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Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment

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ABSTRACT: Fauna have been found to regulate important biogeochemical properties and ecosystem functions in benthic environments. In this study, we focused on how functional biodiversity and species-specific traits of benthic macrofauna affect key ecosystem functions related to organic matter mineralization and cycling of nutrients in surface sediments. Dominant benthic invertebrates from the Baltic Sea and the Skagerrak were classified into functional groups in accordance with their behaviour, feeding and sediment reworking activities. Macrofauna species were added in different combinations to defaunated Baltic sediments in 2 parallel microcosm systems fuelled with brackish and marine water. In total, there were 12 treatments that differed in terms of functional diversity of benthic fauna. The experiments demonstrated that faunal activities directly affected benthic oxygen and nutrient fluxes, sediment reactivity and pore-water distribution under both Baltic and Skagerrak conditions. Benthic fluxes, sediment reactivity and pore-water distribution were similar in Baltic and Skagerrak treatments, in which the same functional biodiversity and species-specific traits of benthic macrofauna were observed. Although no significant effects of functional biodiversity could be detected under Baltic or Skagerrak conditions, treatments with bioturbating fauna from the Skagerrak enhanced oxygen consumption and nutrient fluxes compared to treatments with Baltic fauna and Skagerrak fauna with functional groups similar (parallel) to the Baltic fauna. Moreover, species-specific traits related to the Skagerrak fauna (e.g. the thalassinid shrimp *Calocaris macandreae*) exceeded the effects of all other faunal treatments. This suggests that species-specific traits of macrofauna may override species richness and functional biodiversity of macrofauna when regulating important ecosystem properties and functions in benthic environments.

KEY WORDS: Macrofauna · Bioturbation · Organic matter mineralization · Benthic fluxes · Pore water distribution · Sediment reactivity · Functional biodiversity · Species-specific traits

INTRODUCTION

One of the important challenges in science today is to understand and predict the coupling between biodiversity and ecosystem functions. According to Margalef (1968), ecosystems have evolved to work in a unified, cybernetic manner with feedbacks that synchronize essential ecosystem functions. Regulation of ecosystem functions and corresponding structural variables may be strongly influenced by species-specific traits rather than by species richness per se (Loreau et al. 2001, Bolam et al. 2002, Giller et al. 2004, Hooper et al. 2005). For example, terrestrial studies have shown that species-specific traits and functional biodiversity influence essential ecosystem structures and functions related to the storing and cycling of organic material (Hooper et al. 2005). Similarly, a study by Heemsbergen et al. (2004) demonstrated that functional bio-

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diversity rather than species richness regulated soil respiration and loss of leaf litter mass. Key ecosystem functions related to the cycling and overall fate of organic material in aquatic environments include mineralization in water column and benthic environments, recycling and transport of reactants across the sediment–water interface, and removal of organic and inorganic compounds by sediment burial (Giller et al. 2004).

Activities of marine benthic fauna have far-reaching effects on the oxic-anoxic boundary and the multidimensional distribution of solutes within the sediment, as well as on the transport of reactants and metabolites across the sediment–water interface (Aller 2001). For example, oxygen consumption is a key ecosystem function of benthic environments that combines abiotic and biotic pathways, including respiration by the fauna (Middelburg et al. 2005). Benthic animals not only supply oxygen to anoxic regions of the sediment, but periodic irrigation of their burrows creates repetitive redox oscillations of the adjacent sediment (Aller 1994, Hulthe et al. 1998). Field and laboratory investigations have demonstrated that repetitive successions between oxic, suboxic and anoxic conditions promote efficient mineralization of different types of organic material, and thereby directly reduce the accumulation and storage of organic material in the sedimentary record (Aller 1994, 1998, Hulthe et al. 1998). Fauna may therefore drastically alter the rates and pathways of organic matter mineralization, as well as overall diagenetic properties (e.g. sediment reactivity and capacity for solute mobilization) of the sedimentary environment, from those that would occur in the absence of fauna. However, different species have different activity patterns, and the importance of faunal activities for system regulation is frequently associated with individual species traits.

Functional diversity is a powerful and important component of biodiversity in ecological studies (Petchey & Gaston 2006). In the present study we used a functional group concept that emerged from studies on the behaviour, feeding and sediment reworking of benthic fauna (Aller 1977, Pearson & Rosenberg 1987, Pearson 2001, François et al. 2002). Further, we defined functional biodiversity as the functional group richness of benthic fauna. There are comparably few previous investigations of the importance of functional biodiversity and species-specific traits of macrofauna for organic matter mineralization and transport of reactants in surface marine sediments; those existing studies have examined e.g. how species richness or functional biodiversity affected production of ammonium in surface sediments and benthic oxygen and nutrient fluxes (Emmerson et al. 2001, Raffaelli et al. 2003, Waldbusser et al. 2004, Mermillod-Blondin et al. 2005, Ieno et al. 2006), and the importance of species-specific traits of fauna was exemplified in 1-, 2- or 3-species combinations (Mermillod-Blondin et al. 2004, Karlson et al. 2005, Waldbusser & Marinelli 2006).

In the present study, we further investigated the importance of functional biodiversity and species-specific traits of benthic macrofauna for ecosystem functions related to organic matter mineralization in 2 benthic ecosystems (Baltic and Skagerrak). Based on patterns of behaviour, feeding and sediment reworking of benthic fauna, there are ~25 functional groups in the Skagerrak (north-east North Sea), but only 5 in sediments of the Baltic Sea (Bonsdorff & Pearson 1999). We hypothesized that species functional biodiversity is important for the rates and extent of organic matter mineralization in marine sediments, and that Skagerrak assemblages are more important for ecosystem functions than are Baltic assemblages owing to the higher functional biodiversity and a larger number of species-specific traits present in Skagerrak sediments.

MATERIALS AND METHODS

We measured benthic oxygen and nutrient fluxes, sediment reactivity and pore-water concentrations in 12 different treatments using defaunated Baltic sediments incubated in the presence of various functional group combinations of Baltic and Skagerrak macrofauna (Bonsdorff & Pearson 1999). Sediment and macrofauna were sampled and adapted to experimental conditions (dark, 10°C) similar to those of the Baltic Sea and the Skagerrak. Macrofauna was added to a set of 48 experimental microcosms that were allowed to acclimatize for 26 or 27 d. Oxygen and nutrient fluxes were then measured. Following termination of benthic flux incubations, sediment reactivity and pore-water concentrations were determined. A general overview of sampling and experimental procedures is provided in Table 1.

Sampling of sediment and macrofauna. In May 2003, surface (0 to 15 cm) sediment from the Baltic (Skagsfjärden, outer Stockholm archipelago; 59°25′00″ N, 18°46′28″ E) was collected by grab sampling (depth = 36 m). The top 15 cm of the sediment was separated into a surface (0 to 3 cm) and a deeper (5 to 15 cm) sediment fraction. The 2 fractions were sieved separately through a 1 mm mesh to remove larger debris and select macrofauna to be used in the experiments. In the laboratory, the sieved sediment was homogenized and transferred to a large plastic container (0.7 × 0.8 m; height 0.5 m) in which 3 cm of the surface sediment fraction was placed on top of a layer of ~15 cm sediment from the deeper fraction. The 2 sediment

Table 1. General overview of fauna and sediment sampling and experimental procedures. B: Baltic conditions; S: Skagerrak conditions

Procedure	Day
Collection of sediment and macrofauna from Skagsfjärd (Baltic Sea)	−62
Collection of *Marenzelleria neglecta* from Himmerfjärd (Baltic Sea)	−47
Collection of macrofauna from Gullmarsfjord (Skagerrak)	−38
Microcosms (cores) inserted into sediment and connected to water flow	−5
Start of experiment: introduction of animals to cores	0
Benthic oxygen and nutrient flux incubation (B)	26
Benthic oxygen and nutrient flux incubation (S)	27
Macrofauna, pore water (start of closed sediment incubations) (B)	28 & 29
Macrofauna, pore water (start of closed sediment incubations) (S)	30 & 31
Termination of closed sediment incubations (B)	32 & 33
Termination of closed sediment incubations (S)	34 & 35

layers were left to acclimatize for about 7 wk with an on-line continuous laminar flow of oxygenated deep water above the sediment surface. Seawater (salinity 32) was supplied from the Gullmarsfjord for the Skagerrak treatments. For the Baltic treatments, seawater of appropriate salinity (8) was obtained by diluting deep water from the Gullmarsfjord with double-distilled water.

We collected dominant benthic macrofaunal species both from the Baltic Sea (*Halicryptus spinulosus, Macoma balthica, Marenzelleria neglecta*) and the Skagerrak (*Glycera alba, Abra nitida, Echinocardium cordatum, Amphiura chiajei*, *Amphiura filiformis* and *Calocaris macandreae*). The Skagerrak species are true marine species not found in the Baltic (salinity < 12). *M. neglecta, M. balthica* and *H. spinulosus* are common in the Baltic, but rarely found in the Skagerrak. *H. spinulosus* and *M. balthica* were collected from the Skagsfjärd (Baltic Sea, 30 to 50 m depth, 59°25′N, 18°46′E), while *M. neglecta* was sampled from the Himmerfjärd (Baltic Sea, 1 to 2 m depth, 59°2′30″N, 17°41′45″E). Benthic macrofauna from the Skagerrak was collected from the Gullmarsfjord (Skagerrak, 30 to 90 m, 58°16″N, 11°28″E). Before starting the experiments (Table 1), all macrofaunal species were kept at 10°C under conditions (dark, particle grain size and organic content) similar to those of the Baltic sediment sampling site.

Combinations of fauna and experimental treatments. We used a replacement design for macrofauna, with replicated (n = 4) predefined levels and combinations of functional biodiversity and species-specific traits of macrofauna. Details of species behaviour and species treatment combinations are provided in Tables 2 & 3. Based on their similar functional traits we placed *Halicryptus spinulosus* and *Glycera alba* in one group and *Macoma balthica* and *Abra nitida* in another. For the Skagerrak treatments, 2-species combinations of *Amphiura chiajei* and *Echincardium cordatum,* and of *Amphiura filiformis* and *Calocaris macandreae* were used owing to their co-occurrence, dominance and overall importance in natural communities. Functional diversity was assessed through functional group richness. For each treatment, the biomass was normalized to 2 g wet weight (WW) core^{-1}, corresponding to about 250 g WW m^{-2} (Table 3). Organic matter was not added to the sediment during the experiment (~3 mo duration), but mineralization was assumed to proceed via the utilization of rather refractory organic material. For refractory material, previous studies have demonstrated a significant coupling between redox conditions (aerobic, anaerobic and oscillating conditions) of surface sediments and overall extent of organic matter degradation (Aller 1994, Hulthe et al. 1998).

Benthic flux incubations. After sediment acclimatization, plexiglass cores (inner diameter 10 cm) were carefully inserted into the sediment of the container

Table 2. Main functions of species (with codes) used in experiments. B: Baltic; S: Skagerrak

Species	Code	Function	Area	Source
Halicryptus spinolosus	Hs	Burrowing, predator, gallery builder	B	Powilleit et al. (1994)
Glycera alba	Ga	Burrowing, predator, gallery builder	S	Ockelmann & Vahl (1970)
Macoma balthica	Mb	Burrowing, surface deposit feeder, biodiffuser	B	Karlson et al. (2005)
Abra nitida	An	Burrowing, surface deposit feeder, biodiffuser	S	Maire et al. (2006)
Marenzelleria neglecta	Mn	Deep burrowing, sub-surface deposit feeder	B	Karlson et al. (2005)
Amphiura chiajei	Ac	Burrowing, surface deposit feeder	S	Buchanan (1967)
Amphiura filiformis	Af	Burrowing, suspension & surface deposit feeder	S	Solan & Kennedy (2002)
Echinocardium cordatum	Ec	Burrowing, sub-surface deposit feeder, biodiffuser	S	Lohrer et al. (2005)
Calocaris macandreae	Cm	Deep burrowing, sub-surface deposit feeder	S	Nash et al. (1984)

Table 3. Composition of benthic macrofauna in 12 treatments (with 4 replicates each) which correspond to different functional biodiversity, defined as functional group richness (FGR). Abundance (ABU) varied among treatments but biomass (BIO) was constant. CB: control (no macrofauna) Baltic; CS: control (no macrofauna) Skagerrak. Species codes as in Table 2

Treatment (n = 4)	Abundance (biomass g WW)						FGR	ABU	BIO
Baltic (salinity 8)	Hs	Mb	Mn						
CB	– (–)	– (–)	– (–)				–	–	–
Hs	4 (2.0)						1	4	2.0
Mb		4 (2.0)					1	4	2.0
Mn			15 (2.0)				1	15	2.0
HsMb	3 (1.0)	3 (1.0)					2	6	2.0
HsMbMn	2 (0.7)	2 (0.7)	5 (0.6)				3	6	2.0
Skagerrak (salinity 32)	Ga	An	Ec	Ac	Cm	Af			
CS	– (–)	– (–)	– (–)	– (–)	– (–)	– (–)	–	–	–
GaAn	3 (1.0)	3 (1.0)					2	6	2.0
EcAc			1 (1.0)	3 (1.0)			2	4	2.0
CmAf					1 (1.8 ± 0.4)[a]	2 (0.5)	2	3	2.3 ± 0.4[a]
GaAnAc	2 (0.7)	2 (0.7)		2 (0.6)			3	6	2.0
GaAnEcAcCmAf	1 (0.1)	1 (0.2)	1 (0.5)	1 (0.1)	1 (1.4 ± 0.2)[a]	1 (0.1)	6	6	2.4 ± 0.2[a]

[a]Variances in biomass owing to different sizes of *Calocaris macandreae*

and sealed with a bottom plug. Each core was randomly dispersed and individually connected to an enclosed (1.5 m^3) flow-through system that supplied aerated seawater of salinity 8 (Baltic cores) or 32 (Skagerrak cores). After 5 d, macrofaunal specimens were manually added to randomly dispersed replicate cores (n = 4) of each treatment. Because faunal additions were normalized to biomass, abundances of fauna differed among treatments. However, the biomass in treatments that included *Calocaris macandreae* was slightly higher and more variable than that in the other treatments (Table 3) owing to difficulties in finding similar small-sized animals.

After we had added the animals, the sediment cores were acclimatized for an additional month. At the start of the benthic flux incubations (after 26 or 27 d), the flow-through system was turned off, the overlying water sampled, and the cores sealed with air-tight Plexiglas lids for benthic flux incubations. A Teflon-coated magnetic stirring bar was attached to the top of the lid for mixing the overlying water (40 rpm) during the incubations. Water samples for oxygen consumption (n = 2) and solutes NH_4^+, $\sum NO_3^-$ = (NO_2^- + NO_3^-); hereafter referred to as NO_3^-, HPO_4^{2-} and $Si(OH)_4$ flux rates (n = 3) were removed from the overlying water by glass (oxygen) and propylene (solutes) syringes. Samples were removed before sealing the core tubes and at the end of the ~12 h incubation period. Benthic flux rates were calculated assuming a linear change of solute concentrations in the overlying water with time of incubation. All samples for solute analyses were filtered through 0.45 µm cellulose acetate filters, immediately frozen at –20°C and stored until analysis.

Pore water and sediment. Closed sediment incubations (Martens & Berner 1974, Hulth et al. 1999) for rates of solute (NH_4^+, HPO_4^{2-}) production following macrofaunal manipulations were performed at the end of the benthic flux incubations (Table 1). After siphoning off the overlying water, the 0 to 1, 3 to 7, and 8 to 12 cm sediment layers were removed and sieved (1 mm) to remove the macrofauna from the sediment before transferal to 60 ml centrifuge tubes (jars). Eight jars from each treatment (2 from each core and depth) were sealed without headspace and centrifuged directly (3400 × *g*, 10 min). Two additional jars from each core and depth were transferred to air-tight plastic bags and incubated under anaerobic conditions at 10°C in a bucket of anoxic mud for ~100 h. At the termination of incubation, pore water was separated from the sediment by centrifugation as above. The obtained pore water was filtered on-line through prepacked 0.45 µm cellulose acetate filters. Pore-water samples were immediately frozen at –20°C and stored until analysis. Solute production rates from the solid sediment were calculated from the initial linear change in pore-water concentrations with incubation time. To account for reversible adsorption equilibrium with sediment particles, observed rates of ammonium mobilization were multiplied by the factor 1 + *K*, where *K* is the linear adsorption coefficient (Mackin & Aller 1984). Based on previous experiments in similar sediments (S. Hulth et al. unpubl. data), *K* was assigned a value of 1.

Porosity (φ) was calculated from the weight of water lost after drying 5 ml of sediment at 70°C until constant weight. The sediment porosity was 0.8 in the surface (0 to 1 cm) and 0.7 deeper down (>3 cm). Sediment for solid phase C and N (0 to 1, 3 to 7 and 8 to 12 cm) was centrifuged (3400 × *g*, 3 min), briefly rinsed in distilled water to remove salt crystals, again centrifuged (3400 × *g*, 3 min), and immediately frozen at –80°C. Sediment samples were freeze-dried, crushed and stored at –20°C until analysis.

Chemical analysis. Oxygen (O_2) concentrations during the flux incubations were determined by Winkler titrations. The nutrients NH_4^+, NO_3^-, HPO_4^{2-} and $Si(OH)_4$ in the overlying water and the sediment pore water were analyzed by an automatic analyzer (TRAACS 800, Bran & Luebbe) using standard colorimetric methods (Strickland & Parsons 1972). Solid-phase total carbon (TC), organic carbon (TOC) and nitrogen (TON) were determined on an elemental analyzer (NA 1500 NC, Fisons Instruments) according to Hedges & Stern (1984).

Statistical analysis. Statistical relationships were defined using ANOVA procedures, followed by planned comparisons and exploratory post hoc analyses where appropriate. Prior to analysis, we used graphical exploratory techniques to check data for assumptions concerning normal distribution (probability plots) and homogeneity of variances (box plots) and, where appropriate, data transformations were applied to reduce effects of single outliers and skewed data (Quinn & Keough 2002). The planned comparisons were used to analyze (1) differences between Baltic and Skagerrak systems with 'no macrofauna' treatments (H_0: CB ≠ CS, where CB is the control [no macrofauna] Baltic and CS is the control [no macrofauna] Skagerrak), parallel functional groups (H_0: HsMb ≠ GaAn), and faunal treatments (H_0: Hs + Mb + Mn + HsMb + HsMbMn = GaAn + EcAc + CmAf + GaAnEc + GaAnEcAcCmAf) (see Table 2 for species codes); (2) the 'no macrofauna' treatments compared with all faunal treatments [H_0: (CB + CS)/2 = (Hs + Mb + Mn + HsMb + HsMbMn + GaAn + EcAc + CmAf + GaAnEc + GaAnEcAcCmAf)/10]; and (3) Baltic functional biodiversity [H_0: (Hs + Mb + Mn)/3 = HsMbMn] and Skagerrak functional biodiversity [H_0: (GaAn + EcAc + CmAf)/3 = GaAnEcAcCmAf], where 3 separate treatments were compared with the same functional groups combined. The 2-tailed *t*-test used in the planned pair-wise comparisons adjusted the significance levels if variances were unequal in the compared groups, but significance levels were not corrected for multiple testing.

Effects from treatments on pore water and solute production rates were tested using partly nested, split-plot, repeated measures (RM) ANOVA with the main factor 'Treatment' nested within cores and the repeated factor 'Depth' within each core. Significance levels for the split-plot ANOVA were made more conservative using adjusted degrees of freedom for the *F*-tests, calculated from the Greenhouse-Geisser estimate (ε) based on the index of sphericity (Quinn & Keough 2002). If the interaction was significant, the main factors were only explored further if they showed a strong main effect in the interaction plot. If significance was detected among treatments in the RM-ANOVAs, Tukey's honestly significant difference (HSD) post hoc test grouped treatments into homogenous groups. Homogenous groups were also used for comparing the controls and parallel treatments in the 2 systems for the split-plot design. The ANOVAs, planned comparisons and Tukey's HSD post hoc tests were all performed using the statistical software package SPSS 13.0.

RESULTS

Sediment and macrofauna

The Baltic sediment used in the experiments was silty sand; mean (±SD) TON and TOC of surface (0 to 3 cm) sediment was 0.42 ± 0.09% dry weight (DW) and 3.5 ± 0.47% DW respectively. Deeper down (>3 cm) in the sediment, mean TON and TOC were 0.60 ± 0.06% DW and 4.62 ± 0.72% DW respectively.

During sectioning of the cores, 50 to 100% of the animals were recaptured in the different treatments (Fig. 1). The mean depth for the recaptured species ranged from 2 to 10 cm, with several species found at depths ≥10 cm. In the Baltic treatments, biogenic structures produced by *Halicryptus spinulosus* extended into the oxidized zone of the sediment immediately adjacent to (within 2 to 5 mm of) the burrows down to depths of ~12 cm. A light-brownish zone surrounded the shell of *Macoma balthica* down to ~3 cm into the sediment. Defecation and burrowing activities of *Marenzelleria neglecta* were recorded as fecal pellets on the sediment surface and J-shaped burrows down to 15 cm. In the Skagerrak treatments, burrow structures produced by *Glycera alba* were found down to ~10 cm depth, and sediment immediately adjacent to (within 2 to 5 mm of) the burrows appeared oxidized. *Abra nitida* extended into the oxidized zone above and around the bivalves down to a depth of ~3 cm in the sediment. *Echinocardium cordatum* extended into the oxidized zone down to ~5 cm owing to its bulldozing activity. Activities by *Amphiura chiajei* and *Amphiura filiformis* oxidized the sediment in the top 5 to 8 cm above and around the central disks of the ophiurids. Burrowing and digging activity by *Calocaris macandreae* produced tunnels in the sediment that extended from the surface to the bottom of the cores (~16 cm).

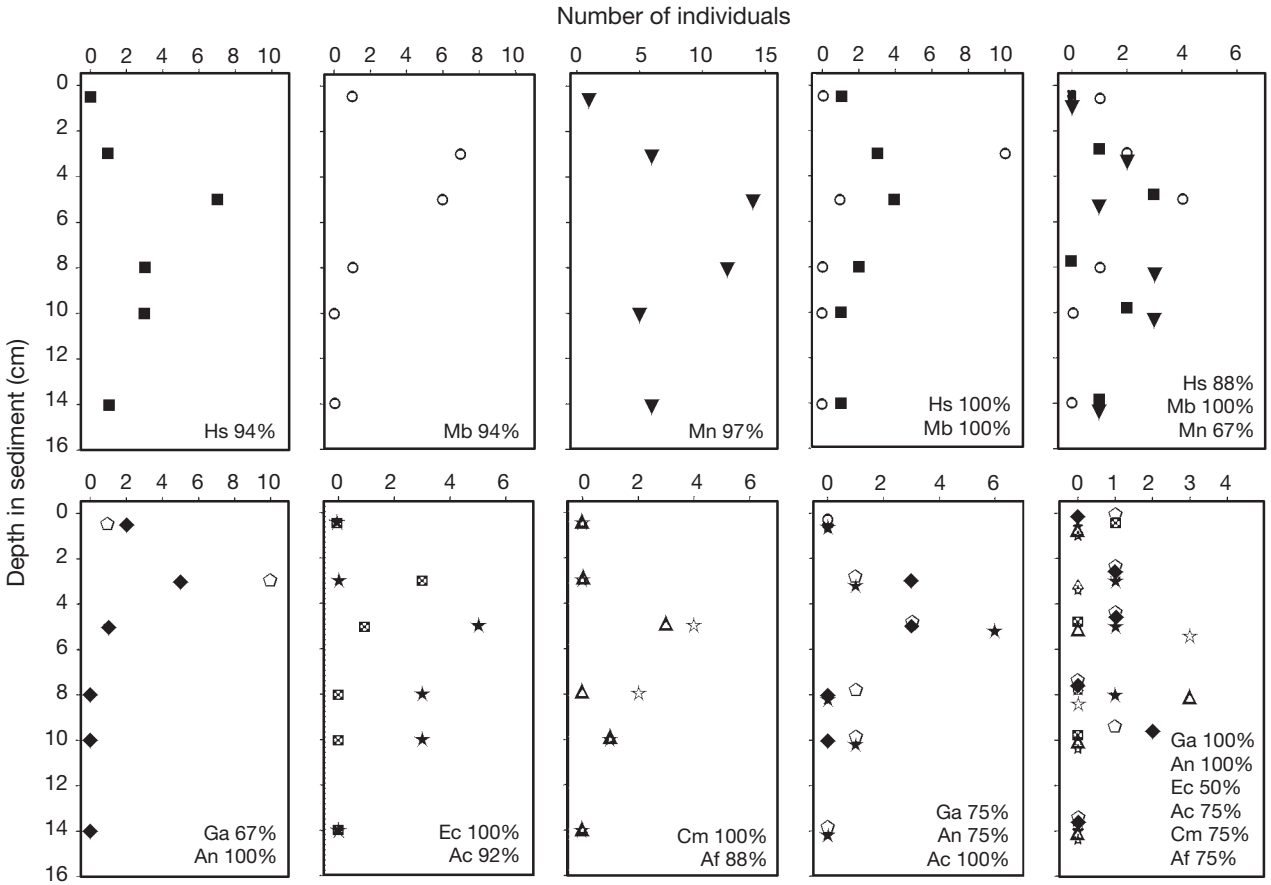

Fig. 1. Vertical distribution of fauna in the sediment and % of each species recaptured in different treatments. ■ = Hs: *Halicryptus spinulosus*; ○ = Mb: *Macoma balthica*; ▼ = Mn: *Marenzelleria neglecta*; ◆ = Ga: *Glycera alba*; ⬠ = An: *Abra nitida*; ⊠ = Ec: *Echinocardium cordatum*; ★ = Ac: *Amphiura chiajei*; △ = Cm: *Calocaris macandreae*; ☆ = Af: *Amphiura filiformis*

Benthic O_2 and nutrient fluxes

There was no significant difference in O_2 and nutrient fluxes between the 2 controls (CB and CS for the Baltic and Skagerrak respectively). $Si(OH)_4$ (silicate) fluxes were the only flux to vary significantly (t = 2.2, p = 0.03) between the parallel treatments GaAn and HsMb (Fig. 2, Table 4a). O_2 and nutrient (except NO_3^-) fluxes of the faunal treatments were significantly lower under Baltic compared with Skagerrak conditions (O_2: t = 8.5, p < 0.001; NH_4^+: t = 2.6, p = 0.02; NO_3^-: t = 0.8, p = 0.4; HPO_4^{2-}: t = 2.7, p = 0.02; $Si[OH]_4$: t = 8.6, p < 0.001; Fig. 2, Table 4a). O_2 and nutrient fluxes in the macrofaunal treatments were significantly higher compared with the control cores with no macrofauna (O_2: t = 6.2, p < 0.001; NH_4^+: t = 4.8, p < 0.001; NO_3^-: t = 2.8, p = 0.02; HPO_4^{2-}: t = 4.3, p < 0.001; $Si[OH]_4$: t = 3.15, p = 0.003; Fig. 2, Table 4a). Under Baltic conditions there was no significant difference in O_2 and nutrient fluxes between single species treatments and treatments with species from 3 functional groups (*Halicryptus spinulosus*, *Macoma balthica* and *Marenzelleria neglecta*). Similarly, under Skagerrak conditions, there was no significant difference in O_2 and nutrient fluxes between treatments with 2 and treatments with 6 functional groups (defined in Table 3).

Rates of O_2 and nutrient (except NO_3^-) fluxes were significantly different (1-way ANOVA) for all 12 faunal treatments (Fig. 2, Table 4b). O_2 consumption in the 2- and 6-species treatments with *Calocaris macandreae* were significantly higher than in all other treatments. Further, NH_4^+ and $Si(OH)_4$ fluxes in these treatments were significantly higher than in the controls (Fig. 2, Table 4c).

Sediment reactivity and pore water distribution

Overall, rates of ammonium (NH_4^+) and phosphate (HPO_4^{2-}) production during the closed sediment incubations differed between sediment depths, and between sediments exposed to faunal activities and sediments from control cores without fauna (Figs. 3 & 4, Table 5a). There was a significant statistical interaction

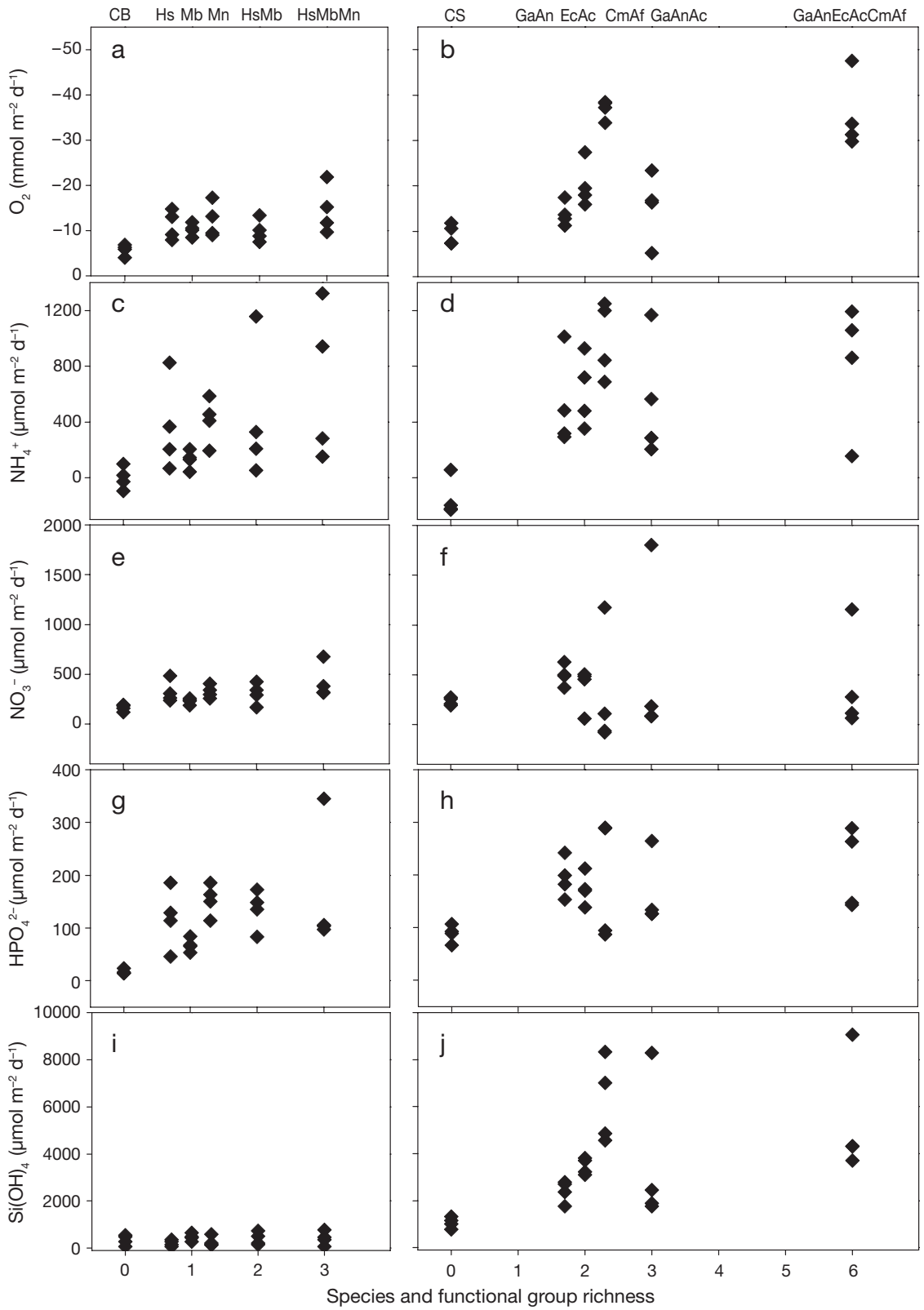

Fig. 2. Functional biodiversity and treatment effects on oxygen and nutrient fluxes during laboratory benthic sediment-water incubations. Benthic fluxes of (a,b) O_2, (c,d) NH_4^+, (e,f) NO_3^-, (g,h) HPO_4^{2-} and (i,j) $Si(OH)_4$ from the sediment and fauna to overlying water during incubation with airtight lid and water mixing. CB: control (no macrofauna) Baltic; CS: control (no macrofauna) Skagerrak. Species codes as in Table 2

Table 4. Summary of (a) planned pair-wise tests between selected treatment combinations and (b) tests of all 12 treatments (1-way ANOVA); (c) mean fluxes of O_2 (mmol m^{-2} d^{-1}) and nutrients (µmol m^{-2} d^{-1}) and results from Tukey's HSD tests. Species codes as in Table 2; CB: no control (Baltic); CS: no control (Skagerrak). ***p < 0.001; **p < 0.01; *p < 0.05; ns: not significant

Dependent variable	O_2	NH_4^+	NO_3^-	HPO_4^{2-}	$Si(OH)_4$
(a) Planned pair-wise test (H_0, *t*-test)					
CB ≠ CS	0.255	0.544	0.782	0.112	0.436
HsMb ≠ GaAn	0.222	0.711	0.444	0.187	*
Baltic fauna = Skagerrak fauna	***	*	0.434	*	***
Controls = all faunal treatments	***	***	*	***	***
Baltic functional biodiversity effect	0.186	0.273	0.229	0.476	0.893
Skagerrak functional biodiversity effect	0.057	0.597	0.951	0.499	0.379
(b) Test of all 12 treatments (ANOVA)	***	**	ns	**	***
(c) Mean fluxes and Tukey's HSD test of all 12 treatments					
CB (no macrofauna, Baltic)	-5.7^{a}	-1.6^{ab}	163	17^{a}	345^{a}
CS (no macrofauna, Skagerrak)	-9.3^{a}	-147^{a}	231	89^{ab}	1063^{abc}
Hs	-11.2^{ab}	366^{abc}	322	118^{ab}	210^{a}
Mb	-10.2^{ab}	129^{ab}	230	68^{ab}	467^{a}
Mn	-12.2^{ab}	410^{abc}	323	153^{ab}	269^{a}
HsMb	-9.9^{ab}	436^{abc}	305	135^{ab}	399^{a}
GaAn	-13.8^{ab}	525^{abc}	495	194^{b}	2404^{abcd}
HsMbMn	-14.6^{ab}	674^{abc}	422	163^{ab}	416^{a}
GaAnAc	-15.4^{ab}	555^{abc}	538	163^{ab}	3593^{cde}
EcAc	-20.2^{b}	619^{abc}	374	173^{b}	3458^{bcde}
CmAf	-36.9^{c}	993^{c}	285	190^{b}	6192^{e}
GaAnEcAcCmAf	-35.5^{c}	817^{bc}	403	211^{b}	5345^{de}

$^{a, b, c, d, e}$Homogeneous subsets of treatments

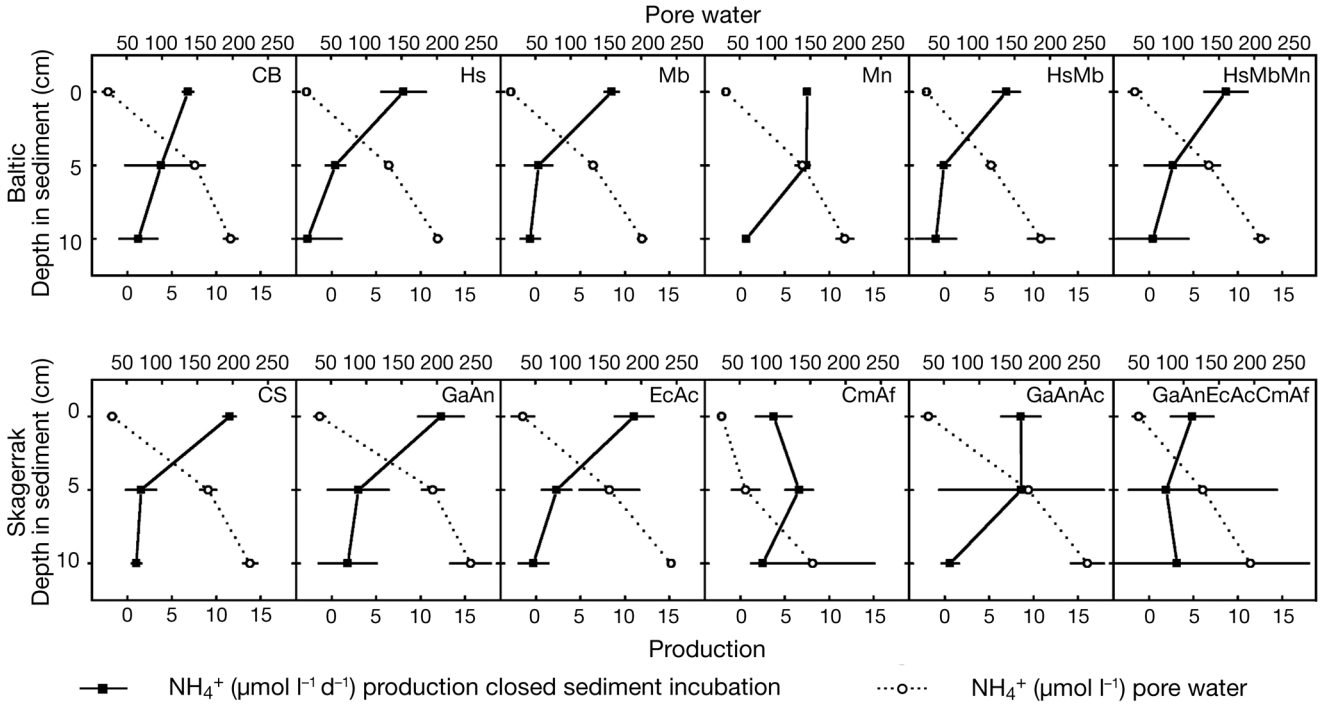

Fig. 3. NH_4^+ pore water concentrations (--O--), and production and consumption rates of NH_4^+ during closed anoxic incubations (—■—) in sediment from Baltic and Skagerrak faunal treatment cores at 3 depth ranges (0–1, 3–7, 8–12 cm). CB: control (no macrofauna) Baltic; CS: control (no macrofauna) Skagerrak. Species codes as in Table 2

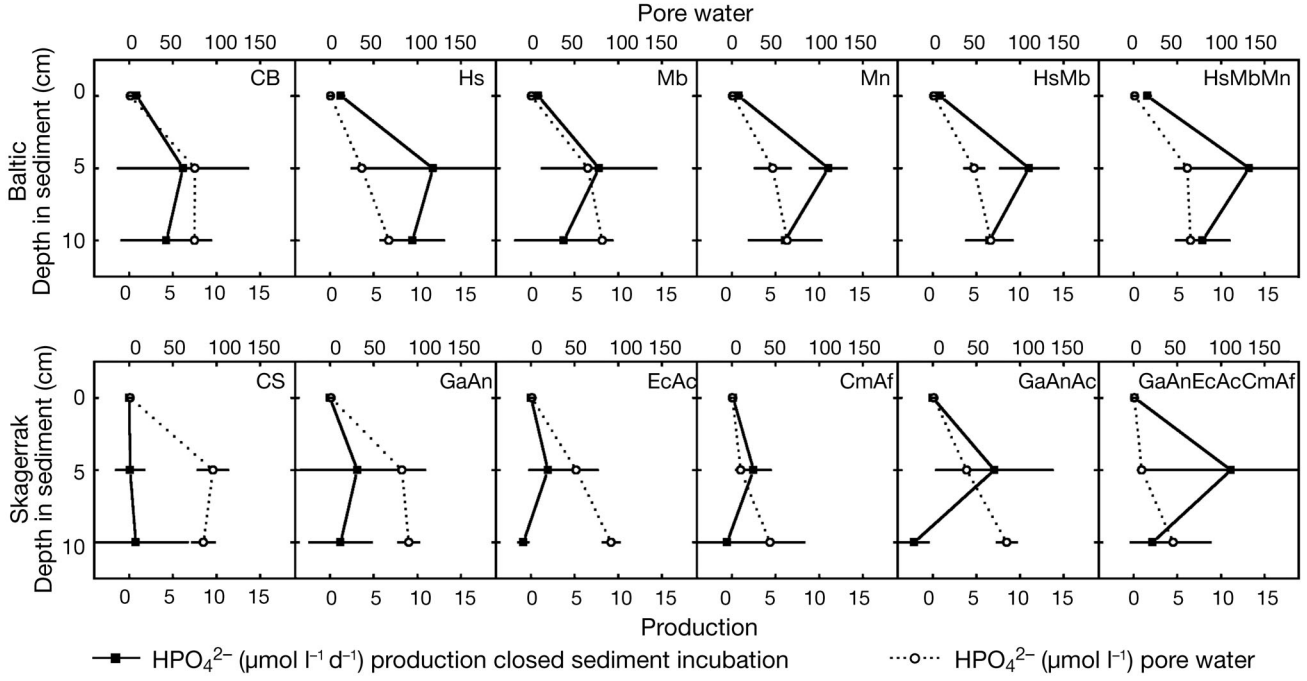

Fig. 4. HPO_4^{2-} pore-water concentrations (···O···), and production and consumption rates of HPO_4^{2-} during closed anoxic incubations (—■—) in sediment from Baltic and Skagerrak faunal treatment cores at 3 depth ranges (0–1, 3–7, 8–12 cm). CB: control (no macrofauna) Baltic; CS: control (no macrofauna) Skagerrak. Species codes as in Table 2

in NH_4^+ production between treatment and sediment depth. This reflected a reduced production (or increased consumption) in the surface sediment, and an increased production at 5 and 10 cm in the CmAf treatment compared with the other treatments (Fig. 3). The production of HPO_4^{2-} differed significantly among treatments. Mean rates of HPO_4^{2-} production were higher under Baltic conditions with fauna than in the Skagerrak control and faunal treatments (Fig. 4). There were significantly different production rates of NH_4^+, NO_3^- and HPO_4^{2-} for the various sediment depths under both Baltic and Skagerrak conditions (Table 5a). NH_4^+ production and NO_3^- consumption both decreased with increasing sediment depth. Overall, NO_3^-concentrations in the pore water were low throughout the anaerobic incubations. After a 4 d incubation, NO_3^- could only be detected in pore water from 6 jars. For all other jars, concentrations were below

Table 5. Summary of partly nested split-plot ANOVAs on (a) solute production and consumption rates and (b) pore-water concentrations in sediments. F_{crit}: calculated critical *F*-ratio for $\alpha = 0.05$, critical *F* values in parentheses; p-values after Greenhouse-Geisser adjustment, ***p < 0.001; **p < 0.01; *p < 0.05. ns: not significant

Dependent variable	df	$F_{crit(0.05)}$	NH_4^+		NO_3^-		HPO_4^{2-}		$Si(OH)_4$	
Source			MS	*F*	MS	*F*	MS	*F*	MS	*F*
(a) Solute production and consumption rate										
Treatment	11	(2.07)	21	2.1*	0.01	1.1 ns	90	4.3***	60	1.0 ns
Cores (Treatment)	36		10		0.009		21		59	
Depth	2	(3.12)	724	83***	0.24	22***	546	36***	68	2.4 ns
Treatment × Depth	22	(1.69)	24	2.7**	0.01	0.9 ns	23	1.4 ns	48	1.7*
Core(Treatment) × Depth	72		9		0.011		17		38	
Total	144									
(b) Pore water concentration										
Treatment	11	(2.07)	5530	3.6**	0.244	2.08*	2165	10.5***	29742	9.9***
Core(Treatment)	36		1554		0.117		206		3000	
Depth	2	(3.12)	399996	627***	4.95	29***	63591	306***	1474	1.9 ns
Treatment × Depth	22	(1.69)	1331	2.1*	0.23	1.3 ns	838	4.0***	480	0.6 ns
Core(Treatment) × Depth	72		638		0.17		208		788	
Total	144									

detection. HPO_4^{2-} production rates were significantly higher at 5 cm than at 1 and 10 cm depth (Fig. 4).

There were significant statistical interactions for pore water concentrations of NH_4^+ and HPO_4^{2-} among treatments and depths, mainly caused by low concentrations at 5 cm in treatments including *Calocaris macandreae* compared with the control (Figs. 3 & 4, Table 5b). Also, in the CmAf treatment, mean concentrations of both NH_4^+ and HPO_4^{2-} were lower than in all other treatments. NH_4^+ and HPO_4^{2-} in the pore water increased significantly with sediment depth, whereas NO_3^- decreased significantly with depth in all treatments (Figs. 3 & 4). Mean pore water concentrations of NH_4^+, NO_3^-, HPO_4^{2-} and $Si(OH)_4$ also differed significantly among treatments (Table 5b). Further, pore-water $Si(OH)_4$ was significantly lower in all Skagerrak treatments than in all Baltic treatments.

DISCUSSION

In this study, we experimentally investigated how functional biodiversity and species-specific traits of macrofauna influence important properties and functions of benthic environments directly associated with organic matter mineralization. Dominant macrofaunal species from the Baltic Sea and the Skagerrak were studied in sieved surface sediment of the same origin. The sediment microcosms were manipulated by adding different combinations of macrofaunal species under salinity conditions resembling those of the Baltic Sea and the Skagerrak respectively. Dominant marine fauna (e.g. crustaceans and echinoderms) from the Skagerrak increased O_2 consumption and nutrient fluxes, sediment reactivity and sediment pore-water concentrations owing to the individual traits of the specific species that comprised the fauna rather than to enhanced functional diversity.

Functional biodiversity and ecosystem functions

We statistically evaluated the effect of functional diversity (i.e. increased richness of species from different functional groups) on O_2 and nutrient fluxes. The fact that no significant difference between single-species or 2-species and multi-species treatments was observed suggests that all species utilized in this study were potentially important for O_2 and nutrient fluxes.

Under Baltic conditions, rates of O_2 consumption ranged from ~5 mmol m^{-2} d^{-1} in the control to 10 to 20 mmol m^{-2} d^{-1} in the faunal treatments. This difference suggests that faunal treatments that had the same species represented at different levels of functional biodiversity could be statistically evaluated without including the control. O_2 and nutrient fluxes in the 3-species treatments with *Halicryptus spinulosus*, *Macoma balthica* and *Marenzelleria neglecta* were not significantly different from the 3 treatments with 1 functional group in each. Effects of faunal species diversity on nutrient regeneration have been observed; however, species identity and density effects often unpin the observed response (Ieno et al. 2006). Investigations into the importance of faunal biodiversity for ecosystem functions have primarily focused on species loss in terrestrial, freshwater or marine systems (Raffaelli 2006). The present study revealed that invasive species (e.g. *M. neglecta*) may affect important functions in the Baltic ecosystem, not only by increasing the functional biodiversity (as a result of habitat modifications by this deep-burrowing, deposit-feeding polychaete), but also because they may occupy new niches and increase overall abundance, biomass and diversity.

Rates of O_2 consumption under Skagerrak conditions ranged between ~10 mmol m^{-2} d^{-1} in the control cores and 35 to 50 mmol m^{-2} d^{-1} in the 2 faunal treatments with *Calocaris macandreae*. In treatments with *C. macandreae*, O_2, NH_4^+ and $Si(OH)_4$ fluxes were also significantly higher than in the control cores (Table 4). Furthermore, O_2 and $Si(OH)_4$ fluxes were significantly higher in the treatments with *C. macandreae* than in all Baltic fauna treatments and to the GaAn treatment. Under Skagerrak conditions, a high functional diversity almost showed enhanced O_2 consumption, but owing to the high variation in function among the three 2-species treatments, means were not significantly different when adjusted for unequal variances ($p = 0.057$). Thus, the high functional biodiversity represented by a surface deposit-feeding bivalve (*Abra nitida*), a gallery-building polychaete (*Glycera alba*), 2 suspension- and deposit-feeding brittle stars (*Amphiura filiformis* and *Amphiura chiajei*), a bulldozing sea urchin (*Echinocardium cordatum*) and a deep tunnel-building crustacean (*Calocaris macandreae*) significantly affected key ecosystem functions compared with fauna combinations equivalent (parallel) to assemblages in the Baltic Sea. In addition, O_2, NH_4^+, HPO_4^{2-} and $Si(OH)_4$ fluxes in the faunal treatments under Skagerrak conditions were higher than in the faunal treatments under Baltic conditions.

In relation to the obvious ecological and biogeochemical relevance, there are comparably few other studies on the importance of functional biodiversity and functional traits of macrofauna for O_2 consumption and benthic solute fluxes. Previous studies suggested that effects from functional biodiversity on ecosystem processes are not additive. Rather, as a result of interspecies interactions, benthic O_2 and nutrient solute

fluxes were reported to be lower for multiple-species than for additive single-species treatments (Waldbusser et al. 2004, Mermillod-Blondin et al. 2005, Ieno et al. 2006). These experimental studies used a subset of complementary species from marine benthic ecosystems similar to the Skagerrak fauna examined in the present study.

Functional traits and ecosystem functions

Benthic O_2 and nutrient fluxes, pore water concentrations (excluding $Si[OH]_4$) and rates of solute mobilization (sediment reactivity) were similar in the Baltic and Skagerrak control cores without macrofauna (Figs. 2 to 4, Tables 4 & 5). *Macoma balthica* and *Abra nitida* are predominantly similar-sized, surface deposit-feeding bivalves, while the worm-like *Halicryptus spinulosus* and the polychaete *Glycera alba* both construct galleries in the sediment. Measured O_2 and nutrient fluxes, pore-water concentrations (excluding $Si[OH]_4$) and sediment reactivity were similar in these parallel treatments with both Baltic and Skagerrak fauna. Because both parallel control cores and the above-described parallel faunal treatments each resulted in similar benthic fluxes, the functional group concept seemed to apply to these faunal combinations under the experimental conditions used in the present study.

O_2, NH_4^+, HPO_4^{2-} and $Si(OH)_4$ fluxes differed significantly among treatments (Table 4b). However, post hoc comparisons showed that the majority of faunal treatments did not differ from the control cores. In contrast, measured fluxes (mean values) in the 2 treatments with *Calocaris macandreae* under Skagerrak conditions were significantly higher (with the exception of NO_3^-) than in all other treatments. Waslenchuk et al. (1983) showed that, owing to pronounced reworking and irrigation activity, *C. macandreae* can regulate mineralization and solute flux rates. Therefore, treatments including particularly active bioturbators such as *C. macandreae* could exceed fluxes and overall mineralization compared to other treatments with a similar biomass. This supports observations that suggest that functional biodiversity, rather than species richness per se, could be important for ecosystem functions in bioturbated sediments (Mermillod-Blondin et al. 2005, Ieno et al. 2006, Raffaelli 2006).

In the present study, the species were added as evenly as possible to the experimental cores with a similar total biomass. Applied densities and biomass per unit area correspond to conditions found in nature. This approach allowed comparisons of biodiversity based on similar biomasses, but not density-dependent effects for different species or combinations. Biomass was not perfectly controlled during our experiments owing to variations in biomass among individuals of *Calocaris macandreae.* Thus, the total biomass in each of the 2- and 6-species combinations with *C. macandreae* was ~20% higher than in the other treatments. Nevertheless, the increased rates of O_2 consumption (>100% greater in treatments with *C. macandreae* than in other faunal treatments, and 400% greater than in the control) could not have been caused by this slightly enhanced biomass.

Functional traits and ecosystem properties

Concentration and distribution patterns of solutes in the pore water are important properties of benthic ecosystems, reflecting rates and pathways of organic matter mineralization in surface sediments (Froelich et al. 1979). In our study, pore water concentrations were similar under both Skagerrak and Baltic conditions (Figs. 3 & 4, Table 5), and comparable in magnitude to similar investigations in Baltic sediments (Karlson et al. 2005). Bioturbating activities by fauna facilitate the ventilation of burrow structures and exchange of reactants and metabolites between the oxygenated overlying water and anoxic pore waters (Hulth et al. 1999, Wenzhöfer & Glud 2004). Thus, faunal activities frequently determine the distribution of solutes in the pore water, and promote biogeochemical reactions that include re-oxidation of reduced compounds (Furukawa et al. 2001). Elevated concentrations in the pore water compared with the overlying water indicate solute production during mineralization in surface sediments and a diffusive transport of solutes from the sediment to the overlying water.

Pore water concentrations of NH_4^+ and HPO_4^{2-} were mainly affected by the activities of *Calocaris macandreae*. In the CmAf treatment, the NH_4^+ concentration decreased at 5 cm depth to approach that found in the surface sediment. Further, effects were most pronounced in Hs and Mn treatments*. Halicryptus spinulosus* and *Marenzelleria neglecta* may ventilate their galleries effectively and reduce pore water concentrations of NH_4^+ and HPO_4^{2-} to levels below those in the 3-species treatment (with *H. spinulosus, Macoma balthica* and *M. neglecta*).

There may be additional feedbacks between fauna and the solid phase of the sediment, in that faunal reworking, feeding and respiration activities directly affect the quality of the organic material that is mineralized. Such feedbacks may be positive (enhanced) or negative (reduced) for overall solute mobilization during mineralization (Aller 1994, Aller & Aller 1998). As O_2 was depleted, NO_3^- was quickly taken up and utilized as an electron acceptor during organic matter

mineralization (denitrification) and oxidation of reduced compounds produced during the closed sediment incubation. Bioturbating fauna increased the ventilation of produced compounds and extended the total zone of denitrification deeper into the sediment, thus contributing to ecosystem functions.

HPO_4^{2-} and NH_4^+ were in general mobilized to the pore water during mineralization and net desorption from mineral surfaces; however, both solutes were occasionally taken up by the sediment. Owing to anoxic conditions, there was no loss of NH_4^+ as a result of aerobic nitrification, or a progressive loss of HPO_4^{2-} as a result of a net adsorption onto iron-oxides (Thamdrup 2000). Therefore, negative mobilization (i.e. uptake) of NH_4^+ and HPO_4^{2-} was likely caused by incorporation of these solutes into the microbial biomass during bacterial growth (King 2005). HPO_4^{2-} production rates seemed higher under Baltic than under Skagerrak conditions, but the only significant difference was observed between the Baltic faunal treatments and the Skagerrak control (Fig. 4, Table 5). The difference in HPO_4^{2-} production between the experimental systems could be an effect of the higher sulphate concentrations under marine (~26 mmol l^{-1}) than brackish-water (~6 mmol l^{-1}) conditions. Significantly higher sulphate concentrations in the overlying water and the pore water imply higher rates of sulphate reduction and thereby a more extensive sequestering of dissolved iron by sulphides in the sediment (Canfield 1993). As a consequence, there is less efficient coprecipitation of HPO_4^{2-} by iron-oxides in the oxidized layer of surface sediments under marine than under brackish-water conditions (Caraco et al. 1989). During the closed sediment incubation, HPO_4^{2-} was therefore subsequently released from the surfaces of iron oxides to a higher degree under Baltic than under Skagerrak conditions. The significant interaction between treatment and depth for NH_4^+ production and HPO_4^{2-} pore water concentrations has lead to an interesting finding that different functional groups affect biogeochemical properties and processes rates. This opens possibilities for further experiments to explore the biogeochemical process rates and properties that result in ecosystem functions and services.

In summary, this study showed that the activities of benthic fauna significantly influence rates and pathways of organic matter mineralization. The Baltic Sea, which has a short geological history, has far fewer benthic species and functional groups than true marine areas such as the Skagerrak. A higher functional biodiversity did not enhance O_2 consumption and nutrient fluxes within the experimental systems. However, deep-burrowing species, which are common in the Skagerrak but rare in the Baltic, were shown to encompass species-specific traits that were more important for ecosystem functions than were those of the other species and species combinations examined in this study.

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