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Habitat modification mediated by motile surface stirrers versus semi-motile burrowers: potential for a positive feedback mechanism in a eutrophied ecosystem

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ABSTRACT: We performed a 4 wk laboratory experiment with the semi-motile burrowers *Macoma balthica* and *Marenzelleria* spp. and the motile surface sediment stirrers *Monoporeia affinis* and *Mysis mixta* to study their effects on the transport of tracer particles (mean diameter [∅] 1 µm) in the sediment, sediment parameters (depth of the oxidized layer, water content, organic matter content), water turbidity, and nutrient fluxes across the sediment-water interface (PO_4^{3-}, $NO_2^- + NO_3^-$, NH_4^+; measured weekly). Two densities were included for each taxon, representing a low and a high field density. *M. balthica* significantly increased particle mixing, the rates being 59.6 and 61.9×10^{-3} cm^2 d^{-1}. While all taxa increased turbidity in the overlying water, the strongest effects were caused by *M. affinis* and *M. mixta*, resulting in 112- and 45-fold increases, respectively. In addition, these 2 motile species increased oxidation of the sediment surface layers. A distinctive difference in the nutrient fluxes was observed between the semi-motile (*M. balthica*, *Marenzelleria* spp.) and the motile taxa (*M. affinis*, *M. mixta*). The former increased the efflux of both PO_4^{3-} and NH_4^+, while the latter suppressed the efflux of NH_4^+ and decreased the sediment uptake of NO_x, indicating enhanced N removal. Higher nutrient exchange rates were observed at the higher animal densities. We conclude that a shift in the benthic communities from the 2 motile to the 2 semi-motile taxa, observed throughout the northern Baltic Sea, may notably alter the regime of benthic nutrient cycling and thereby the performance of the entire ecosystem.

KEY WORDS: Bioturbation · Motile · Semi-motile · Nutrient cycling · Particle mixing · Turbidity

INTRODUCTION

In soft-sediment environments, the habitat is profoundly affected by the activities of its inhabitants in a process termed bioturbation. Sediment-reworking species possess a diversity of functional characteristics, linked to their feeding, burrowing and motility traits (Bonsdorff & Pearson 1999), all of which may exert a specific influence on the environment (e.g. Karlson et al. 2005).

In the Baltic Sea, high external nutrient loading combined with weak vertical mixing between stratified water layers has led to a chronic state of eutrophication. Elevated pelagic production, accelerated benthic oxygen consumption, and expanding near-bottom hypoxia alter the regime of nutrient cycling (Kuparinen & Tuominen 2001). As a consequence, internal processes, namely benthic release of P and N, largely govern the level of nutrients available for primary producers (e.g. Vahtera et al. 2007). In addition to its effects on nutrient dynamics, oxygen deficiency in near-bottom waters has resulted in notable impoverishment of the benthic biota (Karlson et al. 2002, Laine et al. 2007).

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The macrozoobenthos of the northern Baltic Sea is characterized by a low number of species, with the amphipod *Monoporeia affinis* Lindström, the bivalve *Macoma balthica* (L.) and the invasive polychaetes *Marenzelleria* spp. being some of the few key organisms (Laine et al. 1997, Karlson et al. 2002). In addition to sediment-dwelling taxa, the nectobenthic mysid *Mysis mixta* Lilljeborg is an important, although frequently neglected, component of the benthic biota (e.g. Lindström & Sandberg-Kilpi 2008). These taxa, hereafter referred to as *Monoporeia*, *Macoma*, *Marenzelleria*, and *Mysis*, differ in terms of their degree of motility and their burrowing depth: *Mysis* is epibenthic, while the others belong to the infauna, *Marenzelleria* being the only deep-burrowing (>10 cm) taxon. *Monoporeia* and *Mysis* are motile detritivores and carnivores, stirring the sediment surface (Lopez & Elmgren 1989, Viherluoto et al. 2000), while *Macoma* and *Marenzelleria* are semi-motile detritivores, capable of switching between deposit- and suspension-feeding modes (Dauer et al. 1981, Lin & Hines 1994).

Large-scale changes in the relative abundance of these 4 taxa have occurred in the northern Baltic Sea during recent decades (Laine et al. 1997, 2007). *Monoporeia*, formerly predominant over large areas, has declined, whereas *Macoma* and *Marenzelleria* have established dense populations in coastal as well as deeper open-sea habitats (Perus & Bonsdorff 2004, Norkko et al. 2007). In addition, mysids appear to have diminished markedly since the 1980s, probably due to poor oxygen conditions in the Gulf of Finland (M. Lehtiniemi et al. unpubl.). Apart from changes related to eutrophication- and stratification-induced hypoxia, interspecific competition is causing further shifts in Baltic soft-sediment communities (Neidemann et al. 2003).

It is often the case that certain functional characteristics have stronger impacts than others (Mermillod-Blondin et al. 2005, Norling et al. 2007), e.g. species that form and irrigate burrows deep in the sediment enhance mineralization and elemental cycling more efficiently than other species (Ieno et al. 2006). However, which traits cause significant ecosystem responses probably depends on the state of the system. For example, in eutrophied waters, traits that constrain benthic nutrient regeneration may substantially contribute to ecosystem recovery. Moreover, some species, such as *Monoporeia* and *Mysis*, are capable of re-oxygenating anoxic sediments and neutralizing toxic sulphide compounds (Modig & Olafsson 2001, Lindström & Sandberg-Kilpi 2008). In the present study, we aim to describe how the shift in relative abundances of the 4 taxa, encompassing functional shifts—the decrease in motile and increase in semi-motile taxa—may alter benthic habitats and the regime of nutrient cycling in the Baltic Sea.

MATERIALS AND METHODS

Collecting the study material. The animals were collected between 18 and 24 August (*Monoporeia* and *Marenzelleria*), 29 August (*Macoma*), and 4 October (*Mysis*), the sediment was collected on 27 August, and the experiment was carried out between 12 October and 3 November 2005. All material originated from accumulation areas rich in deposited organic matter.

Macoma and *Mysis* were collected from the Gulf of Finland (off the Hanko Peninsula, SW coast of Finland; 59° N, 23° E) and *Monoporeia* and *Marenzelleria* (probably *M. arctia* Chamberline; Bastrop & Blank 2006) from the Gulf of Bothnia (at the regular monitoring stations of the Finnish Institute of Marine Research; 61° N, 20° E) at depths of 35 to 100 m. The bivalves were collected with a bottom trawl (length 7 m, width 4 m, mesh size 10 mm) and the mysids with an epibenthic sledge (mouth opening 41 × 23 cm, net length 115 cm, 1 l cod end). The amphipods and polychaetes were collected with a van Veen grab. All animals were immediately transferred into insulated boxes with seawater from below the thermocline (4 to 10°C), and for infauna, some sediment from the grab was added.

In the laboratory, the animals were placed in 30 to 50 l aquaria (macrofauna with plenty of sediment from the collection site) with continuously flowing unfiltered seawater (5 to 6 psu, 5 to 10°C) and gentle aeration. Prior to initiating the experiment and within 55 d of the field collections, the sediment-dwelling taxa were fed *Nannochloropsis oculata* (Instant Algae® Nannochloropsis 3600; Reed Mariculture) monthly, and the mysids were fed frozen *Daphnia* sp. weekly. Macrofauna survive in good health for several months under laboratory conditions if supplied with sufficient food (e.g. Elmgren et al. 2001). In addition to the food supplied, the sediment used during the pre-experimental and experimental periods was rich in organic matter (13 to 15%).

The sediment used in the experiment was collected from a depth of 35 m in an archipelago area (59° 45.58′ N, 23° 15.23′ E) in close proximity to the Tvärminne Zoological Station, on the SW coast of Finland. An Ockelmann benthic sledge (mouth opening 12 × 30 cm, net length 52 cm, mesh size 150 µm) was used to collect the surface layers of the sediment (the uppermost ca. 5 cm) and a box corer was used to collect the deeper anoxic layers (down to 20 cm). The sediment was kept in insulated boxes until transport to the laboratory (5°C) for processing. To remove the macrofauna, the surface sediment was sieved through a 0.5 mm mesh and the deeper sediment through a 1.0 mm mesh.

Experimental setup. The experiment was carried out at Tvärminne Zoological Station in a temperature-controlled room at 2 to 3°C, approximating *in situ*

temperatures. The deeper sediment was packed in 8.5 cm layers in round experimental cores (diameter 14 cm, height 18 cm, with a movable bottom), and the surface sediment was added in a 2.5 cm layer on the top of each core. The cores were carefully filled with seawater (water column depth 7 cm), and a flow-through system was established using seawater (5 to 6 psu) filtered through a 0.2 µm filter and stored in a container (1 m^3) with aeration to ensure a continuous oxygen supply to the system. A peristaltic pump brought new seawater from the container to the cores, each of which had separate tubing. The flow rate through the pump was set to 1 ml min^{-1}, but was observed to fluctuate between 0.6 and 1.5 ml min^{-1} for the different cores. The cores were allowed to stabilize for 14 d prior to the experiment and were kept unsealed throughout the experiment, allowing the surplus water to overflow.

The experiment comprised 9 treatments, which included 2 densities for each of the 4 species plus the control without fauna (n = 4 for all), yielding a total of 36 cores (Table 1). The higher animal densities corresponded to the higher end of reported field densities (Laine et al. 2007, Norkko et al. 2007); the lower densities were one fifth of the higher densities. To prevent the animals from escaping, the cores were capped with 0.5 mm mesh size steel nets. The experiment lasted for 21 d.

To study the effect of the 4 species on sediment layering and particle mixing, fluorescent microspheres (polystyrene latex spheres, 1 µm in diameter) (Fluoresbrite® YG Microspheres; Polysciences) were added to the top of the sediment (~1.14 × 10^9 particles $core^{-1}$) at the beginning of the experiment (Day 0), before introduction of the animals. At the end of the experiment, for 3 replicate cores in each treatment, the upper 4 cm of the sediment was cut into 1 cm slices and the remaining sediment into three 2 cm slices. One replicate control core (presented in gray in Fig. 5) was excluded from the particle mixing analyses due to problems in the slicing operation. This replicate was, however, included in the nutrient and turbidity analyses.

The slicing apparatus was comprised of a movable piston attached to a stand and a separate cutting plate (Viitasalo 2007). The sediment slices were thoroughly homogenized, and a 30 to 40 ml sample was taken with a syringe for particle analysis. The sediment was lyophilized and the number of microspheres in a 10 mg subsample were counted under a Leica DMIL inverted microscope equipped with an epifluorescence setup (EBQ100 lamp, blue excitation light, filter 450 to 490 nm) and with 200 to 400× magnification. The counts were converted into percentages of the tracer in each depth stratum and the particle-mixing coefficients (D_b), expressing the rate of sediment mixing in cm^2 d^{-1}, were determined using the biodiffusion model (the biodiffusor submodel) developed by François et al. (1997). This model simulates diffusion-like random transport of sediment particles by the fauna over short distances (François et al. 1997).

Turbidity and nutrient fluxes (NH_4^+, NO_2^- + NO_3^-, PO_4^{3-}) were measured on Day 0, before adding the animals, and subsequently at 1 wk intervals. Turbidity as nephelometric turbidity units (NTU) was determined with a 2100P Turbidimeter. To transform NTUs into total suspended solids (TSS), we used the equation given by Ginting & Mamo (2006): $Y = 0.08 \cdot X^{0.76}$, where Y and X are the TSS concentration and NTU, respectively.

The nutrient flux measurements were carried out according to Hietanen et al. (2007), i.e. in an open flow-through system. The tubing bringing the inflowing seawater was put aside and water samples for turbidity (20 ml) and nutrient flux measurements (200 ml) were collected from the cores (43 mm above the sediment surface). Due to fluctuations among the cores, the flow rate in each core was measured prior to sampling.

Table 1. Length of the animals (mean ± SE, number of measurements in parentheses), treatments and species densities (expressed as individuals and dry weights, DW, per core and per m^2) used in the experiment, and recovery and survival percentages of the fauna at the end of the incubation (mean ± SE)

Treatment	Length (mm)	Code	Density				Recovery (%)	Survival (%)
			Ind. $core^{-1}$	Ind. m^{-2}	g DW $core^{-1}$	g DW m^{-2}		
Control	–	Ctrl	0	0	–	–	–	–
Macoma balthica	18.6 ± 1.8 (72)	Mc3	3	190	0.16	10	100	92 ± 8
		Mc15	15	970	0.61	40	100	82 ± 2
Marenzelleria spp.	20.4 ± 4.0 (15)	Mz6	6	390	0.01	0.4	79 ± 8	79 ± 8
		Mz30	30	1950	0.02	1.5	69 ± 9	66 ± 10
Monoporeia affinis	8.0 ± 1.4 (300)	Mo15	15	970	0.02	1.4	93 ± 4	93 ± 0
		Mo75	75	4870	0.11	6.9	86 ± 5	85 ± 2
Mysis mixta	19.0 ± 2.3 (22)	My1	1	65	0.01	0.3	100	100
		My5	5	320	0.03	1.7	100	85 ± 6

In addition, a 200 ml water sample from the storage container was analyzed for nutrients. After sampling, the container was replenished with 0.2 µm filtered seawater. All nutrients were analyzed using standard methods (Grasshoff et al. 1983). The nutrient fluxes per unit area were calculated from the concentration differences between the water collected from the container and the water collected from the cores, divided by the residence time (determined according to the flow rates).

Dead mysids were replaced weekly, after collecting the turbidity and nutrient samples. Altogether, 8 dead mysids were replaced during the incubation. In addition, all mysids were removed on Day 7 for stomach content analyses (data not included in this study) and immediately replaced with new individuals. No other species were replaced.

At the end of the incubation, the mean depth of the light-brown surface layer was estimated with a ruler by means of 2 to 3 measurements per core from outside the core wall. This layer was termed 'oxidized', i.e. characterized by the presence of oxidized compounds (mainly iron) and high redox potential, as demonstrated by Hietanen et al. (2007) with a similar experimental setup and sediments. All cores were photographed for more detailed examination. To determine the water content and the percent of organic matter (OM) in the sediment, a 10 ml sample was taken from each of the sediment slices obtained (see above), dried overnight at 105°C, and ignited at 550°C for 2 h.

After removing subsamples from the slices, the remaining sediment was carefully sieved through 0.5 mm mesh and the animals recovered were preserved in 5% buffered formalin and counted. Prior to the preservation, survival (% of the animals originally added to the cores that were still alive) of the animals was determined based on locomotion and swimming behavior. The lengths of the mysids and the amphipods were measured from the tips of the rostrums to the ends of the telsons. The lengths of the polychaetes were estimated from straightened but non-stretched individuals. The preserved animals were weighed for dry weight (DW) after drying for 24 to 48 h at 60°C (shell-free dry weight for *Macoma*).

Statistical analyses. A one-way *F*-test was used to test the treatment effects on OM and water content in the different depth strata, separately at the low and high animal densities, and with 5 levels: control (Ctrl), *Macoma* (Mc), *Marenzelleria* (Mz), *Monoporeia* (Mo) and *Mysis* (My). The homogeneity of the variances and normality of

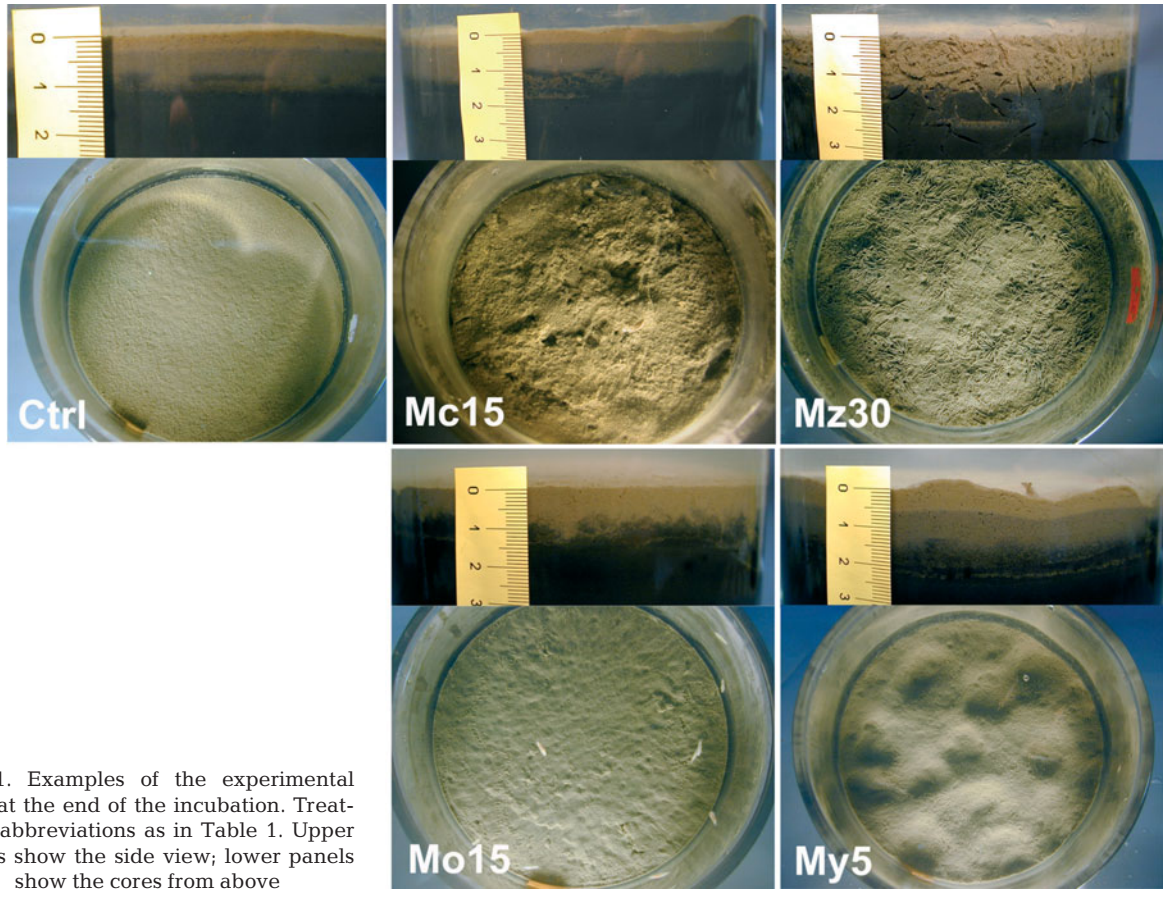

Fig. 1. Examples of the experimental units at the end of the incubation. Treatment abbreviations as in Table 1. Upper panels show the side view; lower panels show the cores from above

the distributions were visually estimated and tested using the Levene and Shapiro-Wilk tests, respectively. A logarithmic transformation was used to fulfill the parametric assumptions. Due to deviations from normality, a Kruskal-Wallis *H*-test was used to test treatment effects on the particle-mixing coefficients, nutrient fluxes across the sediment-water interface and on water turbidity (with 5 levels, separately at the low and high animal densities). For the nutrient and turbidity data, a mean value over the 3 measurement points (excluding Day 0) was calculated. To test the difference between the effects of the semi-motile vs. motile taxa on nutrient dynamics, a non-parametric contrast (*S*-test) was computed using the *H* statistics and the following coefficients: 0 (Ctrl), 0.5 (Mc), 0.5 (Mz), −0.5 (Mo) and −0.5 (My), according to Jar (1999). Other multiple comparisons were made using the Tukey HSD post hoc test. All statistical analyses were performed with SPSS 15.0 software.

RESULTS

Structure of the sediment

In the control cores without animals, the sediment surface was undisturbed and the mean depth of the light-brown oxidized layer was 2.3 mm at the end of the incubation (Figs. 1 & 2). In contrast, distinct patterns of sediment reworking were observed in the cores with macrofauna. The motile species *Monoporeia* and *Mysis* actively stirred the topmost 0.5 to 1 cm of the sediment and produced an evenly mixed oxidized layer of 6.0 to 7.5 mm (*Monoporeia*) and 5.0 to 6.5 mm (*Mysis*). Pits of ~1 cm in diameter were visible in the cores with *Mysis* (Fig. 1). The epibenthic *Mysis* does not penetrate into the sediment and were picked from the water column at the end of the incubation, while *Monoporeia* was mainly recovered from the uppermost 1 to 2 cm (Fig. 3).

In comparison, the deeper-burrowing semi-motile *Macoma* and *Marenzelleria* produced a granular and variable surface appearance (Fig. 1) and were found down to a depth of 6 and 10 cm, respectively (Fig. 3). The depth of the oxidized layer was estimated to be 2.3 to 3.0 mm for *Macoma* and 2.5 to 5.0 mm for *Marenzelleria*, although this estimation was somewhat difficult due to the uneven layering in the presence of these 2 taxa (Fig. 2). The surface of the *Marenzelleria* cores was covered with fecal pellets spreading radially outwards from the burrow openings and the burrows, lined with a light layer of ~1 mm, extended to a depth of 11 cm. The burrow network was dense enough to produce a continuous oxidized layer near the surface, while the interspace between the burrows, characterized by dark-colored reduced sediment, increased notably with depth. The colour of the light-brown oxidized layer is indicative of chemical (oxidizing) reactions that occur in the given sediment layer; it does not indicate the presence of dissolved oxygen, which is generally limited to the uppermost 1.5 mm in such sediments (Hietanen et al. 2007).

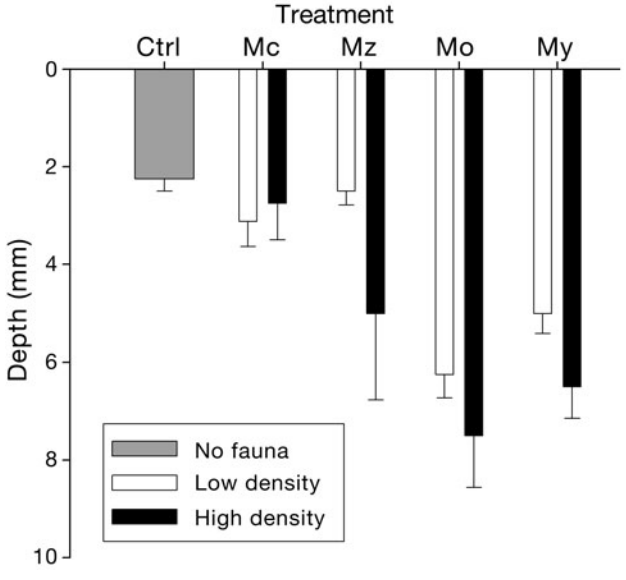

Fig. 2. Depth of the oxidized layer (mean ± SE) in the various treatments at the end of the incubation (n = 4). For treatment codes see Table 1

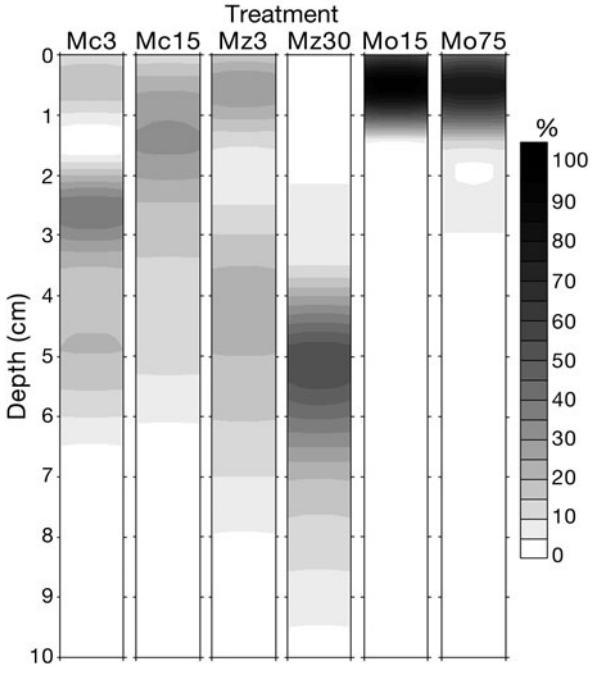

Fig. 3. Proportion of the infauna recovered from the various sediment layers at the end of the experiment. The vertical axis denotes the depth (cm) in the sediment. The contour plot was produced with Surfer 6.0, and the data were interpolated according to the Kriging method. For treatment codes see Table 1

Recovery and survival of the fauna were >80% except for the polychaetes that were cut into numerous pieces during the sediment slicing (Table 1), making the estimation of polychaete recovery and survival difficult.

Sediment properties and turbidity

Both water content and OM were highest near the surface and decreased steadily with depth, the mean maximum values within the topmost 1 cm being 84.9% (water content) and 13.9% (OM). The lowest and highest water contents within the 0 to 1 cm layer were measured in the presence of *Mysis* (84.0%) and *Monoporeia* (86.8%), respectively. *Monoporeia* (at the higher density) significantly increased the water content within the topmost 1 cm of the sediment, compared with the control, *Macoma*, and *Marenzelleria* (Table 2). The lowest OM values within the 0 to 1 cm layer were measured in the cores with *Macoma* (13.4%), whereas the highest values were found in the cores with *Monoporeia* (14.6%); the difference between these 2 species was significant within the 2 uppermost sediment strata (Table 2). No differences in the water content and OM occurred below the 1 to 2 cm stratum.

In the control cores, the turbidity remained low (<1 NTU) throughout the incubation (Fig. 4). All taxa significantly increased turbidity compared with the control (Table 3), the increase for *Macoma*, *Marenzelleria*, *Monoporeia*, and *Mysis* being 13-, 3-, 112-, and 45-fold, respectively (Fig. 4), and the taxa also differed significantly from each other (Table 3). Higher NTU values were measured at the higher animal densities in all taxa (Fig. 4). When these effects were expressed as TSS per unit area, the values remained <10 g m^{-2} in the control cores and in the treatments with *Marenzelleria*, but exceeded 100 g m^{-2} in Mo75 (Fig. 4).

Distinct differences between the animals were found in the profiles of the tracer particles (Fig. 5). In the cores with *Mysis*, 96% of the tracer was recovered within the uppermost 1 cm, while the values were 85% in the control, 76% with *Marenzelleria*, 77% (lower density) and 86% (higher density) with *Monoporeia*, and only 48% (lower density) and 50% (higher den-

Table 2. Test statistics for the effects of the 4 species on particle-mixing coefficients (D_b), sediment water content, and organic matter (OM) within the uppermost 2 cm. Treatment low and treatment high denote the low and high animal densities, respectively. p > 0.05: not significant, ns; *p < 0.05; **p <0.01; ***p<0.001. The treatments that significantly (α = 0.05) differed from each other are specified under 'Tukey HSD'. For treatment codes, see Table 1

Variable	Factor	Between-subject	p	Tukey HSD
D_b	Treatment low	H = 9.8, df = 4	*	Mc vs. others
	Treatment high	H = 9.5, df = 4	*	Mc vs. My
Water content				
(0–1 cm)	Treatment low	$F_{4,10}$ = 1.7	ns	
	Treatment high	$F_{4,10}$ = 6.0	*	Mo vs. Ctrl, Mc, Mz
(1–2 cm)	Treatment low	$F_{4,10}$ = 0.5	ns	
	Treatment high	$F_{4,10}$ = 4.8	*	Mo vs. Mc
OM				
(0–1 cm)	Treatment low	$F_{4,10}$ = 0.2	ns	
	Treatment high	$F_{4,10}$ = 4.2	*	Mo vs. Mc
(1–2 cm)	Treatment low	$F_{4,10}$ = 0.3	ns	
	Treatment high	$F_{4,10}$ = 4.2	*	Mo vs. Mc

Table 3. Effects of the 4 taxa on the sediment-water nutrient fluxes and turbidity (mean values over Days 7 to 21). Statistics from the semi-motile vs. motile contrast (S-test) and the Tukey HSD (treatments that significantly differed from each other at α = 0.05) are specified under 'Post hoc'. Other notations as in Table 2

Variable	Factor	Between-subject	p	Post hoc	p
PO_4^{3-}	Treatment low	H = 12.0, df = 4	*	S = 2.7, df = 4	ns
	Treatment high	H = 16.3, df = 4	**	S = 3.1, df = 4	*
NH_4^+	Treatment low	H = 14.0, df = 4	**	S = 3.4, df = 4	*
	Treatment high	H = 17.1, df = 4	**	S = 3.9, df = 4	**
NO_x	Treatment low	H = 10.9, df = 4	*	S = 2.7, df = 4	*
	Treatment high	H = 15.1	**	S = 3.6, df = 4	*
Turbidity	Treatment low	H = 17.9, df = 4	**	Mc vs. Ctrl; Mo, My vs. all	
	Treatment high	H = 18.3, df = 4	**	All vs. all	

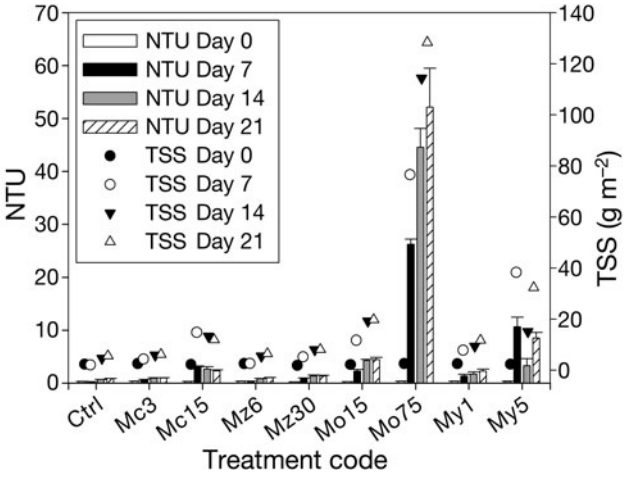

Fig. 4. Water turbidity (mean ± SE) in the various treatments (n = 4) as optically measured nephelometric turbidity units (NTUs) and as converted to total suspended solids (TSS). For treatment codes, see Table 1

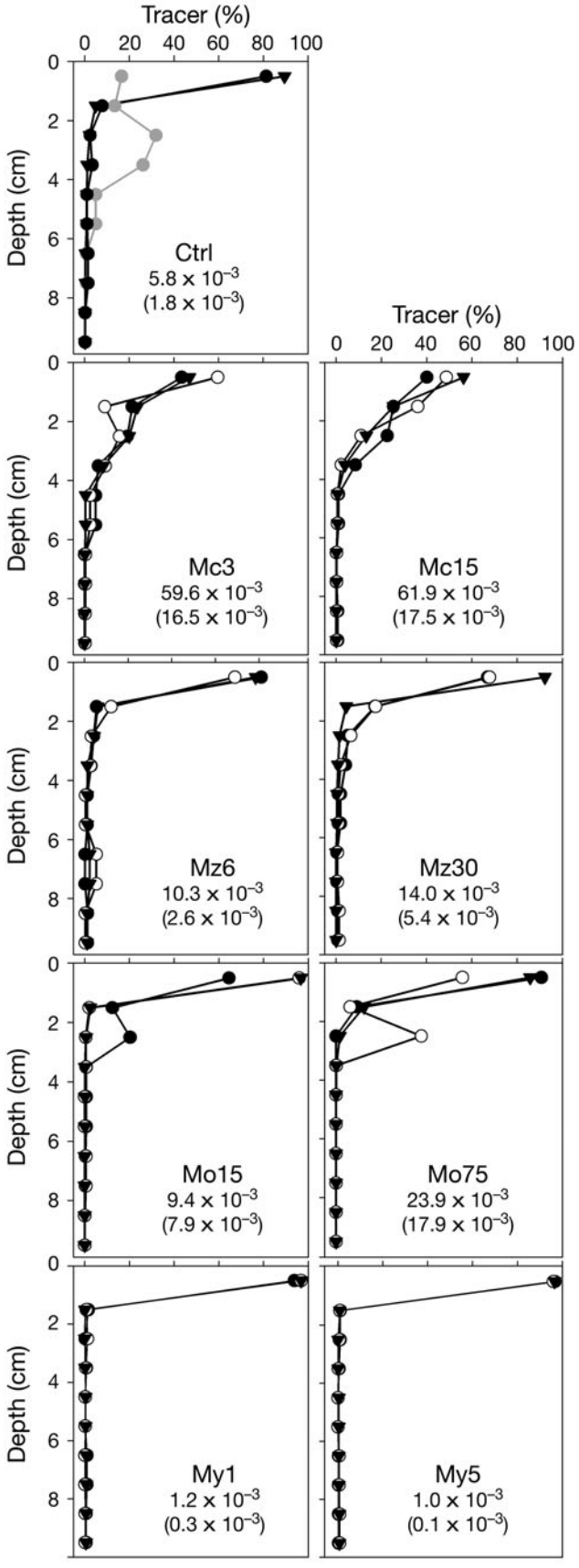

Fig. 5. Depth profiles of the fluorescent tracer in 3 replicate cores of the various treatments. Particle-mixing coefficients are noted under the treatment codes as means in $cm^2\ d^{-1}$ (SE in parentheses). The replicate shown in gray in the control is excluded from the analysis (see 'Materials and methods for details). For treatment codes, see Table 1

sity) with *Macoma* (Fig. 5). The D_b values were highest for *Macoma* (59.6 and 61.9×10^{-3} $cm^2\ d^{-1}$ at the lower and higher densities, respectively) and lowest for *Mysis* (1.1 and 1.2×10^{-3} $cm^2\ d^{-1}$) (Fig. 5). At the lower density *Macoma* significantly increased the D_b relative to the control and the other species, while at the higher density the difference between *Macoma* and *Mysis* was significant (Table 2).

Nutrient fluxes

The nutrient fluxes to and from the sediment were significantly affected by the various macrofaunal taxa and increased with increasing animal density (Fig. 6). Moreover, there was a significant difference in all nutrient fluxes between the motile and semi-motile taxa (Table 3).

The PO_4^{3-} fluxes remained <0.1 mmol $m^{-2}\ d^{-1}$ in the control cores throughout the experiment. The fluxes were significantly higher in the presence of *Macoma* (up to 1.1 mmol $m^{-2}\ d^{-1}$) and *Marenzelleria* (up to 0.5 mmol $m^{-2}\ d^{-1}$), compared with *Monoporeia* and *Mysis* (indicated by the semi-motile vs. motile contrast; Table 3), although there was a general decrease in the fluxes over time (Fig. 6).

The NO_x fluxes in the control cores were directed from the water to the sediment throughout the incubation, but a trend toward a decrease with time was observed: the NO_x uptake by the sediment decreased from 0.5 to 0.2 mmol $m^{-2}\ d^{-1}$ over the control in the course of the experiment. A similar pattern was observed in the cores with *Macoma* and *Marenzelleria*: a decrease from 0.7 to 0.1 mmol $m^{-2}\ d^{-1}$ occurred in the sediment uptake. Compared with the semi-motile taxa, *Monoporeia* and *Mysis* caused a significant reduction in the sediment NO_x uptake (Fig. 6, Table 3), resulting in a suppression of the NO_x fluxes in only 7 d to a level of <0.1 mmol $m^{-2}\ d^{-1}$, and on Day 21 the amphipods at the higher density even triggered an efflux of NO_x from the sediment to the water (Fig. 6).

The fluxes of NH_4^+ showed a contrasting pattern: in the control and with *Macoma* and *Marenzelleria* the fluxes were high (>1 mmol $m^{-2}\ d^{-1}$) and were directed from the sediment to the water throughout the 3 wk experiment, whereas *Monoporeia* and *Mysis* attenuated the NH_4^+ efflux to the water, down to 0.2 mmol $m^{-2}\ d^{-1}$ (*Monoporeia*) and <0.1 mmol $m^{-2}\ d^{-1}$ (*Mysis*)

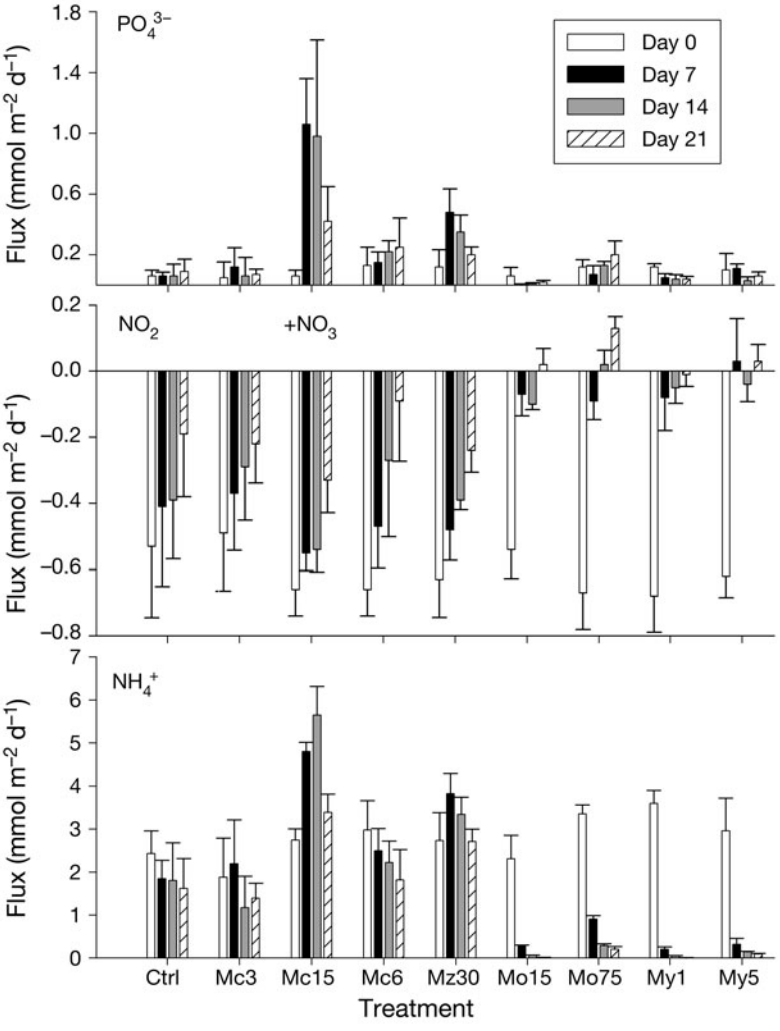

Fig. 6. Nutrient fluxes (mean ± SE) between sediment and water (n = 4). Negative fluxes are directed from water to sediment. For treatment codes, see Table 1

(Fig. 6). The difference was significant between the motile and semi-motile taxa (Table 3). As in the case of PO_4^{3-} and NO_x, there was an overall decrease in the NH_4^+ fluxes with time.

DISCUSSION

The 4 taxa had markedly different influences on their habitats, best indicated by differing effects on nutrient fluxes and turbidity. All 4 taxa are surface deposit feeders (although *Macoma* and *Marenzelleria* may also feed on suspended material), demonstrating that the area of food collection is not a proper criterion for identifying a species' influence on its habitat. In contrast, the marked similarity between *Monoporeia* and *Mysis* on the one hand and between *Macoma* and *Marenzelleria* on the other hand, appears to relate best to their degree of motility, as judged by traditional functional group classification (Bonsdorff & Pearson 1999).

Reworking of the sediment

Changes in sediment water content, stability, and resuspension may have detrimental effects on meiofauna (e.g. Sundelin & Elmgren 1991) and may inhibit settling or decrease the survival of recruits of other sediment-dwelling species (Rhoads & Young 1970). In the present study, *Monoporeia* and *Mysis* increased turbidity and the amount of suspended solids in the water column, indicating that activities by these species loosen the structure of the sediment surface. Comparable bioresuspension has been observed in the presence of benthivorous fish and chironomids (Tarvainen et al. 2005) and the estuarine mysid *Neomysis integer* (Roast et al. 2004). The lower order of magnitude turbidity values in the cores with *Macoma* and *Marenzelleria* reflect their differing motility traits and may result from deposition of a multitude of fecal pellets on the sediment surface, making it less prone to being resuspended. These 2 taxa also efficiently collect resuspended particles from the water column (Dauer et al. 1981, Lin & Hines 1994).

Monoporeia was the only taxon that significantly increased the sediment water content, probably due to active burrowing, as well as passage across the sediment-water interface. *Marenzelleria* formed a dense burrow network but did not elevate the sediment water content, perhaps reflecting insufficient vertical resolution in sediment slicing. Alternatively, the polychaetes may construct their burrows so that the sediment is pushed aside and packed near the mucus-cemented burrow walls, resulting in a horizontally variable sediment structure with water-filled burrow interiors, but unaltered average water content.

In the fluorescent tracer profiles, some mixing occurred in the control, which was probably due to activities by the meiofauna. Additionally, transport of the tiny particles may occur via movements along the interstitial water (Bradshaw et al. 2006). In the animal cores, *Macoma*, *Marenzelleria*, and *Monoporeia* all created typical biodiffuser profiles i.e. they transported particles in the upper layers of the sediment up and down in a more or less random pattern. Although the

burrows and individuals of *Marenzelleria* penetrated deepest into the sediment, *Macoma* mixed the sediment layers more efficiently and much deeper than the other species.

Physical mixing, i.e. introduction of reduced compounds to the sediment surface and burial of oxidized particles beneath the surface, stimulates organic matter turnover (Kristensen 2001). Consistent with the increased particle mixing, *Macoma* decreased the sediment OM content, although this is a somewhat coarse measure of changes in the organic matter pool. This is in agreement with the study by Karlson et al. (2005) in which *Macoma* increased mineralization more than *Monoporeia* and *Marenzelleria* did.

In a study by Bradshaw et al. (2006) *Macoma* did not significantly affect the D_b values, while *Marenzelleria viridis* showed 3 to 4 times higher mixing rates relative to the defaunated control in Quintana et al. (2007). These results contrast with our findings, which may partly result from the different types of particles used. Bradshaw et al. (2006) and Quintana et al. (2007) used luminophores of varying sizes (unknown size in Bradshaw et al. 2006; 125 to 250 µm in Quintana et al. 2007), whereas we used latex balls 1 µm in diameter. On the other hand, the present results are similar to our previous results in which *Macoma* buried asymmetric and relatively large (~400 µm) cladoceran eggs down to 4 cm, while *Monoporeia* and *Marenzelleria* had no effects on egg distribution (Viitasalo 2007).

Although *Monoporeia* actively stirs the sediment in search of food, it generally inhabits the top few centimeters of the sediment and does not therefore mix deeper layers. Particle mixing by *Macoma*, in turn, probably results from depth adjustments and feeding and defecation processes, whereas *Marenzelleria* may mix particles through continuous construction of new burrows (Quintana et al. 2007). The insignificant effect of *Marenzelleria* in the present study was unexpected, given the formation of burrow networks close to the sediment surface. Although the microspheres were small enough to be transported within the burrows by irrigation, the thin membrane-like mucous lining of the burrow walls may hinder transport of adjacent sediment particles, irrespective of water movement inside the burrows.

In contrast to the infauna, *Mysis* had a negligible contribution to particle mixing, although it deepened the oxidized sediment layer. The fact that even less mixing was observed in the presence of *Mysis* than in the control (the difference was not statistically significant) may result partly from the influence of the mysids as predators on meiofauna (M. Lehtiniemi et al. unpubl.), which may have decreased meiofauna activity. Also, efficient bioresuspension may have inhibited tracer incorporation into the sediment.

Biogeochemical cycling

To simulate winter conditions with a low supply of fresh organic matter, no additional food was provided to the system. Organic input, however, largely determines the rates of macrofaunal metabolism and thereby the benthic nutrient dynamics (Kristensen 2001, Karlson et al. 2007), which should be noted when interpreting the present results. Although biodeposition by *Macoma* and *Marenzelleria*, capable of both suspension and deposit feeding, could build up the sediment organic pool (Christensen et al. 2000), such an input was presumably negligible in the present study, due to the lack of suspended food. It must be noted that dead individuals, especially in the polychaete treatments, may potentially have affected the overall biogeochemistry in the cores, decreasing faunal-mediated particle mixing and pore-water irrigation.

The weekly flux measurements revealed evolution of the system with time. The sediment uptake of NO_x and the efflux of NH_4^+ were attenuated in all treatments during the incubation (Fig. 6). In addition, the pulse of high P release recorded on Day 7 probably resulted from accelerated pore-water mobilization following faunal colonization. Such non-steady-state effects are a common feature in experiments with manipulated sediments (Welsh 2003).

Higher effluxes of both PO_4^{3-} and NH_4^+ were observed at the higher animal densities, implying that sediment metabolism and the rate of mineralization were elevated in relation to the macrofaunal density. A notable difference in the exchange dynamics of inorganic P and N was observed between the semi-motile taxa that form burrows down to the reducing sediment strata (*Macoma* and *Marenzelleria*), and the motile taxa that actively stir the sediment surface (*Monoporeia* and *Mysis*).

Macoma and *Marenzelleria* increased the fluxes of PO_4^{3-} compared with the control 17- and 8-fold, respectively, and the increases in the fluxes of NH_4^+ were 3.1- (*Macoma*) and 2.1-fold (*Marenzelleria*). In contrast, the motile *Monoporeia* and *Mysis* suppressed the fluxes of inorganic P and N. For example, the total dissolved inorganic nitrogen (DIN) fluxes (NH_4^+ + NO_x) out of the sediment in the presence of the semi-motile taxa were 0.9 to 5.1 mmol m^{-2} d^{-1} (*Macoma*) and 1.7 to 3.4 mmol m^{-2} d^{-1} (*Marenzelleria*), while the corresponding values with the motile *Monoporeia* and *Mysis* were 0 to 0.8 mmol m^{-2} d^{-1} and 0 to 0.4 mmol m^{-2} d^{-1}, respectively.

The enhanced nutrient fluxes induced by the semi-motile burrowers indicate faunal-mediated escalation of organic matter mineralization (production of inorganic P and N) and transport of pore-

water solutes from reduced sediments to the overlying water (Kristensen 2001). While *Macoma* probably stimulated mineralization, the oxidized burrow walls created by *Marenzelleria* suggest enhanced pore water flushing, although this taxon is not a particularly efficient irrigator (Hietanen et al. 2007, Quintana et al. 2007).

The motile surface stirrers, in turn, deepened the oxidized layer of the sediment and increased the number of particles with oxidized surfaces in the water column (seen as increased turbidity) by vigorous bioresuspension. Such activities can enhance P retention through increased P binding to metal oxides in the sediment, a process that depends upon the redox conditions, provided that free absorption sites are available (Sundby et al. 1992). Moreover, although direct evidence regarding the pathways of N mineralization cannot be presented, the reduction in the DIN fluxes indicates increased N removal, e.g. via denitrification, which is enhanced by the supply of excreted NH_4^+ as well as the presence of oxic-anoxic interfaces (Seitzinger 1988).

These results are in agreement with previous studies in which *Monoporeia* reduced pore-water concentrations of both PO_4^{3-} and NH_4^+ (Tuominen et al. 1999) and sediment reactivity (pore-water production of PO_4^{3-} and NH_4^+) (Karlson et al. 2007). In addition, *Monoporeia* stimulated N_2 formation (Tuominen et al. 1999, Karlson et al. 2005), while *Marenzelleria* (Karlson et al. 2005, Hietanen et al. 2007) and *Macoma* (Karlson et al. 2005) had less influence on denitrification. In turn, both *Macoma* (Karlson et al. 2005) and *Marenzelleria* (Hietanen et al. 2007) increased effluxes of PO_4^{3-} and NH_4^+. However, such a clear difference between these taxa with respect to their motility traits has not previously been established.

It is worth noting that excretion by the fauna often plays a highly significant but variable role in the net fluxes triggered by bioturbation (Magni et al. 2000). For example, the weight-specific excretion rate of NH_4^+ by *Macoma* is 0.1 µmol g^{-1} wet weight h^{-1} (Henriksen et al. 1983), which equates to 12 µmol g^{-1} DW d^{-1} (assuming a dry to wet weight ratio of 0.20), while those by *Monoporeia* are between 25 to 45 µmol g^{-1} DW d^{-1} (Lehtonen 1995). Accordingly, excretion comprised 0.1 to 0.2% of the total NH_4^+ fluxes with *Macoma* and 1 to 6% with *Monoporeia*. In terms of net fluxes induced by the animals (after subtracting the control fluxes), the contribution of excretion becomes higher, especially with *Monoporeia*, which caused negative (decreased) NH_4^+ fluxes compared with the control. Nevertheless, these calculations suggest that excretion does not explain the differences between the motile and semi-motile taxa in their effects on NH_4^+ exchange.

Bioturbation and ecosystem performance in the northern Baltic Sea

Large-scale ecosystem changes (e.g. eutrophication and near-bottom hypoxia) may strongly alter biodiversity – and more importantly, functional diversity – but also vice versa, i.e. biodiversity and functional complexity modify processes contributing to ecosystem performance (Naeem 2002). However, species identity and the presence of certain functional traits are often more important than diversity as such (Ieno et al. 2006), and in terms of ecosystem recovery, the key traits may be context dependent, i.e. there is a real interplay between the biota and the environment.

Multispecies effects were not investigated in the present study, so net effects of mixed communities cannot be deduced. The results show, nevertheless, that in natural communities dominated by one species at a time, especially if the communities are subject to species shifts, the identity of the dominant species is of substantial importance. While the semi-motile burrowers provoke high nutrient release, indicating accelerated mineralization rates, the motile surface stirrers may enhance ecosystem performance through other mechanisms, e.g. by stimulating N removal. We emphasize especially the importance of epifauna, given the already marked impact of mysids at low (65 ind. m^{-2}) densities.

The significance of motility appears to be especially great in eutrophied ecosystems, particularly if the semi-motile and motile species respond differently to eutrophication-driven ecosystem changes. This is the case in the Baltic Sea, in which the macrofaunal communities have experienced notable changes (Laine et al. 1997, 2007). In the Gulf of Bothnia, *Monoporeia* densities in the 1990s that were similar to those in Mo75 were gradually replaced during the 2000s by *Marenzelleria* at densities corresponding to those in Mz30 (Norkko et al. 2007). *Monoporeia* populations have drastically declined in the Gulf of Finland, mainly due to deep-water hypoxia (Laine et al. 2007), whereas in shallow archipelago waters with higher oxygen levels *Macoma* and *Marenzelleria* have spread abundantly at the expense of *Monoporeia* (Perus & Bonsdorff 2004).

In the present state of the Baltic Sea, efficient nutrient cycling within the system generates a strong feedback that inhibits its recovery (Vahtera et al. 2007). Our study suggests that another feedback mechanism may operate as well. Species sensitive to hypoxia, i.e. *Monoporeia* and *Mysis*, increase N removal and sediment P-binding capacity, processes contributing to the system's resistance to accelerated nutrient cycling. As eutrophication progresses and deep-water oxygen conditions deteriorate, *Monoporeia* and *Mysis* are era-

dicated and replaced by the more resistant *Macoma* and *Marenzelleria*, which may further hamper the recovery of these 'positive' species.

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