between porewater total CO_2 (TCO_2) in control (C) sediment and the corresponding faunated sediments (M, N and MN) at Days (A) 16 and (B) 31. Lines drawn according to least-squares linear regression and the obtained equations are shown. The 1:1 lines shown for comparison. See Fig. 1 for core definitions

rapid transport of water through the U-shaped burrow and back to the overlying water with only radial diffusive and limited advective porewater solute exchange (Davey & Watson 1995, Kristensen & Hansen 1999). *M. viridis*, on the other hand, lives in deep and blind-ended L- or J-shaped burrows. Some of the water ventilated into the burrow must therefore percolate up through the sediment, carrying solutes efficiently back to the overlying water (Quintana et al. 2011). The irrigation mechanism of *M. viridis*, in principle, functions as for the lugworm *Arenicola marina* (Timmermann et al. 2002, Meysman et al. 2005), except that the ventilated water percolates into the sediment along the entire shaft of *M. viridis* burrows and not only through the dead-end (Quintana et al. 2011). *M. viridis* certainly irrigates porewater solutes much more efficiently than *N. diversicolor* despite an order of magnitude lower ventilation: an effect that is greatly amplified by the much greater depth of sediment influenced by *M. viridis* irrigation.

Ecological consequences of replacing *Nereis diversicolor* with *Marenzelleria viridis*

A replacement of the native *Nereis diversicolor* with the invasive *Marenzelleria viridis* as the dominant burrow-dwelling polychaete in shallow coastal areas, which is a current concern, may have serious biogeochemical and ecological implications. As predicted by our hypotheses, activities of the deep burrowing *M. viridis* alter the balance of biogeochemical pathways by increasing sulfate reduction at the expense of aerobic processes, and its stronger porewater irrigation enhances the transport of porewater metabolites, such as sulfide, towards the sediment–water interface. The presence of near-surface sulfide in *M. viridis* inhabited sandflats of Odense Fjord is visually evident (even from Google Earth) as a purple coloration of the sediment surface due to purple sulfur bacteria (authors' pers. obs.). Consequently, organisms tolerant to and dependent on sulfide (e.g. sulfur oxidizing bacteria and opportunistic polychaetes) will be favored at the expense of sensitive species (e.g. large polychaetes and crustaceans) (Levin et al. 2009). Actually, *M. viridis* itself is highly tolerant to low oxygen and high sulfide (Schiedek 1997). Such a shift in species composition yields altered trophic structures and energy flow pathways, as previously observed for other anthropogenically induced hypoxia events (Karlson et al. 2002). Although we found no change in overall rates of benthic metabolism and inorganic nitrogen dynamics when *M. viridis* replaced *N. diversicolor* in our short-term experiment, it is likely that the more reduced conditions over longer time scales will hamper carbon oxidation and enhance the release of inorganic nitrogen and phosphorus to the overlying water (Kristensen & Holmer 2001). The species composition, functioning and stability of the ecosystem may therefore be in jeopardy if the well-oxidized conditions maintained in the upper sediment layers by *N. diversicolor* through its strong ventilation is replaced with the more sluggish ventilation, but much stronger and deeper irrigation, of *M. viridis*.

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