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Effects of bioirrigation by the three sibling species of *Marenzelleria* spp. on solute fluxes and porewater nutrient profiles

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ABSTRACT: The spread of the sibling polychaete species *Marenzelleria neglecta*, *M. viridis*, and *M. arctia* in the Baltic since the early 1980s has been accompanied by various effects on the biogeochemistry of bioturbated sediments. Their influence on benthic nutrient fluxes (NH_4^+, NO_3^- PO_4^{3-}) and oxygen uptake was examined in a laboratory experiment. Confirming a previous experiment, *M. neglecta* and *M. viridis* are more similar to each other with respect to their direct and indirect ecosystem function than to *M. arctia*. In contrast to the predominantly non-local transport mode of the deep-burrowing species *M. viridis* (solute transport coefficient $\alpha = 284.1\ yr^{-1}$) and *M. neglecta* ($\alpha = 277.1\ yr^{-1}$) in the sediment, the solute transport mode of *M. arctia* is more diffusive in character (11.8-fold enhanced diffusivity and $\alpha = 4.3\ yr^{-1}$). While the release of ammonium and phosphate, as well as the total oxygen uptake (TOU) of the sediment, was stimulated by the presence of all polychaetes, the fluxes (NH_4^+, PO_4^{3-}, TOU) in cores colonized with *M. viridis* and *M. neglecta* were substantially higher than those of *M. arctia*. The presence of *M. arctia* had only slight stimulatory effects on nitrification, whereas *M. neglecta* and *M. viridis* enhanced nitrification. This suggests negligible stimulation of denitrification for *M. arctia* and leaves the source of ammonium in *M. neglecta* and *M. viridis* unresolved. Consequently, *M. viridis* and *M. neglecta* may affect eutrophication-related benthic fluxes considerably more than *M. arctia*, and a functional grouping of all 3 sibling species in terms of bioirrigation is not reasonable.

KEY WORDS: *M. viridis* · *M. neglecta* · *M. arctia* · Solute transport · Ammonium · Nitrate · Phosphate · Functional diversity

INTRODUCTION

Spionid polychaetes of the genus *Marenzelleria* in the Baltic Sea comprise 3 sibling species which are morphologically difficult to distinguish. *M. neglecta*, *M. viridis*, and *M. arctia* are therefore primarily identified by molecular analysis (Bick & Burckhardt 1989, Bastrop 1997, Blank et al. 2008). A precise characterization of the biology, ecology, and distribution of these sibling species is essential to assess their environmental impact (Knowlton 1993). They have been found in the Baltic Sea since the 1980s, and it is assumed that *M. neglecta* is now established over the whole Baltic Sea, whereas *M. viridis* and *M. arctia* are still spreading (Blank et al. 2008). *M. neglecta* and *M. viridis* inhabit estuarine sandy and muddy sediments in abundances of several thousand individuals per square meter (Kube et al. 1996, Delefosse 2012) and can occur sympatrically in the eastern Baltic Sea. *M. arctia* mainly occurs in various sediments in deeper, cooler habitats in the northern Baltic region, at reported abundances of 4000 ind. m^{-2} (Hietanen et al. 2007), and can be found there sympatric with the other 2 species (Blank et al. 2008). *M. neglecta* and *M. viridis* are known to construct L-, J-, or I-shaped, unbranched mucus-lined burrows deep into the sediment (25 to 35 cm deep; 2 mm mean diameter) (Essink & Kleef 1988, Zettler et al.

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1994, Quintana et al. 2011). In contrast, *M. arctia* creates J-, Y-, or U-shaped burrows with a thin transparent membrane lining to maximum depths of 6 to 8 cm (Renz & Forster 2013). Feeding modes of *Marenzelleria* spp. include facultative deposit feeding and suspension feeding (Fauchald & Jumars 1979, Dauer et al. 1981, Sikorski & Bick 2004), although for *M. arctia* no information is available.

Bioturbating macrofauna determine the input and vertical depth distribution of organic material in the sediment and its mineralization (Shull 2009). Beside biomass, density, and species composition (Welsh 2003), the burrowing depth (Aller 1982) and the morphology of burrows (i.e. open or blind ended), as well as the ventilation rate, are constitutive characteristics, determining the effects of bioirrigation on porewater transport (Kristensen et al. 2012). While the construction of burrows and feeding activities increases the sediment–water interface and, therefore, the effective area for any solute exchange and for biogeochemical reactions (Forster & Graf 1992), porewater irrigation as a consequence of burrow ventilation leads to enhanced water exchange between overlying water and porewater (Graf & Rosenberg 1997). Thus, bioturbation also stimulates microbial activities by providing additional electron acceptors (e.g. oxygen, nitrate, and sulfate) for benthic mineralization (Andersen & Kristensen 1988) and by removing toxic metabolites (e.g. ammonium and sulfide) (Quintana et al. 2013).

The influence of *Marenzelleria* spp. on sediment nutrient dynamics is poorly understood, and, though a few studies have investigated the effects of *M. viridis* (Karlson et al. 2005, Kristensen et al. 2011, Quintana et al. 2013) and *M. arctia* (Hietanen et al. 2007, Viitasalo-Frösen et al. 2009), no information on the biogeochemical influence of *M. neglecta* is available. The missing taxonomic identification of species in several recent studies (Bonaglia et al. 2013, Urban-Malinga et al. 2013) renders the interpretation of some of their results difficult. Recent studies have shown that the mineralization of organic material is increased and sulfate reduction is stimulated by the presence of *M. viridis* (Kristensen et al. 2011, Quintana et al. 2013). On the other hand, the influence of *M. arctia* and *M. viridis* on denitrification is minor despite increased ammonium fluxes from the sediment (Hietanen et al. 2007, Kristensen et al. 2011). The high fluxes of nitrate into the sediment apparently stimulate dissimilatory reduction of nitrate to ammonium (DNRA) more than denitrification (Karlson et al. 2005). The efflux of phosphate from the sediment is increased by the presence of *M. arctia* (Hietanen et al. 2007, Viitasalo-Frösen et al. 2009), but Hietanen et al. (2007) speculated that the oxygenation of the sediment surface may lead to improved long-term retention of phosphorus and, therefore, enhance the amount of Fe-bound P in sediments (Norkko et al. 2012).

The concept of grouping benthic animals by ecological equivalency into functional groups sharing common biogeochemical and interspecific attributes (Gérino et al. 2003), has been used to link bioturbation aspects with ecosystem functions in a conceptual framework (Mermillod-Blondin & Rosenberg 2006). Ecosystem engineering comprises direct or indirect modifications by organisms that modulate the physical environment (Jones et al. 1994) and, therefore, cause qualitative and quantitative changes in the distribution and availability of resources for other species (Kristensen et al. 2012). Especially invasive species have been identified to cause extensive changes in the function of ecosystems (Leppäkoski & Olenin 2000). *Marenzelleria* spp. in the Baltic Sea is known to affect populations of the polychaete *Hediste diversicolor* (Delefosse 2012) and the amphipod *Monoporeia affinis* (Kotta et al. 2006) and, consequently, their contribution to the remobilization of buried contaminants (Granberg et al. 2008, Josefsson et al. 2011).

Based on the classification of different mixing modes (François et al. 2002), the mechanical sediment reworking of all 3 sibling species of *Marenzelleria* can be assigned to the 'biodiffuser' functional group from a model point of view (Renz & Forster 2013), causing vertical transport of particles by random translocation over short distances and time intervals (François et al. 1997, 2002). However, sediment reworking by all 3 sibling species is negligible compared to their pronounced effects on the solute transport pattern (Renz & Forster 2013).

In the present study we examined the effects of the 3 closely related polychaetes on solute fluxes (bromide), nutrient dynamics (NH_4^+, NO_3^-, PO_4^{3-}), and oxygen uptake to emphasize potential differences among them. Due to the similarity in morphological characteristics, these species are thought to have only minor, if any, functional differences. We hypothesize that differences in nutrient release and total oxygen uptake are driven by differences in size and burrowing depth of the species. We predicted that these morphologically similar organisms would differ in their direct (solute transport) and indirect functions (biogeochemical effects) and that the 3 sibling species, therefore, cannot be categorized as a single functional group.

Table 1. Sites where *Marenzelleria* spp. were sampled, and abiotic parameters. Temperature at Askö was measured at the surface, and in the bottom water at other sites

Sampling site	Species	Position	Water temp. (°C)	Depth (m)	Salinity	Sediment type
Askö (Sweden)	*M. arctia*	58° 50′ N, 17° 32′ E	15.3	30	6.1	Mud
Langenwerder, Poel (Germany)	*M. viridis*	54° 03′ N, 11° 49′ E	17.0	1	14.0	Sand
Banzelwitz, Rügen (Germany)	*M. neglecta*	54° 52′ N, 13° 41′ E	15.6	1.2	8.3	Sand

MATERIALS AND METHODS

Sampling and experimental design

Sediment was collected in July 2008 in a shallow brackish water bay (Schnatermann, Warnow River) near Rostock, Germany. Sediment was pre-sieved through 1000 and 500 µm mesh and homogenized. Grain size and loss on ignition (500°C, 12 h) were determined before establishing the sediment cores (Bale & Kenny 2005). Polychaetes were collected in September 2008 at 3 different sampling sites in the Baltic Sea as specified in Table 1 and were kept in aquaria with sediment for approximately 2 wk under constant conditions (14°C, salinity: 10) for acclimation.

Transparent 55 cm long PVC tubes (internal diameter: 10 cm) were filled with 40 cm homogenized sediment overlaid by 1 l seawater (salinity: 10). Cores were sealed with plastic wrap and pre-incubated for 5 wk with air-saturated water in a dark, temperature-controlled (14°C) container to restore near-steady conditions after sediment homogenization. Aeration of the water column in each core provided convection and, thus, a complete mixing of the overlying water, while care was taken not to resuspend the sediment. Salinity was controlled daily and diluted with fresh water if necessary, and the height of the overlying water was noted.

The experimental set-up consisted of 4 treatments with 3 replicate cores each, comprising azoic controls (C) and cores colonized with *Marenzelleria arctia* (MA), *M. neglecta* (MN) and *M. viridis* (MV), taking into account the natural densities of the polychaetes. Individuals were of typical size for adults of the respective species from the Baltic Sea (Sikorski & Bick 2004, Bick 2005). Given the small size (around 1 to 2 cm) of *M. arctia*, the number of individuals per core differed among the treatments (MA: n = 20 ind. core^{-1}, equating to 2546 ind. m^{-2}; MV and MN: n = 10 ind. core^{-1} equating to 1273 ind. m^{-2}). Total fresh weight of polychaetes per core (MA: 0.5 ± 0.1 g; MN: 1.0 ± 0.1 g; MV: 1.7 ± 0.2 g) was determined before introducing the animals to the randomly chosen sediment cores on Day 1 (d_1) (Fig. 1). All animals buried immediately into the sediment of the microcosms.

Oxygen and nutrient exchange

To assess benthic oxygen uptake, the ventilation of all cores was stopped on d_7 and the cores were sealed with tight lids. Magnetic stirrers ensured mixing of the water column during the respiration measurements (stirring speed of approximately 60 rotations min^{-1}). Oxygen concentrations were measured with 2 optodes integrated into the lids (oxygen sensor spots SP-PSt3-PSUP-YOP-D5, PreSens), and the fluxes were calculated from changes in O_2 concentrations over time for all cores. The measurements were stopped when oxygen depletion reached 80 % saturation. The optodes were calibrated in distilled water (Arain et al. 2005), and O_2 concentrations were checked by the Winkler titration technique (Grasshoff et al. 1983).

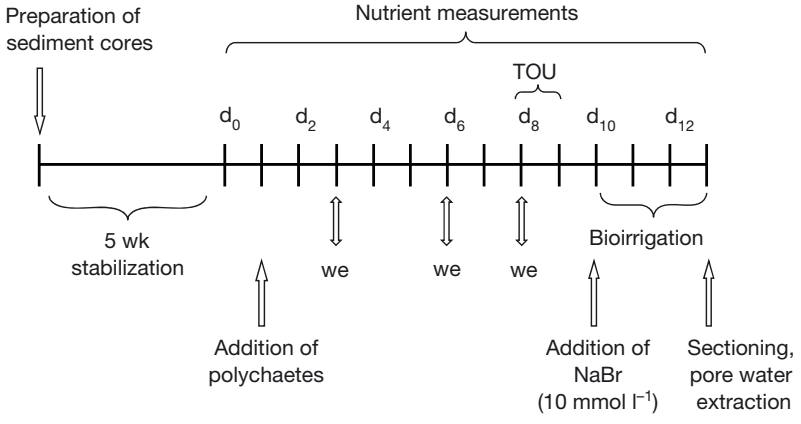

Fig. 1. Timeline of the laboratory experiment with a total length of 48 d (d_x). Water exchange (we) was conducted 3 times, and measurement of total oxygen uptake (TOU) was performed on Day 8 (d_8) of the experiment

Samples of 10 ml water for N and P nutrient analysis were taken from the overlying water of each core before animals were introduced on d_0, to control variability among cores. Similar samples were taken daily from d_2 to d_{13} to determine nutrient fluxes from concentration differences in the overlying water against time. The overlying water was replaced 3 times (d_3, d_6, and d_8) with sea water stored in a reservoir, to avoid exceedingly high nutrient levels, resulting in 3 sequential incubations. The nutrient concentrations of the reservoir (NH_4^+: 3.4 ± 0.9 µmol l^{-1}; NO_2^-: 1.8 ± 0.6 µmol l^{-1}; NO_3^-: 20.0 ± 1.3 µmol l^{-1}; PO_4^{3-}: 0.17 ± 0.18 µmol l^{-1}) were monitored daily during the experiment to assure that no changes occurred.

The microcosms were sectioned at the end of the experiment on d_{13}. The overlying water was first removed, and 1 cm slices were taken from the sediment cores at variable depths depending on treatment (C: 1–10, 15, and 20 cm; MA: 1–10, 12, 14, 16, 18, 20 cm; MV and MN: 1–20, 22, 24, 26, 28, 30, 35 cm). The remaining layers were discarded. Residence depth of polychaetes was noted during sectioning, and collected worms were preserved in 80% ethanol for molecular identification. Sediment layers were weighed fresh and dry (60°C) for porosity (φ) determination. Porewater was extracted from a subsample of each slice by centrifuging (1 min, 500 rpm) through GF/F filters as described by Saager et al. (1990). Of the porewater retrieved, ~5 ml was collected and frozen (–18°C) for nutrient analysis and 2 ml was stored dark and cold (5°C) for bromide measurements.

Ammonium and phosphate were analyzed spectrophotometrically immediately after sampling (Parsons et al. 1984). Samples for nitrate and nitrite were preserved (–18°C) and measured using the spongy cadmium technique (Jones 1984). Methods were modified for small sample volumes of 1 ml for all nutrient analyses.

Total nutrient fluxes (F_{olw}) were calculated for each stage from concentration changes in the overlying water using a linear regression against time.

Bromide tracer transport

Porewater irrigation was quantified from vertical sediment profiles after the addition of sodium bromide to a final concentration of 10 mmol l^{-1} to the overlying water on d_{10} of the experiment (Martin & Banta 1992, Forster et al. 1999). After an initial incubation time of 15 min, 2 ml water samples were taken sequentially after 0.25, 2, 5, 9, 24, 32, 50, 69, and 70.5 h. The samples were stored cold (5°C) in the dark until analysis.

Bromide was analyzed by anion exchange chromatography (Sykam, IBJ A06 column, Merck-Hitachi L-4200 UV-VIS detector), with a 25 mM NaCl eluent and a constant flow rate of 1 ml min^{-1}. Peak areas were compared to standards. Analytical precision was ±0.1 mmol l^{-1}, and the detection limit was 0.4 mmol l^{-1} Br^-.

Bromide tracer results were interpreted with a numerical model, described in detail by Andersson et al. (2006) within the flexible environment for mathematically modeling the environment (FEMME) (Soetaert et al. 2002). Solute transport was specified with a factor of enhanced diffusion (ε), a non-local exchange coefficient (α), or as a combination of both. The tracer concentration C in the sediment is described by:

$$\phi\frac{\partial C}{\partial t} = \frac{\partial}{\partial x}\left(\varepsilon D_s\phi\frac{\partial C}{\partial x}\right) + \alpha\phi(C_{olw} - C) \quad (1)$$

where ϕ is the porosity, as a function of depth, t is time, D_s is the diffusion coefficient in porewater calculated according to Archie's Law with $m = 2$ (Ullman & Aller 1982), x is sediment depth, ε is a factor of enhancement over molecular diffusion, and α is the non-local exchange coefficient, defined as volume fraction per unit time, that is exchanged between porewater and the overlying water (C_{olw}). ε (and by analogy α) are assumed to be constant down to a bioturbated layer L_b and to decrease exponentially with an e-folding depth ($k_{\varepsilon,\alpha}$) (Andersson et al. 2006) below L_b:

$$\varepsilon(x) = \begin{cases} \varepsilon, & \text{if } x \le L_b \\ \varepsilon \cdot e^{-(x-L_b)/k_{\varepsilon,\alpha}}, & \text{if } x > L_b \end{cases} \quad (2)$$

The parameters used for the irrigation model have been described by Renz & Forster (2013). A calibration analysis (Soetaert et al. 2002), using the Levenberg-Marquardt algorithm, was used to fit the model to the observed data and to obtain the solute transport parameters.

Statistical analyses

Differences in treatments were tested using the Kolmogorov-Smirnov test to test for normality. When the distribution of data was normal, pairwise comparison among treatments was performed with Student's t-test. Otherwise, non-parametric tests after Whitney and Mann (U-test) or Kruskal and Wallis (H-test) were used on raw data. With these tests, all treatments during each incubation period were tested pairwise at a 95% level.

A non-parametric multivariate analysis (cluster and SIMPER) on modeled co-dependent solute transport parameters (PRIMER 6.0) was conducted to show resemblance between the treatments and to test for significant differences (SIMPROF, $p < 0.05$) (Clarke & Warwick 2001, Clarke et al. 2008). Raw data were fourth-root transformed, and for the resemblance Bray-Curtis similarity was used (stress: 0.01). A linear regression analysis ($p < 0.01$) was conducted to test the correlation between ammonium fluxes and the bromide-affected sediment depth.

RESULTS

Visual observations

Control cores appeared distinctly layered and with an organic-rich, brown-green fluff layer at the sediment surface, followed by an approximately 0.5 cm thin bright oxidized layer. Below, the sediment of control cores was uniform and grey to greyish-black in colour. In populated microcosms the fluff layer appeared less distinct. Burrow linings of *Marenzelleria arctia* were U- and J-shaped and reached a sediment depth of approximately 6 cm. Burrows of both *M. neglecta* and *M. viridis* were J-shaped. Bright, oxidized halos with a width of 2 mm along the burrow linings of *M. viridis* and *M. neglecta* reflected the penetration of oxygen from burrow walls into the surrounding sediment. In *M. arctia* cores, halos were discontinuous and of a much smaller extent. In a few cores colonized with *M. viridis* and *M. neglecta*, sporadic white patches of *Beggiatoa* spp. (1 cm diameter) could be noted at the sediment surface.

Recovery and molecular identification

In our experiments recovery of polychaetes from sediment cores differed between the treatments (18.3% MA, 46.7% MN, and 50% MV). Overall 33% of all introduced individuals were found. Recovery of organisms during sectioning of sediment cores and subsequent porewater extraction is generally difficult. Mortality of polychaetes can easily be judged when dead or injured individuals are found on the sediment surface. When relying on recovery to estimate mortality, it therefore remains unclear whether animals were truly dead or not found during handling. In some cases worms had been cut into pieces, but only head pieces were counted and used for identification. The molecular species identification (Blank & Bastrop 2009) that was done with recovered polychaetes and reference animals from the sampling sites (data not shown) confirmed the successful grouping of polychaete sibling species in separate experimental treatments as originally intended.

Sediment properties

The sediment was classified as fine to very fine sand, with a median particle size of 178 µm (sorting 0.31; Folk & Ward 1957) and an organic content of 0.47 ± 0.02% dry weight (n = 3). Mean sediment porosity near the sediment surface was 0.51 ± 0.08 and decreased with depth to 0.38 ± 0.01.

Solute transport

The natural background concentration of bromide was 0.37 ± 0.11 mmol l^{-1}, indicating a uniform distribution within the microcosms at the beginning of the experiment. Porewater tracer profiles (Fig. 2) of control cores exhibited a highly reproducible and steep decrease within all replicates, basically driven by vertical molecular diffusion. Bromide background concentration was reached at a depth of 6.8 ± 1.1 cm. *M. arctia*-inhabited sediment cores showed a less steep decrease of bromide concentrations between the sediment surface and a depth of approximately 3 cm, followed by a significantly higher level compared to control cores from 3 to 13 cm depth. The background level was reached at 14.1 ± 1.2 cm. The biological impact declined with depth, and vertical molecular diffusion apparently dominated below a bioturbated layer (L_b) of approximately 7 cm. The tracer profiles of the MV treatment were characterized by fluctuating but slowly declining bromide concentrations to a depth of 29.5 ± 3.3 cm, where the background level was reached. The bromide profiles of the MN treatment were comparable in shape but lower in concentrations than those of the MV treatment, and reached the natural background concentration at 24.7 ± 2.0 cm. The bioturbated layer (L_b) of both these polychaetes was approximately 20 cm.

The volume of overlying water transported into the sediment, calculated from bromide inventory per core and time, divided by the concentration in the overlying water, amounted to 0.8 ± 0.2 ml h^{-1} (*M. arctia*), 3.6 ± 0.9 ml h^{-1} (*M. neglecta*), and 5.8 ± 1.4 ml h^{-1} (*M. viridis*).

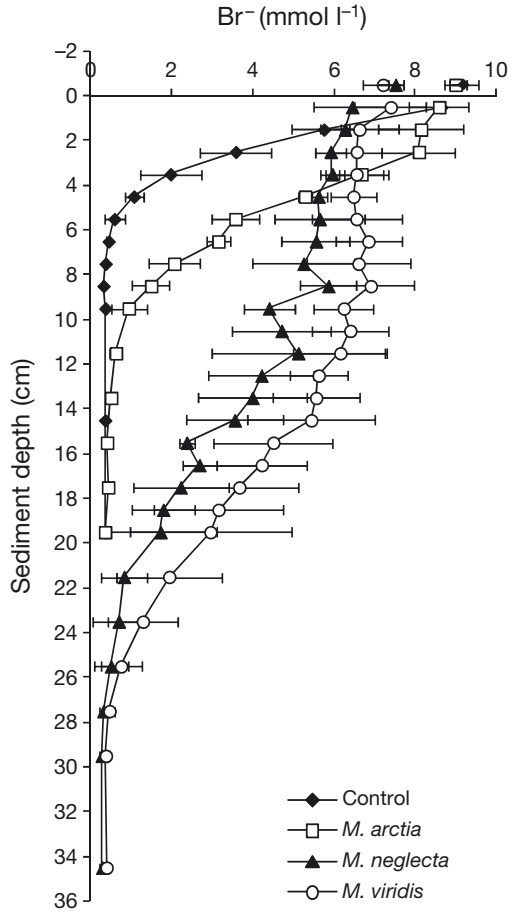

Fig. 2. Average porewater bromide concentrations after an incubation time of 70.5 h. Single symbols displayed above the sediment surface represent mean bromide concentration in overlying water (C_{olw}) at the end of the experiment. Standard deviation obtained from 3 replicates treatment^{-1}

Modeled solute transport

Molecular diffusion is assumed to be the single driving force for any solute exchange in azoic control cores. In one control core the decrease of measured bromide concentrations below a depth of 4 cm was less than in modeled data. In this core an enhanced diffusion coefficient (ε) 3.0-fold higher than molecular diffusion resulted in the best fit. Therefore, diffusion coefficients of the control cores were 1.7 ± 1.1 fold enhanced (Table 2, Fig. 3). Multivariate analysis resulted in 3 clusters (control, *M. arctia*, and *M. viridis*/*M. neglecta*) and showed significant differences (SIMPROF, p > 0.05) between polychaete treatments and control cores (Table 2).

The SIMPER analysis (Clarke & Warwick 2001) thereby confirmed the species-specific differences described as similarities or dissimilarities with regard to the different transport parameters (Table 3). The modeled solute transport coefficients for *M. arctia* yielded a combination of 11.8 ± 4.2 fold enhanced molecular diffusion (similarity of 39.07%) and a small non-local transport coefficient α, with mean values of 4.3 ± 3.9 yr^{-1} (similarity of 18.78%). The non-local transport α was the dominant mechanism influencing solute transport patterns in *M. neglecta* and *M. viridis* cores (similarity of 43.2%), and the enhanced diffusion was seemingly negligible.

Oxygen uptake

Compared to control cores with a mean total oxygen uptake (TOU) of 8.5 ± 1.3 mmol m^{-2} d^{-1} (Table 4), the presence of polychaetes significantly (*U*-test, p < 0.05) increased TOU 2.8-fold (*M. arctia*), 8.9-fold (*M. neglecta*), and 10.8-fold (*M. viridis*). While the effects of *M. viridis* (91.5 ± 13.1 mmol m^{-2} d^{-1}) and *M. neglecta* (75.6 ± 7.8 mmol m^{-2} d^{-1}) were statistically not different from each other, TOU in *M. arctia* cores (23.9 ± 6.3 mmol m^{-2} d^{-1}) was significantly smaller than for the former species.

Nutrient fluxes

At the beginning of the experiment (d_0), before animals were introduced, concentrations in the water column of ammonium (4.3 ± 8.2 µmol l^{-1}), nitrite (3.5 ± 1.5 µmol l^{-1}), and phosphate (2.9 ± 2.2 µmol l^{-1}) were similar and low in all 12 replicates. In contrast, nitrate concentrations varied considerably (56.7 ± 35.2 µmol l^{-1}), indicating non-uniform starting condi-

Table 2. Modeled solute transport (bioirrigation) with FEMME (flexible environment for mathematically modeling the environment). Parameters ε, α, $k_{\varepsilon,\alpha}$, and L_b were obtained from modeling. Significant differences (SIMPROF, p < 0.05) from multivariate analysis between the treatments are labelled with an asterisk (polychaete treatments compared to control cores). Standard deviation obtained from 3 replicates treatment^{-1}

Treatment	ε	α (yr^{-1})	$k_{\varepsilon,\alpha}$ (cm)	L_b (cm)
Control	1.7 ± 1.1	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 0.0
*M. arctia**	11.8 ± 4.2	4.3 ± 3.9	3.3 ± 2.9	3.4 ± 4.8
*M. viridis**	6.3 ± 3.3	277.1 ± 336.6	4.4 ± 0.7	9.4 ± 4.0
*M. neglecta**	4.9 ± 4.6	284.1 ± 184.6	3.7 ± 2.1	13.1 ± 1.4

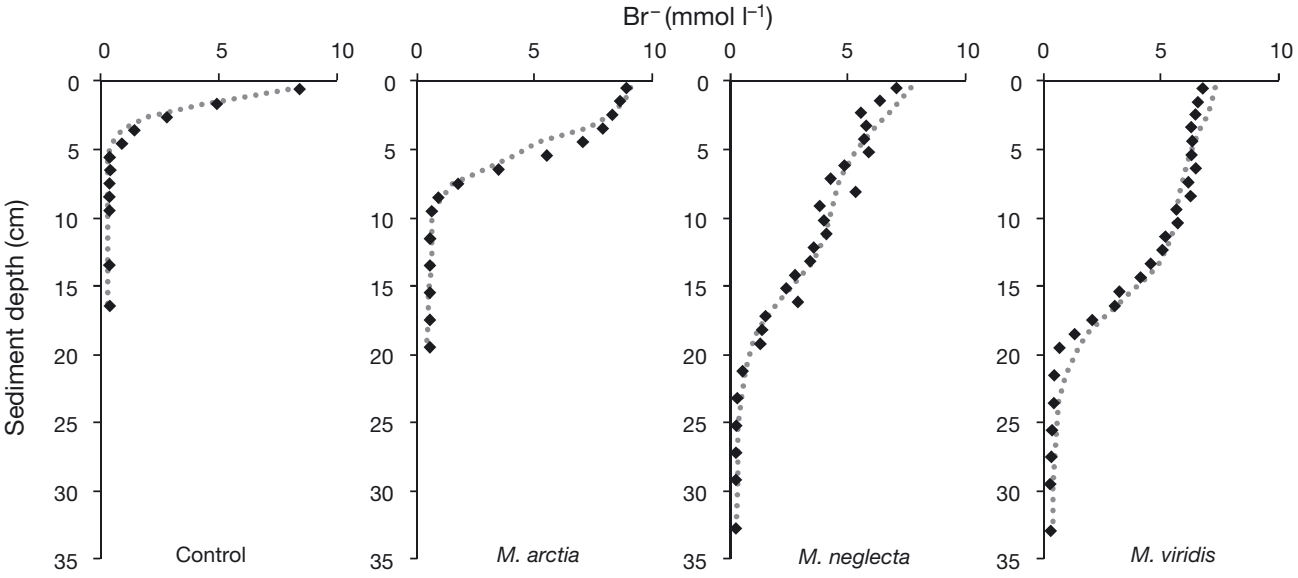

Fig. 3. Examples of individual cores (control [C3], *Marenzelleria arctia* [MA6], *Marenzelleria viridis* [MV12], and *M. neglecta* [MN17]) from the bromide tracer experiments shown in Fig. 2. Dotted lines indicate model fit obtained for the concentration depth profiles

tions. Ammonium and phosphate concentrations in the water column stayed at a steady low level in control cores, while these nutrients increased with time in almost all polychaete treatments (Fig. 4, left-hand panels). Only concentrations of phosphate decreased from d_7 to d_8 in C, MA, and MN treatments. NH_4^+ concentrations on d_{13} were excluded from calculations due to analytical problems. Microcosms colonized by *M. viridis* and *M. neglecta* displayed considerably higher increases in ammonium and phosphate concentrations than those with *M. arctia*. In contrast to increasing nitrate concentrations with time in azoic controls and cores colonized with *M. arctia*, NO_3^- concentrations in *M. neglecta* and *M. viridis* microcosms were significantly lower and tended to decrease during the experiment.

Ammonium fluxes derived from the concentration changes in the overlying water in each incubation period (Fig. 4, right-hand panels) were directed out of the sediment and increased with time, except for control cores on d_4 to d_6. The efflux of NH_4^+ in all polychaete cores was significantly enhanced compared to the control cores (*U*-test, $p < 0.05$). The highest effluxes in *M. viridis* cores did not significantly differ from cores colonized with *M. neglecta*, except on d_9 to d_{10}. The fluxes in both these treatments were significantly higher than fluxes in *M. arctia*-inhabited cores, except on d_6 to d_7.

Nitrate fluxes of control and *M. arctia* cores were directed out of the sediment and increased with time, except from d_9 to d_{13}. The NO_3^- fluxes of cores colonized with *M. viridis* and *M. neglecta* were directed into the sediment, except for *M. neglecta* on d_7 to d_8 and significantly differed from control and *M. arctia* cores, respectively, except on d_6 to d_7 (*U*-test, $p < 0.05$). No statistical differences were found for *M. viridis* compared to *M. neglecta*, except on d_9 to d_{13}.

Phosphate fluxes were highly variable and in the majority of cases directed out of the sediment, except for d_7 to d_8 when fluxes in almost all treatments were

Table 3. Similarity and dissimilarity (SIMPER analysis) of modeled solute transport parameters. Average similarity or dissimilarity (in parentheses) within or between the groups obtained from 3 replicates treatment^{-1}. C: control; MA: *Marenzelleria arctica*; MV + MN: *M. viridis* + *M. neglecta*

Similarity (%)	C	MA	MV + MN
Within group	(94.91)	(81.20)	(90.04)
ε	52.30	39.07	16.85
L_b	47.70	17.92	22.67
α	0.00	18.78	43.20
$k_{\varepsilon,\alpha}$	0.00	24.23	17.28
Dissimilarity (%)	**C – MA**	**C – (MV + MN)**	**MA – (MV + MN)**
Between groups	(49.03)	(61.95)	(28.36)
$k_{\varepsilon,\alpha}$	36.23	21.63	6.61
α	33.35	58.38	65.56
ε	20.42	5.99	9.80
L_b	10.00	14.00	18.03

Table 4. Total oxygen uptake (TOU), estimated respiration rates (R_r) of the polychaetes, and calculated oxygen uptake of the burrow walls (OU_{bw}). Values in parentheses are related to the total oxygen uptake (% of TOU). R_r and OU_{bw} were calculated considering initial and recovered abundances (subscripted i and rec, respectively)

	Control	*M. arctia*	*M. neglecta*	*M. viridis*
TOU (mmol m^{-2} d^{-1})	8.5 ± 1.3	23.9 ± 6.3	75.6 ± 7.8	91.5 ± 13.1
$TOU_{control}$ (% of TOU)		8.5 (35.4 %)	8.5 (11.2 %)	8.5 (9.2 %)
R_r (mmol m^{-2} d^{-1})		$0.4_{rec} - 2.1_i$ ($1.8_{rec} - 8.9_i$%)	$1.6_{rec} - 3.3_i$ ($2.2_{rec} - 4.4_i$%)	$2.7_{rec} - 5.4_i$ ($2.9_{rec} - 5.9_i$%)
OU_{bw} (mmol m^{-2} d^{-1})		$13.3_i - 15.0_{rec}$ ($55.7_i - 62.8_{rec}$%)	$63.9_i - 65.5_{rec}$ ($84.5_i - 86.6_{rec}$%)	$77.6_i - 80.3_{rec}$ ($84.9_i - 87.8_{rec}$%)

low and directed into the sediment. Beside the significantly higher fluxes of inhabited cores compared to control cores, only marginal statistical differences were found for phosphate fluxes (*U*-test, $p < 0.05$).

Porewater profiles

Ammonium porewater profiles (Fig. 5) of control cores were characterized by increasing concentrations within the first sediment layers, a typical subsurface maximum

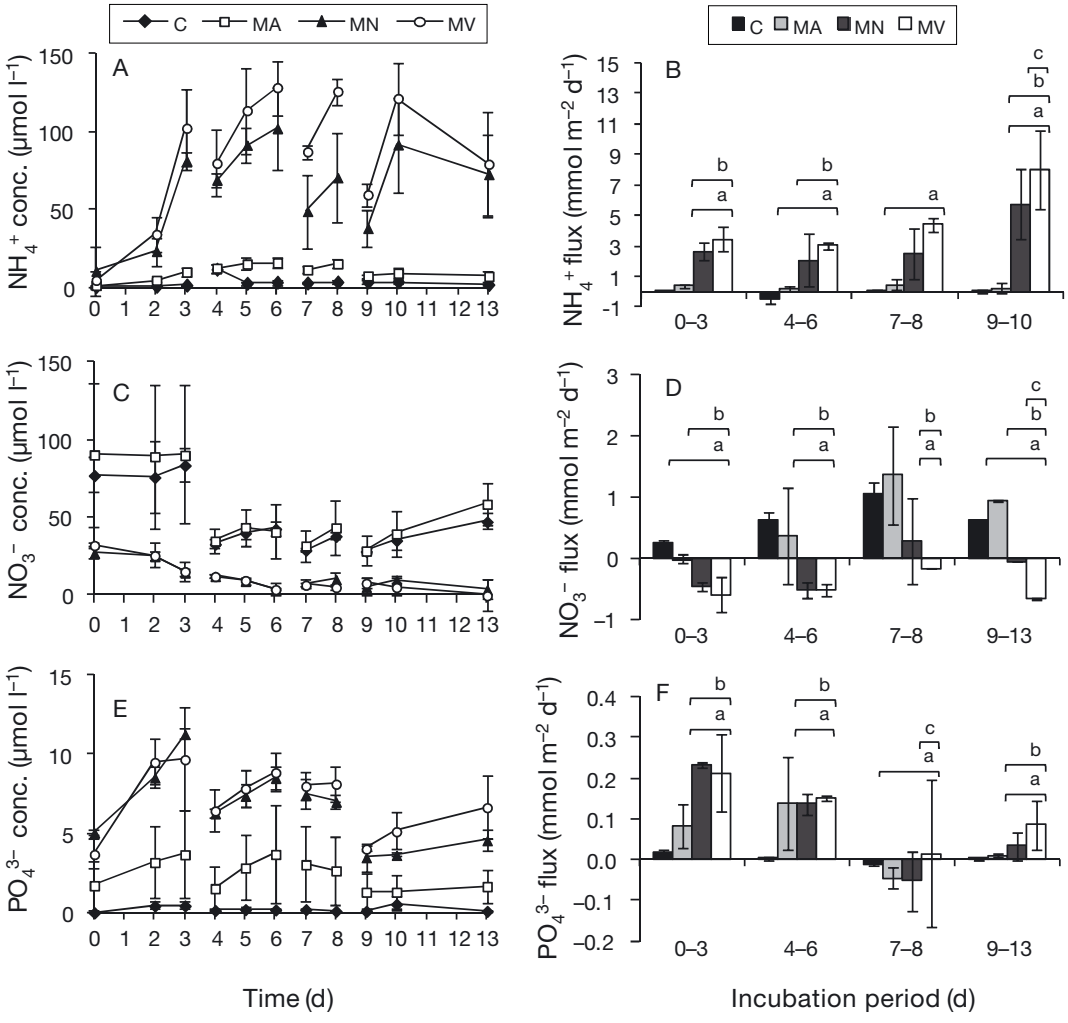

Fig. 4. Nutrient concentrations (A,C,E) and fluxes (B,D,F) calculated from concentration gradients in the water column. Standard deviation obtained from 3 replicates treatment^{-1}. MA: *Marenzelleria arctia*; MN: *M. neglecta;* MV: *M. viridis.* Significant differences (*U*-test; $p < 0.05$) of fluxes during each incubation period were tested pairwise. Differences in the respective treatments are labelled with lowercase letters—a: treatments compared to control cores; b: MN or MV compared to MA; c: MN compared to MV

at a sediment depth of 3.5 cm (205.5 ± 10.6 µmol l^{-1}), and a subsequent slight decrease in concentrations. The porewater NH_4^+ concentration gradient and subsurface maximum in MA cores (189.2 ± 34.9 µmol l^{-1}) were smaller than in control cores. NH_4^+-concentrations in MN and MV cores increased within the first sediment layers, followed by fluctuation at approximately 160 and 145 µmol l^{-1}, respectively.

The nitrate porewater profiles of control and *M. arctia* cores were characterized by highest concentrations within the first sediment layer (C: 20.8 ± 18.8 µmol l^{-1}; MA: 12.0 ± 5.3 µmol l^{-1}), followed by a continuous decrease with depth to a mean value of

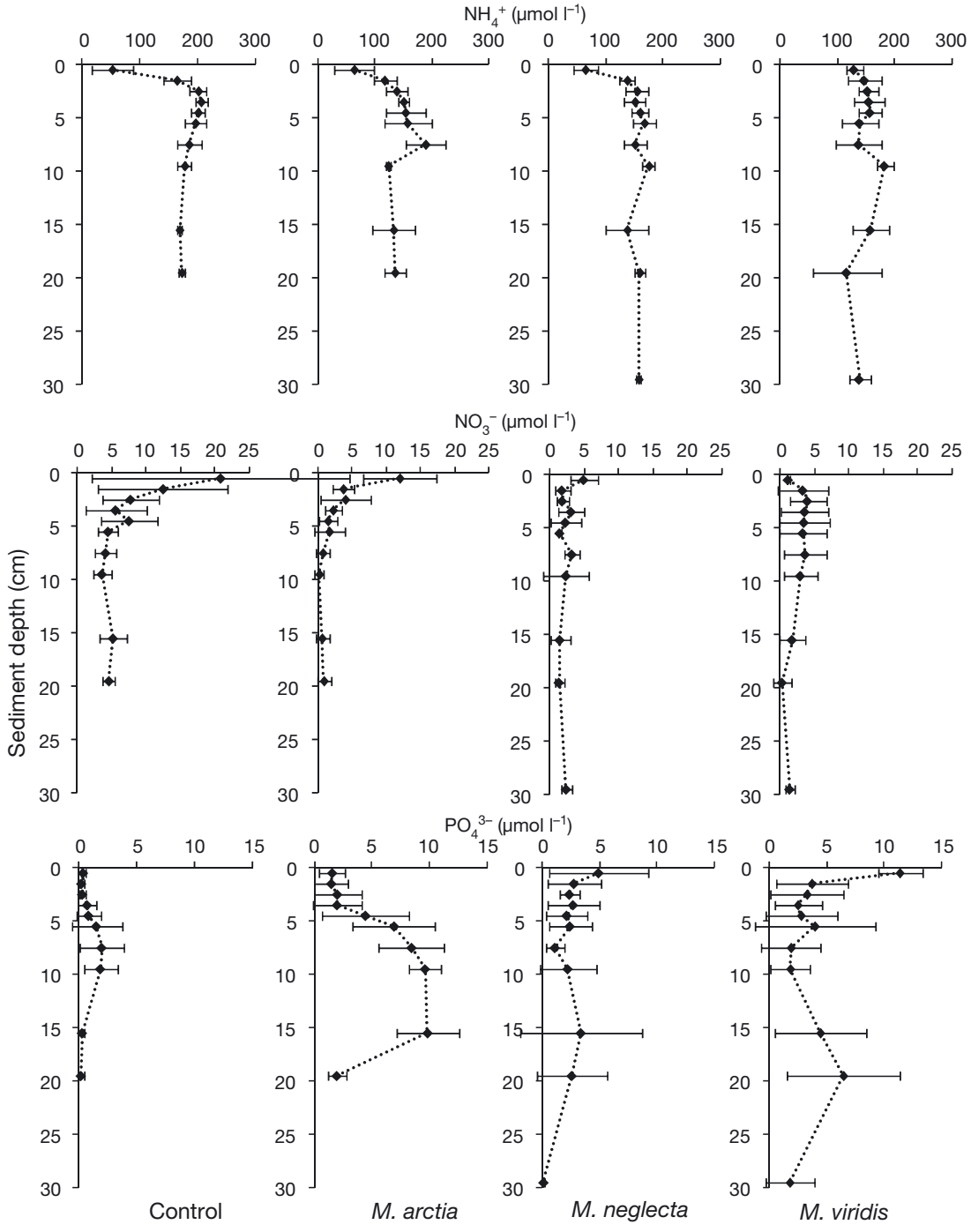

Fig. 5. Nutrient porewater profiles at the end of the experiment. Standard deviation obtained from 3 replicates treatment^{-1}

4.3 ± 0.6 and 0.7 ± 0.3 µmol l^{-1}, respectively. Microcosms colonized by *M. neglecta* likewise displayed highest nitrate values within the first sediment layer (4.9 ± 2.0 µmol l^{-1}), followed by decreasing levels to a depth of 2.5 cm, and subsequent fluctuating concentrations around a mean value of 2.2 ± 0.7 µmol l^{-1}. In cores inhabited by *M. viridis* almost no nitrate was detected in the surface layer (1.2 ± 0.3 µmol l^{-1}), and below a subsurface maximum at a sediment depth of 2.5 cm concentrations decreased.

The control porewater profiles of phosphate were characterized by a typical subsurface maximum (2.0 ± 1.9 µmol l^{-1}) at a sediment depth of 6 to 9 cm. The concentrations in *M. arctia*-inhabited cores did not change considerably from the sediment surface to a sediment depth of approximately 4 cm. Below this depth, the concentrations increased to approximately 9.9 ± 2.7 µmol l^{-1} at a depth of 15 cm, followed by a decrease. In contrast, the maximum concentrations of phosphate in the porewater profiles of *M. neglecta* (4.9 ± 4.3 µmol l^{-1}) and *M. viridis* (11.4 ± 1.9 µmol l^{-1}) were observed within the first sediment layer. Subsequently, decreasing concentrations to a sediment depth of 3 cm were followed by porewater distribution patterns that were inconsistent in shape and fluctuating in concentrations.

DISCUSSION

To compare the biogeochemical impact of the 3 *Marenzelleria* sibling species, natural, sieved sediment was used in laboratory experiments. At the polychaete sampling sites abiotic parameters and sediment characteristics varied considerably. Consequently, unknown ecological constraints to the behaviour of the polychaetes may emerge that cannot be addressed here. The use of homogenized sediment in artificial cores requires that sufficient time is given to facilitate steady-state conditions with regard to porewater profiles and solute fluxes across the sediment–water interface (Hansen & Kristensen 1998). Despite a stabilization period of 5 wk, the initial starting conditions within the replicates varied, reflecting the individual growth and evolution of microorganisms in each sediment core. To reduce effects related to these differences and to facilitate comparable starting conditions, the choice of cores during the colonization with polychaetes was random. Nevertheless, starting conditions in NO_3^- concentrations incidentally fell into distinct groups (C and MA vs. MN and MV), reflecting for example the slow growth of nitrifying bacteria compared to denitrifying bacteria (Welsh 2003).

Morphology of burrows and their ventilation

The different burrowing depth and morphology of burrows are thought to be of major importance, when assessing the various effects of bioturbation and bioirrigation on the complex system of oxygen and nutrient dynamics (Kristensen & Kostka 2005). While the burrows of *M. arctia* appear to create a 'dense network' close to the interface, if viewed from outside the core, the polychaetes construct individual, unbranched, and twisted burrows of ~0.5 mm diameter, which are mainly U-shaped (Renz & Forster 2013). Thereby, the bioirrigation depth remains restricted to the initial 10 cm of the sediment. In contrast, the L-, J-, or I-shaped burrows of the 'deep burrowing' species (authors' obs.), i.e. burrows of *M. viridis* (Essink & Kleef 1988) and *M. neglecta* (Zettler et al. 1994), with mean diameters of 2 mm and maximum lengths of 35 cm, are similar in shape and length and clearly differ from those of *M. arctia*.

Only limited information about the burrow ventilation of *Marenzelleria* spp. is available. The ventilation mechanism of *M. viridis* is described as a combination of ciliar and muscular pumping of water into and out of the blind-ending burrows (Quintana et al. 2011). There is no information concerning the ventilation behaviour of *M. neglecta* and *M. arctia* so far either, but based on the similar results obtained for *M. neglecta* and *M. viridis*, comparable ventilation patterns may be assumed for these species. In contrast, the U-shaped burrows of *M. arctia* allow unidirectional ventilation of burrows, with probably less energy demand. The enhanced diffusive porewater transport originating from open-ended burrows, however, is thought to be less intensive and deep compared to the advective irrigation of porewater from blind-ended burrows (Kristensen et al. 2012). While details of irrigation patterns remain unknown, some studies suggest that continuous ventilation in open-ended burrows creates a more stable environment compared to oscillating conditions (Forster & Graf 1992, Kristensen & Kostka 2005). This may add to the differences observed here between the species.

Influences on solute transport

With respect to their solute transport patterns *M. neglecta* and *M. viridis* are more similar to one another than to *M. arctia*. While the modeled solute transport mode of *M. arctia* is largely determined by enhanced diffusivity, the deep-burrowing species *M. viridis* and *M. neglecta* affect tracer distributions in

the sediment predominantly through a non-local, advective transport mode. The solute transport coefficients of *M. viridis* and *M. neglecta* in the prevailing study are comparable to the findings of Quintana et al. (2007) and Hedman et al. (2011), respectively. No information on the magnitude of solute transport for *M. arctia* is available from the literature. However, based on the fact that the chosen settings clearly affect the magnitude of coefficients, the comparison of modeled transport coefficients in general has to be made with care.

The volume of overlying water transported into the sediment per individual, calculated from bromide porewater inventory divided by the overlying water concentration at the end of the incubation period, was 13.9-fold and 9.2-fold higher for *M. viridis* and *M. neglecta*, respectively, compared to the water exchange of *M. arctia.* The results correspond well to findings in a previous study (Renz & Forster 2013) and to recent investigations, where *M. viridis* transported 12 ml d^{-1} $ind.^{-1}$ (Quintana et al. 2011) and *M. neglecta* 6.6 ml d^{-1} $ind.^{-1}$ (Hedman et al. 2011) into the sediment. In all these studies, including the present one, mortality poses a problem (see next subsection). Still, all results deviate by <30% from one another, indicating reproducibility in the incubation methods used.

Total oxygen uptake

Benthic oxygen uptake reflects the oxygen demand of the heterotrophic activity of fauna and bacteria, as well as the reoxidation of reduced inorganic products that are released during the anaerobic heterotrophic degradation (Glud 2008). The increased TOU in sediments colonized with polychaetes is caused by effects such as stimulation of microbial degradation, as well as directly by the metabolism of macrofauna. There might be additional oxygen consumption associated with decomposing dead individuals if polychaetes not recovered are assumed to have died.

The impact of animal respiration is still controversial, with ranges cited from 10 to 41% of the total benthic metabolism in the case of *Marenzelleria* spp. (Quintana et al. 2007, 2013, Bonaglia et al. 2013, Urban-Malinga et al. 2013). No information on the respiration rates of *M. neglecta* and *M. arctia* are available from the literature; we roughly estimated the respiration rates (R_r) based on biomass (Mahaut et al. 1995) of all 3 polychaetes according to Urban-Malinga et al. (2013), using the relation $R_r = 0.0174 W^{0.844}$ (mg C d^{-1}) (Braeckman et al. 2010). To assess the impact of reduced biomass (recovery) on the oxygen budgets, we also calculated the respiration rates considering the reduced abundance for each treatment (Table 4). With 0.4 to 2.1 mmol m^{-2} d^{-1}, the respiration rate of *M. arctia* was slightly lower than the 1.6 to 3.3 and 2.7 to 5.4 mmol m^{-2} d^{-1} for *M. neglecta* and *M. viridis*, respectively. Subsequently, oxygen uptake at the burrow walls (OU_{bw}), estimated from $OU_{bw} = TOU - TOU_{control} - R_r$, was comparable in *M. neglecta* and *M. viridis* cores (84.5 to 86.6% of TOU and 84.9 to 87.8% of TOU) and differed considerably from that at *M. arctia* burrow walls (55.7 to 62.8% of TOU). This indicates that sediment–water interfaces are the most intense sinks for oxygen. Consequently, changing respiration rates of the estimated magnitude (Table 4, initial or recovered abundances) would not affect this conclusion in either case. In the case of mortality, reduced burrow wall surface would affect the above calculations, increasing the importance of oxygen removal at these sediment–water interfaces. Therefore, absolute numbers should be interpreted with caution.

The high TOU, especially in cores colonized by *M. neglecta* and *M. viridis*, indicate stimulation of the anaerobic bacterial processes around the burrows. Therefore, a considerable amount of the oxygen uptake in the sediment cores was likely due to the reoxygenation of reduced components. *M. viridis* is known to increase sulfate reduction (Kristensen et al. 2011, Quintana et al. 2013), and the appearance of *Beggiatoa* spp. in *M. neglecta* and *M. viridis* cores at the sediment surface indicates reduced conditions near the sediment surface by reason of upward drifting sulfide.

Influence on nutrient fluxes

Shortly after their introduction to sediment cores, the polychaetes affected the nutrient fluxes. Overall, concentrations of ammonium were higher in sediments than in overlying water, driving a constant nutrient release from the sediment. Compared to azoic control cores, the presence of burrowing polychaetes enhanced the effluxes of ammonium, thus reflecting the grouping of the sibling species, as also shown in solute-transport and oxygen-uptake patterns, with the strongest impact of 'deep-burrowing' *M. neglecta* and *M. viridis* compared to that of *M. arctia*.

The burrowing and ventilating polychaetes influence the magnitude of nutrient fluxes in several ways. As a result of the established burrow structures, the additional sediment–water interface and therefore the effective area of exchange for any solutes increases. In a previous study, *M. viridis* formed approximately 2.8 m^2; *M. neglecta*, 2.1 m^2; and *M. arctia*, 0.4 m^2 of

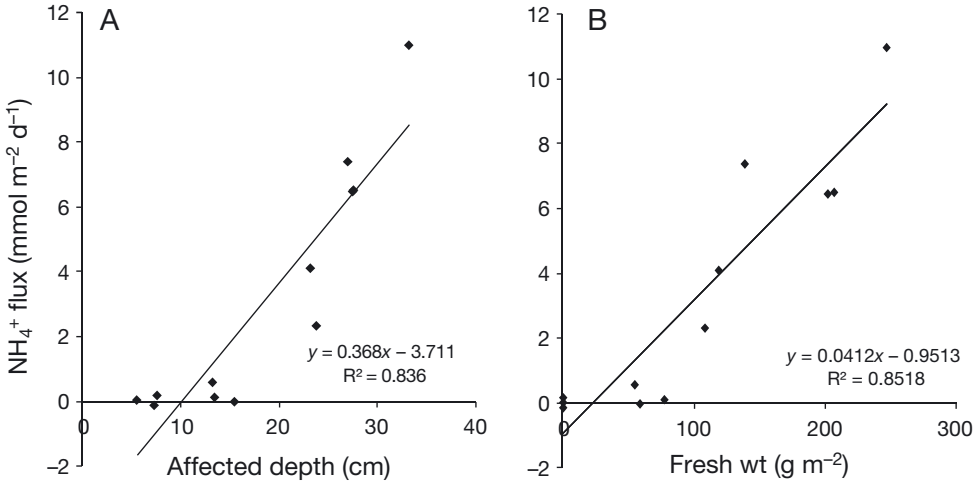

Fig. 6. Linear regression of ammonium fluxes with (A) the bromide-affected sediment depth and (B) the fresh weight of polychaetes. Points represent the individual cores

burrow walls below each square meter of sediment (1273 ind. m^{-2}) (Renz & Forster 2013). Since biomass, size, and abundance of macrofauna, as well as the specific burrowing depth, have a major impact on the geometry of diffusion and the vertical solute concentration gradient (Aller 1982), deeper irrigation will increase porewater solute exchange most. To assess the influence of burrowing depth and the biomass of polychaetes on nutrient dynamics, the ammonium efflux determined at the end of the experiment was correlated with the simultaneously measured bromide-affected sediment depth and with the biomass used in the different treatments (Fig. 6). Thereby, ammonium fluxes significantly correlate with both biomass ($n = 12$, $p < 0.01$, $R^2 = 0.85$) and sediment irrigation depth ($n = 12$, $p < 0.01$, $R^2 = 0.84$). Thus, the magnitude of ammonium fluxes of *M. viridis* and *M. neglecta* compared to *M. arctia* can be directly linked to the differences in biomass and irrigation depth, but no evidence can be gleaned on the causality of parameters (e.g. size-dependent burrowing depth) influencing the magnitude of fluxes. In addition, as drawn from the calculated water exchange and from solute transport coefficients, the ventilation patterns of the 3 sibling species are different in magnitude and quality, which, consequently, affect the stimulation of microbial nutrient mineralization differently.

A part of the produced ammonium is assumed to be transported to the water column by the ventilation current, as is visible in the decreasing ammonium porewater inventories in the polychaete treatments compared to control cores. In the water column and oxidized surface sediments, ammonium can be directly nitrified to nitrite and nitrate. In control and *M. arctia* cores, the increasing nitrate concentrations in overlying water (e.g. between d_9 and d_{13}), in combination with the porewater nitrate distributions, suggest high nitrification rates within the water column. The nitrate produced will be transported into the sediment and possibly fuel benthic denitrification. However, compared to control cores, *M. arctia* had no significant stimulatory effects on nitrification; hence, the stimulatory effect on denitrification is assumed to be minor.

In sharp contrast to the control and *M. arctia* cores, nitrate concentrations in the overlying water of *M. neglecta* and *M. viridis* cores continuously decreased during the experiment. This decrease is even higher when considering that an additional amount of nitrate (20 µmol l^{-1}) was added with each water exchange. If rates of nitrification and denitrification match, a steady-state condition exists, as no net nitrate fluxes across the sediment–water interface are evident (Hietanen et al. 2007). Nitrate porewater concentrations in the present investigation remain low, suggesting a little transport of nitrate across the sediment–water boundary. Consequently, no considerable accumulations of nitrate occur within the sediment, and any nitrate produced will either be denitrified or used as substrate for DNRA. Ammonium fluxes from the sediment and small nitrate fluxes into the sediment agree with results of other studies of *M. arctia* (Hietanen et al. 2007, Viitasalo-Frösen et al. 2009) and *M. viridis* (Karlson et al. 2005, Kristensen et al. 2011). Hietanen et al. (2007) found the influence of *M. arctia* on denitrification to be minor. Similarly, in a study by Karlson et al. (2005), the effects of *M. viridis* on denitrification were low and DNRA was thought to be the major pathway of nitrate removal in reduced sediments. No information on the influence of the nutrient dynamics of *M. neglecta* is currently available

from the literature. While the pathway of nitrate removal cannot be deduced from this study, the literature suggests DNRA as the likely mechanism.

The phosphate porewater profiles of *M. arctia*-inhabited cores are typically S-shaped (Slomp et al. 1998) and characterized by a sharp increase in phosphate concentrations below the oxidized surface sediment. Below this subsurface maximum the declining concentrations are caused by a general decrease in metabolic activity with depth. The similar shape, but generally lower concentrations, of profiles in control cores indicate a stimulation of the microbial production of phosphate, as well as enhanced desorption in the presence of *M. arctia*. Consequently, the produced phosphate will be transported upward by diffusion to the more oxidized sediment layers at the sediment surface, where an adsorption on Fe-oxides is likely. The potential irrigation effect of *M. arctia*, caused by non-local transport of dissolved phosphate from below the oxidized sediment layers, is minor, as indicated by only slowly increasing phosphate concentrations in the water column. Therefore, the phosphate-buffering capacity of the sediment will not be exploited. Similar effects of *M. arctia* on the remobilization of phosphate have been reported by Hietanen et al. (2007) and Viitasalo-Frösen et al. (2009).

The porewater phosphate profiles of *M. neglecta* and *M. viridis* are completely different from those of the control and *M. arctia* cores. Highest phosphate concentrations occur within the surface layer, followed by decreasing concentrations with depth. Below a sediment depth of 10 cm, the higher phosphate concentrations indicate a stimulated release in both treatments, resulting from enhanced microbial production, as well as from enhanced desorption. The produced phosphate will enter the surrounding sediment via diffusion along a concentration gradient and is transported via non-local transport to the water column. The latter process may partly explain the unusually high phosphate concentrations near the sediment surface. However, the bulk may result from a shift to a more intense anaerobic metabolism, also consistent with the appearance of *Beggiatoa* spp. in these cores. As a consequence of increased sulfate reduction in the upper sediment layers, the produced sulfide causes desorption of phosphate, which diffuses into the water column (Heijs 2000). The phosphate release caused by *M. viridis* is comparable to that found in a study by Karlson et al. (2005), with a benthic flux of approximately 0.1 mmol m^{-2} d^{-1}, and to the measured flux of 0.09 to 0.12 mmol m^{-2} d^{-1} found in a study by Urban-Malinga et al. (2013), most likely caused by *M. neglecta* (pers. comm.); these data are consistent with the results of the present investigation.

Functional diversity

A classification of benthic organisms into functional groups or traits is helpful when assessing their direct and indirect ecological effects. Since feeding types of *Marenzelleria* spp. are assumed to be consistent, comprising surface deposit and suspension feeding (Fauchald & Jumars 1979, Dauer et al. 1981, Sikorski & Bick 2004), and owing to close taxonomical and morphological similarity, functional differences of the 3 sibling species are frequently assumed to be negligible (Hietanen et al. 2007, Norkko et al. 2012), although for *M. arctia* no information is available. In a previous tracer experiment, Renz & Forster (2013) found all 3 sibling species to be biodiffusers in terms of particle transport (François et al. 2001, Gérino et al. 2003). However, confirming the results of the present study, a disparity was found. *M. arctia* was shown to affect solute transport primarily by enhanced molecular diffusion, while *M. viridis* and *M. neglecta* exhibit non-local solute transport.

The indirect functions measured as changes in nutrient dynamics and oxygen uptake in the present investigation emphasize the complexity of macrofaunal bioturbation activities and their effects on microbial communities (Meysman et al. 2006). Thereby, the 3 closely related polychaetes emerged with different activity patterns related to their individual species traits. With regard to their oxygen consumption as a key ecosystem function (Norling et al. 2007), the periodic irrigation of the blind-ended burrows of *M. viridis* and *M. neglecta* creates oscillating redox conditions in the surrounding sediment, consequently stimulating the rates of mineralization of organic material (Forster & Graf 1992, Aller 1994, Kristensen & Kostka 2005). Due to the different individual species traits (e.g. burrow structure and irrigation patterns), a similar magnitude of stimulation may not occur in the presence of *M. arctia*. Assessing the relevance of the 3 morphologically similar species related to all these indirect functions, the deep-burrowing species *M. viridis* and *M. neglecta* may, therefore, cause profound changes in resources, acting as important ecosystem engineers. They should, therefore, belong to one functional group, distinctly different from that of *M. arctia*. The ecological consequences of a potential spread of *M. arctia* into the southern areas of the Baltic Sea are assumed to be less dramatic than a comparable spread of *M. viridis*.

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LITERATURE CITED

Aller RC (1982) The effects of macrobenthos on chemical properties of marine sediment and overlying water. Plenum Publishing Company, New York, NY

Aller RC (1994) Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. Chem Geol 114:331–345

Andersen FÄ, Kristensen E (1988) The influence of macrofauna on estuarine benthic community metabolism: a microcosm study. Mar Biol 99:591–603

Andersson JH, Middelburg JJ, Soetaert K (2006) Identifiability and uncertainty analysis of bio-irrigation rates. J Mar Res 64:407–430

Arain S, Weiss S, Heinzle E, John GT, Krause C, Klimant I (2005) Gas sensing in microplates with optodes: influence of oxygen exchange between sample, air, and plate material. Biotechnol Bioeng 90:271–280

Bale AJ, Kenny AJ (2005) Sediment analysis and seabed characterization. In: Eleftheriou A, McIntyre A (eds) Methods for the study of marine benthos. Blackwell Science, Oxford

Bastrop RR (1997) Where did *Marenzelleria* spp. (Polychaeta: Spionidae) in Europe come from? Aquat Ecol 31: 119–136

Bick A (2005) A new Spionidae (Polychaeta) from North Carolina, and a redescription of *Marenzelleria wireni* Augener, 1913, from Spitsbergen, with a key for all species of *Marenzelleria*. Helgol Mar Res 59:265–272

Bick A, Burckhardt R (1989) Erstnachweis von *Marenzelleria viridis* (Polychaeta, Spionidae) für den Ostseeraum, mit einem Bestimmungsschlüssel der Spioniden der Ostsee [First evidence of *Marenzelleria viridis* Polychaeta (Spionidae) for the Baltic Sea region, with a sorting key for spionides of the Baltic Sea]. Mitt Zool Mus Berlin 65: 237–247

Blank M, Bastrop R (2009) Phylogeny of the mud worm genus *Marenzelleria* (Polychaeta, Spionidae) inferred from mitochondrial DNA sequences. Zool Scr 38:313–321

Blank M, Laine A, Jürss K, Bastrop R (2008) Molecular identification key based on PCR/RFLP for three polychaete sibling species of the genus *Marenzelleria*, and the species' current distribution in the Baltic Sea. Helgol Mar Res 62:129–141

Bonaglia S, Bartoli M, Gunnarsson JS, Rahm L and others (2013) Effect of reoxygenation and *Marenzelleria* spp. bioturbation on Baltic Sea sediment metabolism. Mar Ecol Prog Ser 482:43–55

Braeckman U, Provoost P, Gribsholt B, Van Gansbeke D and others (2010) Role of macrofauna functional traits and density in biogeochemical fluxes and bioturbation. Mar Ecol Prog Ser 399:173–186

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymouth

Clarke KR, Somerfield PJ, Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. J Exp Mar Biol Ecol 366:56–69

Dauer DM, Maybury CA, Ewing RM (1981) Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. J Exp Mar Biol Ecol 54:21–38

Delefosse M (2012) Macrobenthic community response to the *Marenzelleria viridis* (Polychaeta) invasion of a Danish estuary. Mar Ecol Prog Ser 461:83–95

Essink K, Kleef HL (1988) *Marenzelleria viridis* (Verril, 1873) (Polychaeta: Spionidae): a new record from the Ems Estuary (The Netherlands/Federal Republic of Germany). Zool Bijdr 38:3–13

Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. Oceanogr Mar Biol Annu Rev 17:193–284

Folk RL, Ward WC (1957) Brazos River Bar: a study in the significance of grain size parameters. J Sediment Petrol 27:3–26

Forster S, Graf G (1992) Continuously measured changes in redox potential influenced by oxygen penetrating from burrows of *Callianassa subterranea*. Hydrobiologia 235–236:527–532

Forster S, Glud RN, Gundersen JK, Huettel M (1999) *In situ* study of bromide tracer and oxygen flux in coastal sediments. Estuar Coast Shelf Sci 49:813–828

François F, Poggiale JC, Durbec JP, Stora G (1997) A new approach for the modelling of sediment reworking induced by a macrobenthic community. Acta Biotheor 45: 295–320

François F, Poggiale JC, Durbec JP, Stora G (2001) A new model of bioturbation for a functional approach to sediment reworking resulting from macrobenthic communities. In: Aller J, Woodin A, Aller RC (eds) Organism–sediment interactions. University of South Carolina Press, Columbia, SC

François F, Gerino M, Stora G, Durbec JP, Poggiale JC (2002) Functional approach to sediment reworking by gallery-forming macrobenthic organisms: modeling and application with the polychaete *Nereis diversicolor*. Mar Ecol Prog Ser 229:127–136

Gérino M, Stora G, François-Carcaillet F, Gilbert F and others (2003) Macro-invertebrate functional groups in freshwater and marine sediments: a common mechanistic classification. Vie Milieu 53:221–232

Glud RN (2008) Oxygen dynamics of marine sediments. Mar Biol Res 4:243–289

Graf G, Rosenberg R (1997) Bioresuspension and biodeposition. J Mar Syst 11:269–278

Granberg ME, Gunnarsson JS, Hedman JE, Rosenberg R, Jonsson P (2008) Bioturbation-driven release of organic contaminants from Baltic Sea sediments mediated by the invading polychaete *Marenzelleria neglecta*. Environ Sci Technol 42:1058–1065

Grasshoff K, Kremling K, Ehrhardt M (1983) Methods of seawater analysis. Wiley-VCH, Weinheim

Hansen K, Kristensen E (1998) The impact of the polychaete *Nereis diversicolor* and enrichment with macroalgal (*Chaetomorpha linum*) detritus on benthic metabolism and nutrient dynamics in organic-poor and organic-rich sediment. J Exp Mar Biol Ecol 231:201–223

Hedman JE, Gunnarsson JS, Samuelsson G, Gilbert F (2011) Particle reworking and solute transport by the sediment-living polychaetes *Marenzelleria neglecta* and *Hediste diversicolor*. J Exp Mar Biol Ecol 407:294–301

Heijs SK (2000) Sulfide-induced release of phosphate from

sediments of coastal lagoons and the possible relation to the disappearance of *Ruppia* sp. Aquat Microb Ecol 23: 85–95

Hietanen S, Laine AO, Lukkari K (2007) The complex effects of the invasive polychaetes *Marenzelleria* spp. on benthic nutrient dynamics. J Exp Mar Biol Ecol 352:89–102

Jones MN (1984) Nitrate reduction by shaking with cadmium: alternative to cadmium columns. Water Res 18: 643–646

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Josefsson S, Leonardsson K, Gunnarsson JS, Wiberg K (2011) Influence of contaminant burial depth on the bioaccumulation of PCBs and PBDEs by two benthic invertebrates (*Monoporeia affinis* and *Marenzelleria* spp.). Chemosphere 85:1444–1451

Karlson K, Hulth S, Ringdahl K, Rosenberg R (2005) Experimental recolonisation of Baltic Sea reduced sediments: survival of benthic macrofauna and effects on nutrient cycling. Mar Ecol Prog Ser 294:35–49

Knowlton N (1993) Sibling species in the sea. Annu Rev Ecol Syst 24:189–216

Kotta J, Kotta I, Simm M, Lankov A, Lauringson V, Põllumäe A, Ojaveer H (2006) Ecological consequences of biological invasions: three invertebrate case studies in the north-eastern Baltic Sea. Helgol Mar Res 60:106–112

Kristensen E, Kostka JE (2005) Macrofaunal burrows and irrigation in marine sediment: microbiological and biogeochemical interactions. Interactions between macro- and microorganisms in marine sediments. Am Geophys Union 60:125–157

Kristensen E, Hansen T, Delefosse M, Banta GT, Quintana CO (2011) Contrasting effects of the polychaetes *Marenzelleria viridis* and *Nereis diversicolor* on benthic metabolism and solute transport in sandy coastal sediment. Mar Ecol Prog Ser 425:125–139

Kristensen E, Penha-Lopes G, Delefosse M, Valdemarsen T, Quintana CO, Banta GT (2012) What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar Ecol Prog Ser 446:285–302

Kube J, Zettler ML, Gosselck F, Ossig S, Powilleit M (1996) Distribution of *Marenzelleria viridis* (Polychaeta: Spionidae) in the southwestern Baltic Sea in 1993/94 — ten years after introduction. Sarsia 81:131–142

Leppäkoski E, Olenin S (2000) Non-native species and rates of spread: lessons from the brackish Baltic Sea. Biol Invasions 2:151–163

Mahaut ML, Sibuet M, Shirayama Y (1995) Weight-dependent respiration rates in deep-sea organisms. Deep-Sea Res I 42:1575–1582

Martin WR, Banta GT (1992) The measurement of sediment irrigation rates: a comparison of the Br tracer and $^{222}Rn/^{226}Ra$ disequilibrium techniques. J Mar Res 50:125–154

Mermillod-Blondin F, Rosenberg R (2006) Ecosystem engineering: the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. Aquat Sci 68:434–442

Meysman FJR, Middelburg JJ, Heip CHR (2006) Bioturbation: a fresh look at Darwin's last idea. Trends Ecol Evol 21:688–695

Norkko J, Reed DC, Timmermann K, Norkko A and others (2012) A welcome can of worms? Hypoxia mitigation by an invasive species. Glob Change Biol 18:422–434

Norling K, Rosenberg R, Hulth S, Grémare A, Bonsdorff E (2007) Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. Mar Ecol Prog Ser 332:11–23

Parsons TR, Maita Y, Lalli CM (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, Oxford

Quintana CO, Tang M, Kristensen E (2007) Simultaneous study of particle reworking, irrigation transport and reaction rates in sediment bioturbated by the polychaetes *Heteromastus* and *Marenzelleria*. J Exp Mar Biol Ecol 352:392–406

Quintana CO, Hansen T, Delefosse M, Banta G, Kristensen E (2011) Burrow ventilation and associated porewater irrigation by the polychaete *Marenzelleria viridis*. J Exp Mar Biol Ecol 397:179–187

Quintana CO, Kristensen E, Valdemarsen T (2013) Impact of the invasive polychaete *Marenzelleria viridis* on the biogeochemistry of sandy marine sediments. Biogeochemistry 115:95–109

Renz JR, Forster S (2013) Are similar worms different? A comparative tracer study on bioturbation in the three sibling species *Marenzelleria arctia*, *M. viridis*, and *M. neglecta* from the Baltic Sea. Limnol Oceanogr 58:2046–2058

Saager PM, Sweerts JP, Ellermeijer HJ (1990) A simple pore-water sampler for coarse, sandy sediments of low porosity. Limnol Oceanogr 35:747–751

Shull DH (2009) Bioturbation. In: John HS, Karl KT, Steve AT (eds) Encyclopedia of ocean sciences (2nd edn). Academic Press, Oxford

Sikorski AV, Bick A (2004) Revision of *Marenzelleria mesnil*, 1896 (Spionidae, Polychaeta). Sarsia 89:253–275

Slomp CP, Malschaert JFP, Raaphorst WV (1998) The role of adsorption in sediment–water exchange of phosphate in North Sea continental margin sediments. Limnol Oceanogr 43:832–846

Soetaert K, DeClippele V, Herman P (2002) FEMME, a flexible environment for mathematically modelling the environment. Ecol Modell 151:177–193

Ullman WJ, Aller RC (1982) Diffusion coefficients in nearshore marine sediments. Limnol Oceanogr 27:552–556

Urban-Malinga B, Warzocha J, Zalewski M (2013) Effects of the invasive polychaete *Marenzelleria* spp. on benthic processes and meiobenthos of a species-poor brackish system. J Sea Res 80:25–34

Viitasalo-Frösen S, Laine AO, Lehtiniemi M (2009) Habitat modification mediated by motile surface stirrers versus semi-motile burrowers: potential for a positive feedback mechanism in a eutrophied ecosystem. Mar Ecol Prog Ser 376:21–32

Welsh D (2003) It's a dirty job but someone has to do it: the role of marine benthic macrofauna in organic matter turnover and nutrient recycling to the water column. Chem Ecol 19:321–342

Zettler ML, Bochert R, Bick A (1994) Röhrenbau und Vertikalwanderung von *Marenzelleria viridis* (Polychaeta: Spionidae) in einem inneren Küstengewässer der südlichen Ostsee [Tube size and vertical distribution of *Marenzelleria viridis* (Polychaeta: Spionidae) in a coastal water of the southern Baltic]. Rostock Meeresbiol Beitr 2: 215–225

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