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ORIGINAL PAPER

Sulfide oxidation in deep Baltic Sea sediments upon oxygenation and colonization by macrofauna

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Abstract

Coastal and shelf sediments affected by transient or long-term bottom water anoxia and sulfidic conditions undergo drastic changes in macrofauna communities and abundances. This study investigates how early colonization by two macrofaunal functional traits (epifauna vs. infauna) affects oxygen, sulfide, and pH dynamics in anoxic sediment upon recent bottom water oxygenation. Large mesocosms (area 900 cm^2) with 150-m-deep Baltic Sea soft sediments were exposed to three treatments: (1) no animals; (2) addition of 170 polychaetes (*Marenzelleria arctia*); (3) addition of 181 amphipods (*Monoporeia affinis*). Porewater chemistry was investigated repeatedly by microsensor profiling over a period of 65 days. Colonization by macrofauna did not significantly deepen penetration of oxygen compared to the animal-free sediment. Bioturbation by *M. affinis* increased the volume of the oxidized, sulfide-free sediment by 66% compared to the animal-free control already after 13 days of incubation. By the end of the experiment *M. affinis* and *M. arctia* increased the oxidized sediment volume by 87 and 35%, respectively. Higher efficiency of epifaunal amphipods in removing hydrogen sulfide than deep-burrowing polychaetes is likely due to more substantial re-oxidation of manganese and/or nitrogen compounds associated with amphipod mixing activity. Our results thus indicate that early colonization of different functional groups might have important implications for the later colonization by benthic macrofauna, meiofauna and microbial communities that benefit from oxidized and sulfide-free sediments.

Introduction

Large amounts of settling organic matter are metabolized in coastal marine sediments due to the interaction and activity of benthic macrofauna, meiofauna and microorganisms (Middelburg et al. 1993; Kristensen 2000; Nascimento et al. 2012). Coastal sediments worldwide host abundant macrofauna populations, whose activities increase rates of solute transport, mineralization, nitrification, and denitrification in the sediment by factors of up to three (Aller 1982; Kristensen and Blackburn 1987; Aller 1994). This stimulation is due to the ability of macrofauna to ingest and redistribute particles, create and maintain burrows (bioturbation), and to ventilate burrows introducing oxygen into otherwise anoxic sediment layers (bioirrigation) (Kristensen et al. 2012). Bioturbating macrofauna may also play an important role in regulating the fate of hazardous substances by enhancing aerobic biodegradation of organic pollutants before their burial in reducing sediment compartments (Gilbert et al. 1996).

Marine coastal environments bounded by catchment areas with high anthropogenic activity, such as the central Baltic

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Sea, receive high loads of nutrients and organic matter leading to algal proliferation and eutrophication (Glibert and Burkholder 2006). When eutrophication and water stratification coexist, algal degradation in the water and in the sediment increases oxygen consumption and eventually leads to water column hypoxia and anoxia (Diaz 2001). Since higher water temperatures enhance metabolic processes and decrease oxygen solubility, ocean de-oxygenation may be further enhanced by global warming (Keeling et al. 2010). Oceanic models anticipate an expansion in the area of dead-zone sediments globally in the next decades (Breitburg et al. 2018). Under these severely hypoxic or anoxic conditions, benthic aerobic processes slow down or even stop, while anaerobic processes such as denitrification, sulfate reduction and methanogenesis are promoted (Howarth 1984). In coastal and shelf sediments bacterial sulfate reduction generally dominate anaerobic rates of organic matter oxidation (Jørgensen 1982; Canfield 1989).

Microbial sulfate reducers produce sulfide, which in marine sediments usually binds to Fe(II), precipitating as amorphous FeS or as the more stable pyrite (FeS_2) (Berner 1984). However, in ecosystems that are characterized by very high organic loading and relatively low reactive iron such as oxygen minimum zones, the anoxic regions of the Baltic Sea and the Black Sea, free sulfide accumulates in the surface sediment or even in the bottom water (Dyrssen and Kremling 1990; Brüchert et al. 2003; Jørgensen et al. 2004). A vast body of literature shows that free hydrogen sulfide (H_2S) is toxic and leads to respiratory stress to benthic organisms already at micromolar concentrations (Völkel and Grieshaber 1992; Diaz and Rosenberg 1995; Jahn and Theede 1997). Results from a modeling experiment demonstrated that H_2S at concentrations > 14 µM have negative effects on marine benthic macrofauna at population level (Vaquer-Sunyer and Duarte 2010).

Hydrogen sulfide is toxic to most benthic invertebrate organisms as it inhibits the last enzymatic reaction of the respiratory chain in the mitochondria when it binds to cytochrome aa3 (Nicholls 1975). Other inhibition mechanisms of sulfide on marine invertebrates are reviewed in Völkel and Grieshaber (1995). Epifaunal species such as the amphipod *Monoporeia affinis*, for example, cannot even tolerate sulfide in the low micromolar range (Sandberg-Kilpi et al. 1999). However, there are a few resistant macrofaunal species that evolved detoxification mechanisms against H_2S. The Baltic clam *Macoma balthica* (now *Limecola balthica*), for example, can tolerate H_2S as it reduces gas diffusion by temporary reduction of valve opening (Jahn and Theede 1997). It has also been shown that the polychaete *Marenzelleria viridis* has the ability to oxidize sulfide in its mitochondria at concentrations < 50 µM (Hahlbeck et al. 2000).

Long-term efforts to reduce nutrient inputs to the Baltic Sea have led to mitigation of eutrophication in the last 10 years (Andersen et al. 2017). When eutrophication and hypoxia fade, it follows sediment colonization by aerobic microorganisms and macrofauna (Stigebrandt et al. 2015). More than 3 decades ago, it was recognized that macrobenthos have a drastic effect on chemical properties of sediments, which mainly depends on the functional groups forming the benthos (Aller 1982). Diverse macrofaunal groups also have different effect on sediment oxygen dynamics and on redox profiles (Weissberger et al. 2009). Not fully understood is, however, the influence of macrofauna colonization on sediment oxygen and sulfide concentrations in previously azoic sediments. For example, it is still unclear whether epifaunal species such as amphipods, which unceasingly dig in the surficial sediment (Tuominen et al. 1999), may extend oxygen distribution and sulfidic horizon. On the contrary, certain strictly infaunal organisms may even enhance sulfide concentrations in the porewater as in *Marenzelleria arctia* bioturbated sediments (Bonaglia et al. 2013; Danielsson et al. 2018), possibly by increasing the rates of sulfate reduction due to their intense bioirrigation (Quintana et al. 2018).

The aim of this study is to better understand how different types of macrofauna influence oxygen, sulfide and pH dynamics in sediments that were naturally reducing with high sulfide concentrations, but subsequently underwent transient (2 weeks) and long-term (2 months) oxygenation. We studied two contrasting types of bioturbators: *M. arctia*, an invasive and opportunistic polychaete species that lives exclusively in sediment and creates J-, Y- or U-shaped burrows down to 10 cm into the sediment (Renz and Forster 2013; Quintana et al. 2018); and *Monoporeia affinis*, a very common amphipod species in the Baltic Sea, which digs in the sediment during daytime and performs nocturnal swimming in the bottom water (Hill and Elmgren 1987). These two types of invertebrates were added to oxygenated mesocosms that were containing previously anoxic Baltic Sea sediment naturally devoid of macrofauna. Measurements of porewater O_2, H_2S and pH were performed at in situ temperature and salinity, thus resembling Baltic Sea sediment conditions, by means of microsensor setup over a 2-month incubation period.

Methods

Sampling for sediment and macrofauna

Intact and undisturbed sediment samples were collected from 149 m depth with a modified boxcorer that minimizes resuspension (Blomqvist et al. 2015) in the northwestern Baltic proper (58°26.2095′N, 18°25.3751′E) in August 2012 onboard *R/V Fyrbyggaren*. Retrieved sediment boxes (area: 30 × 30 cm) had a sediment height of ca. 34 cm and a water column height of ca. 12 cm. The water overlying sediment had salinity 11, temperature 5.6 °C, and concentrations of dissolved O_2 measured in situ were between 0 and 8 µM (Ekeroth et al. 2016a). Visual inspection indicated that the sediment was completely devoid of macrofauna. Sediment boxes were immediately transported to Askö Laboratory (Stockholm University's Baltic Sea Centre), where they were placed in a dark and temperature-controlled room at in situ temperature.

Macrofauna sampling was performed at 28 m depth by means of a benthic sled (Blomqvist and Lundgren 1996) in Yttre Hållsfjärden, close to Askö laboratory (Ekeroth et al. 2016a). The macroinvertebrates were extracted from the sediment by sieving with a mesh size of 0.5 mm. From the macrofauna extract, only the amphipod *Monoporeia affinis* and the polychaete *Marenzelleria arctia* were carefully picked from the sieves with tweezers and kept in plastic containers with aerated water until the addition to the sediment boxes (see next section).

Mesocosm setup

Three boxcores (hereafter mesocosms) were incubated for this experiment and their lids were connected to external tubes, which supplied sand-filtered brackish seawater with an average particulate organic carbon (POC) concentration of 50 µg L^{-1} at a rate of 30 mL min^{-1} pumped directly from the Baltic Sea from ca. 20 m depth (Björk and Gilek 1996). This water was fully oxygenated and had salinity and temperature in the range of the water collected in situ. An outlet placed on the side of each mesocosm allowed a continuous flow of water, while an aquarium pump was placed inside each mesocosm to maintain the water conditions homogenous. Inlets, outlets and aquarium pumps were all equipped with nets, which prevented removal and unintentional import of invertebrates. The mesocosms were equipped with optical sensors (models 3830 and 4835; Aanderaa Data Instruments AS, Norway) for oxygen and temperature monitoring. Oxygen saturation ranged between 70 and 80% and temperature was kept at 5.5 ± 1 °C (always < 8 °C) throughout the course of the experiment (Ekeroth et al. 2016a).

Twenty days after the water aeration started, macrofauna individuals were added to each mesocosm. Under these conditions, the top dark gray fluffy sediment layer had turned into a 1-cm-thick brown sediment layer. One of the three mesocosms was left without infauna and served as control. Here, no sign of macrofauna bioturbation was detected throughout the course of the experiment. The second mesocosm received 170 *M. arctia* individuals, while the third mesocosm received 181 *M. affinis* individuals. To mirror the natural size distribution of Baltic Sea bioturbated sediments, macroinvertebrates of all sizes were randomly added to the mesocosms. The animal additions corresponded to abundances of 2020 *M. arctia* ind. m^{-2} and 2150 *M. affinis* ind. m^{-2}. These densities of macroinvertebrates represent the range generally reported for Baltic Sea sediments (Villnäs and Norkko 2011; Kauppi et al. 2015). Details of the mesocosm setup and macrofauna handling are described in the companion paper by Ekeroth et al. (2016a). Converse to that study, measurements here were carried in one mesocosm per treatment. This was justified by the low heterogeneity of the sediment as confirmed by the low variability in biogeochemical processes within the sampling site (Ekeroth et al. 2016a). As a matter of fact, all nutrient fluxes strongly dependent on redox conditions, i.e., N, P and Si fluxes, were not significantly different between mesocosms before the introduction of the animals, but became significantly different right after macrofauna addition—see Fig. 3 of Ekeroth et al. (2016a).

Microelectrode profiling

Microscale depth distribution of oxygen (O_2), hydrogen sulfide (H_2S) and pH were measured via microsensors (Revsbech and Jørgensen 1986) in the three mesocosms, hereafter simply called (1) Control, (2) *Marenzelleria*, and (3) *Monoporeia*. The first O_2 profiles were measured 1 day after the addition of the macroinvertebrates to determine if there was an immediate effect of the animal addition on O_2 dynamics, while the complete microprofiling array (O_2, H_2S and pH) was performed 13 and 65 days after the addition of the invertebrates to establish the medium- and long-term effects of animal activity on solute distribution and sediment porewater geochemistry. Microprofiles were measured directly inside each mesocosm with stirring system on using a micromanipulator (MM33, Unisense, DK) and microsensors with a tip diameter of 50 µm (OX-50, H2S-50, pH-50; Unisense, DK). Oxygen profiles were carried out first and were followed by simultaneous determination of H_2S and pH, with electrodes mounted on a double-headed micromanipulator (Unisense, DK). Three to four profiles were measured at each time for each solute in each mesocosm. A total of 70 microprofiles was carried out. For each day of measurement, O_2 microelectrodes were calibrated at O_2 saturation and under anoxic conditions using a two-point calibration according to the manufacturer's recommendation. Hydrogen sulfide microelectrodes were calibrated daily in fresh Na_2S solutions that were prepared with washed and cleaned Na_2S crystals in anoxic water and calibrated using the methylene blue method of Cline (1969). pH microelectrodes were calibrated with commercial pH standards of 4.00, 7.00 and 10.00 (Fisher Scientific, Gothenburg, Sweden). Concentrations of total hydrogen sulfide ($\Sigma H_2S = [H_2S] + [HS^-] + [S^{2-}]$) was calculated at each depth from the measured H_2S and pH values (Jeroschewski et al. 1996). Diffusive sulfide flux J in the sediment was calculated from the sulfide depth profiles using Fick's first law corrected for sediment porosity:

$$J\Sigma H_2S = \phi \, Ds \, \mathrm{d}\left[\Sigma H_2S\right]/\mathrm{d}x,$$

where ϕ is the porosity of the sediment, Ds is the diffusion coefficient of sulfide in the sediment, which was estimated from the porosity and the free diffusion coefficient of sulfide at infinite dilution (D_{HS}) using the approximation $Ds = \phi^2 \times D_{\mathrm{HS}}$ (Ullman and Aller 1982), and $\mathrm{d}[\Sigma H_2S]/\mathrm{d}x$ indicates the ΣH_2S concentration gradient with depth in the linear interval below the sulfidic horizon. Sediment porosity (vol/vol) was determined from dry sediment density (2.65 g ml^{-1}) and water content of 5-mm-thick sediment slices. Water content was quantified by loss of weight on drying each sediment slice at 60 °C until constant weight (Andrews and Bennett 1981). For the sake of conciseness, we defined the sulfidic horizon as the specific sediment depth where sediment became sulfidic (depth with $[\Sigma H_2S] > 1$ µM). The OPD (oxygen penetration depth) was defined as the depth at the bottom of the oxygen profile where $[O_2]$ was < 1 µM.

Statistical tests and data presentation

The effects of factors *Day* (Day 1, Day 13 and Day 65 for OPD; Day 13 and Day 65 for sulfidic horizon and sulfide fluxes) and Treatment (Control, *Marenzelleria* and *Monoporeia*) were tested on our dependent variables (OPD, sulfidic horizon and sulfide fluxes) by means of a two-way repeated measures ANOVA test. Normality (Shapiro–Wilk test) and equal variance (Brown–Forsythe test) were tested before running the ANOVA and these assumptions were always met. The level of significance was set to $p < 0.05$. When the differences were greater than expected by chance, pairwise multiple comparison was performed (Holm–Sidak test). Statistical analyses were performed using SigmaPlot 14.0 (Systat Software, Inc., USA). Data synthesis and graphing were performed on SigmaPlot 14.0 and Origin Viewer 9.6.5 (OriginLab Corporation, USA). If not stated otherwise, measurements are reported as average mean value with associated standard error of the mean.

Results

Sediment and macroinvertebrate conditions

The upper two centimeters of sediment had very similar water contents (91−92%) and porosities (0.96−0.97) in the control, *Marenzelleria* and *Monoporeia* treatments. The added macrofauna immediately colonized and burrowed the re-oxygenated sediment. Bioturbation by *Monoporeia affinis* extended to a maximum of 1.5−2.0 cm in the sediment, while *Marenzelleria* penetrated to a maximum depth of 6−7 cm (visual observations). No signs of stress or dead animals lying on the surface were detected until ca. 90 days after addition to the mesocosms. After that, several individuals of *M. affinis* and relatively fewer individuals of *Marenzelleria* were found lying on the surface of the sediment suggesting stress, likely induced by the relatively limited amount of food (i.e., phytodetritus) supplied from the flow-through system. Thus, we interrupted the experiment after 90 days and only present results up to 65-day incubation period within which animals were alive and active.

Oxygen, pH and sulfide porewater profiles

One day after animal introduction, the oxygen penetration depth (OPD) was 0.83 ± 0.02 cm in the *Monoporeia* mesocosm, 0.88 ± 0.07 cm in the *Marenzelleria* mesocosm and 0.87 ± 0.03 cm in the Control mesocosm (Figs. 1, 2). OPD was not significantly different between treatments ($p = 0.496$) and between the three different times ($p = 0.467$) (Table 1). After 13 days of incubation in the control mesocosm, oxygen and sulfide profiles slightly overlapped indicating the onset of an aerobic sulfide oxidation zone at 0.83 cm depth (Fig. 1). The pH decreased rapidly from the water column value of 7.5 to a minimum of 6.9 in proximity of the sulfide oxidation zone (0.9 cm depth). pH values increased slightly with depth to a pH of 7.1 at 3 cm. In the *Marenzelleria* treatment, oxygen penetrated 2 mm deeper (1.03 ± 0.04 cm) compared to the control (0.83 ± 0.04 cm). Overall *Marenzelleria* showed similar patterns to Control indicated by the overlapping oxygen and sulfide profiles and the corresponding pH minimum at the depth of sulfide disappearance. In the *Monoporeia* treatment, the OPD (0.78 ± 0.02 cm) was similar to the one measured in the Control (Table 1, Fig. 2). However, sulfide and pH profiles showed a deepening of the sulfide oxidation zone and a development of a 0.75-cm-thick zone devoid of both oxygen and sulfide (Fig. 1). As a consequence, the sulfidic horizon was situated deeper in *Monoporeia* (1.47 ± 0.09 cm) than in *Marenzelleria* (0.82 ± 0.07 cm) and in Control (0.85 ± 0.01 cm) (Fig. 2).

On day 65, microprofiles in Control showed a 0.27-cm separation between the oxic and sulfidic zones. The pH profile showed a small maximum close to the sediment–water interface and a minimum in proximity to the sulfidic horizon. In the *Marenzelleria* treatment, oxygen penetrated down to 1.06 ± 0.03 cm (Fig. 1). The sulfidic horizon and the pH minimum deepened to approximately 1.53 ± 0.04 cm indicating the development of an anoxic sulfide-free zone approximately 0.5 cm thick. In the *Monoporeia* treatment, the OPD remained stable compared to day 13; however, the anoxic sulfide-free zone had expanded to a thickness of 1.3 cm. In all mesocosms, the sulfidic horizons significantly moved deeper with time ($p < 0.001$; Table 2) and at day 65 they were situated at 1.13 ± 0.02 cm, 1.53 ± 0.04 cm and 2.12 ± 0.02 cm depth

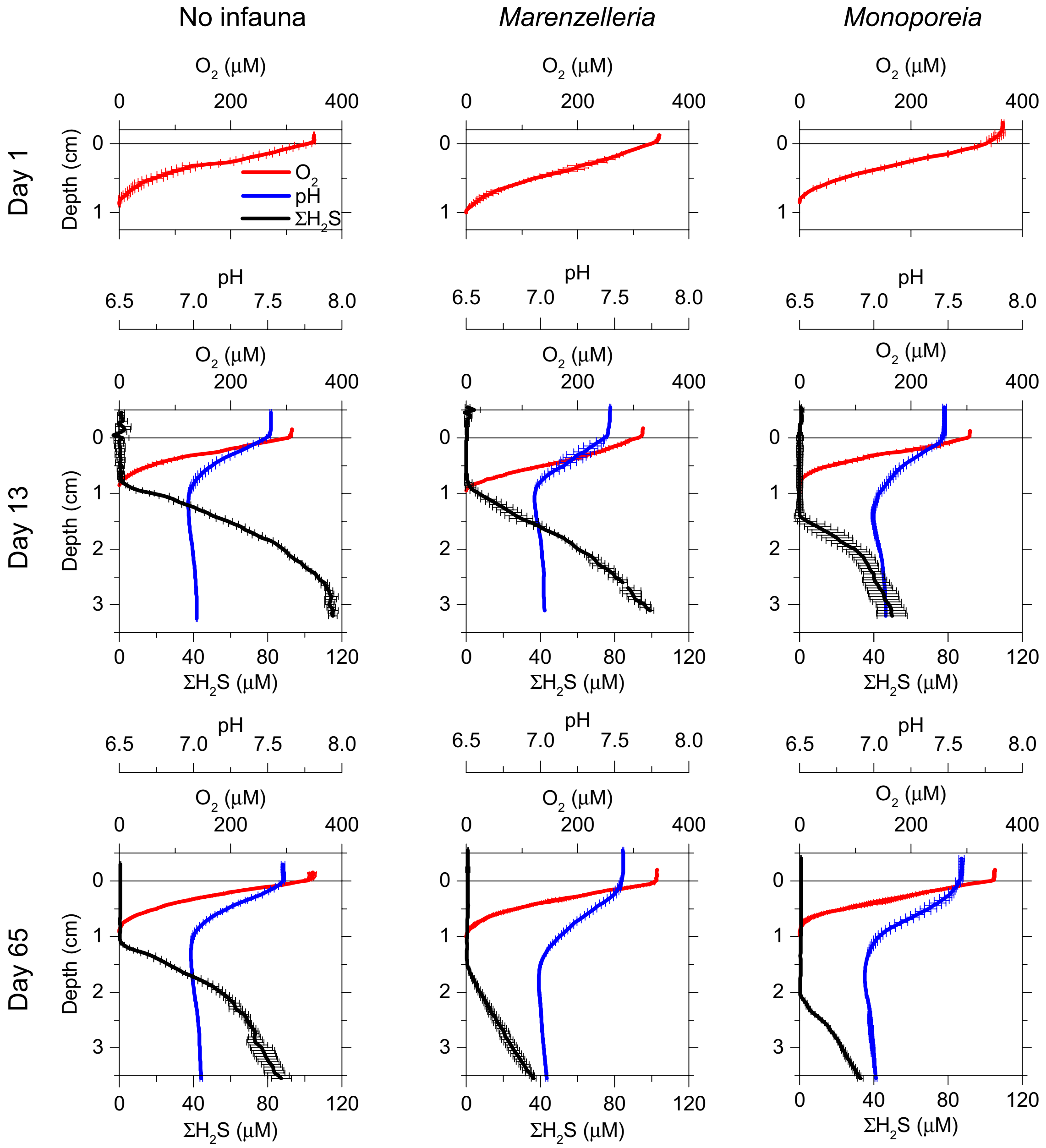

Fig. 1 Sediment microprofiles in the three mesocosms. Oxygen (red), pH (blue) and H_2S (black) lines indicate sediment microprofiles carried out inside (from left to right) control mesocosm, mesocosm amended with *Marenzelleria arctia* and mesocosm amended with *Monoporeia affinis*. Bold lines indicate average microprofiles, while error bars represent standard error of the mean ($n = 3{-}4$). Horizontal black lines corresponding to 0 cm depth indicate the sediment–water interface

in Control, *Marenzelleria* and *Monoporeia*, respectively (Fig. 2). Throughout the course of the experiment, the sulfidic horizon of *Monoporeia* was significantly deeper than in Control ($p < 0.001$) and *Marenzelleria* ($p < 0.001$) (Table 2). *Marenzelleria* was significantly deeper than Control too ($p = 0.016$) (Table 2).

Sulfide fluxes

The calculated sulfide fluxes only identify the diffusional transport of sulfide, omitting his advective component, which is an intrinsic characteristic of bioturbated sediments. Thus, sulfide fluxes should be considered representative of

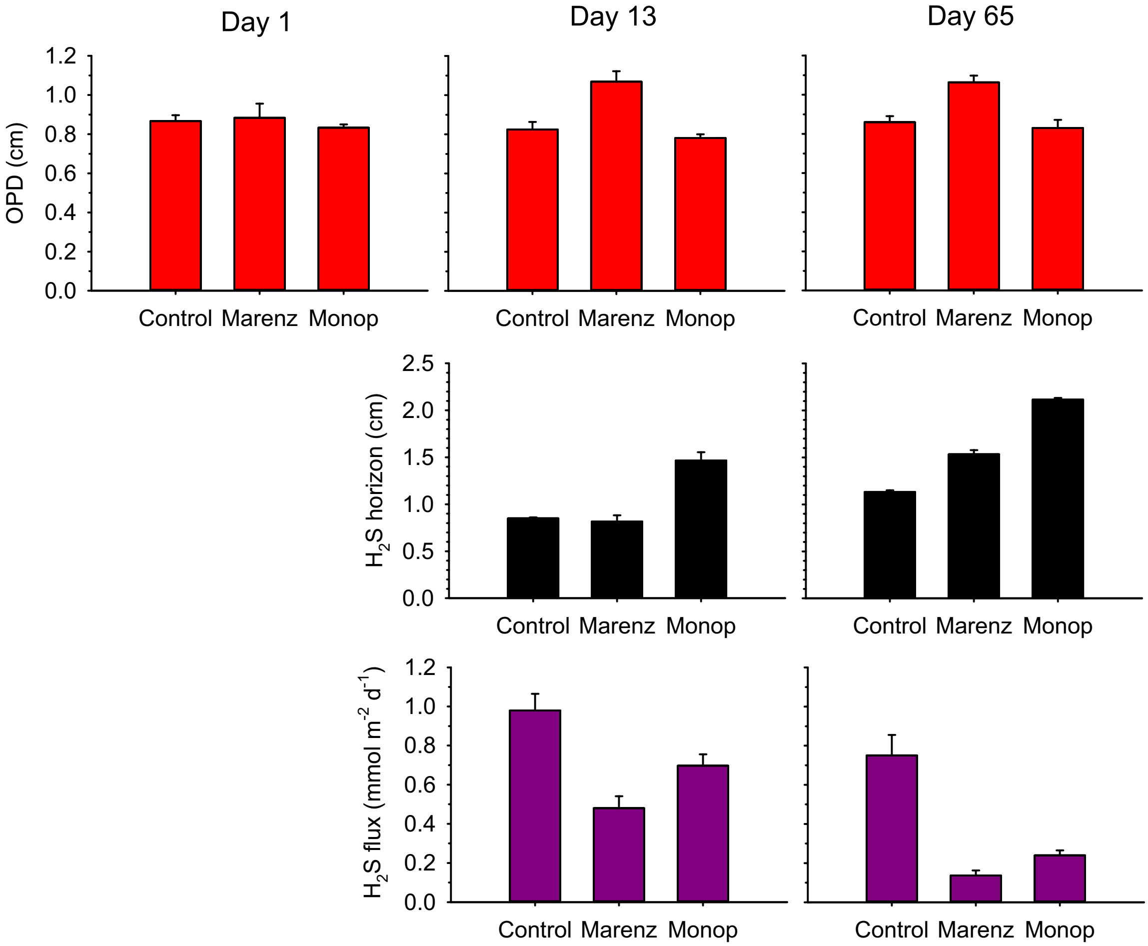

Fig. 2 Summary of the measured oxygen penetration depths (OPDs), depth of the sulfide horizon and diffusive sulfide fluxes in the sediment. For each day of measurement, from left to right: Control = control mesocosm; Marenz = mesocosm amended with *Marenzelleria arctia*; Monop = mesocosm amended with *Monoporeia affinis*. Colored bars indicate average values and error bars represent standard error of the mean ($n = 3–4$)

Table 1 Summary of the results of the two-way repeated measures ANOVA performed to test the effect of factors Day (Day 13 and Day 65) and Treatment (Control, *Marenzelleria*, *Monoporeia*) on dependent variables (OPD = oxygen penetration depth; sulfidic horizon; sulfide flux)

Dependent variable	Factor	*DF*	SS	MS	*F*	*p*
OPD	Day	2	4.638	2.319	0.9	0.467
	Treatment	2	4.545	2.272	0.8	0.496
	Day × treatment	4	11.21	2.802	1.0	0.445
Sulfidic horizon	Day	1	1.361	1.361	1666.8	< 0.001
	Treatment	2	2.108	1.054	167.6	< 0.001
	Day × treatment	2	0.163	0.0817	5.5	0.070
Sulfide flux	Day	1	0.53	0.53	345.6	0.003
	Treatment	2	0.986	0.493	41.9	0.002
	Day × treatment	2	0.0386	0.0193	3.1	0.154

the overall H_2S transport for the control, non-bioturbated sediment, but considered as underestimation of the total flux for the *Monoporeia* (bioturbation down to 1.5–2.0 cm), and especially for the *Marenzelleria* treatment (bioturbation reaching up to 7 cm depth and active bioirrigation).

After 13 days of incubation, the diffusive flux of sulfide in the sulfidic horizon was 51% and 29% lower in the *Marenzelleria* and *Monoporeia* treatments, respectively, compared to Control (Fig. 2). Sulfide fluxes were 0.48 ± 0.06 mmol m^{-2} day^{-1} in *Marenzelleria*, 0.70 ± 0.06 mmol m^{-2} day^{-1} in

Table 2 Summary of pairwise multiple comparison procedures (Holm–Sidak method)

Comparisons for factor	Comparison	Sulfidic horizon				Sulfide flux			
		Diff Means	*t*	*p*	$p<0.05$	Diff Means	*t*	*p*	$p<0.05$
Time	Day 13 vs. Day 65	0.550	40.827	< 0.001	Yes	0.343	18.591	0.003	Yes
Treatment	*Marenzelleria* vs. *Monoporeia*	0.617	13.469	< 0.001	Yes	0.160	2.554	0.063	No
	Marenzelleria vs. Control	0.183	4.004	0.016	Yes	0.557	8.888	0.003	Yes
	Control vs. *Monoporeia*	0.800	17.473	< 0.001	Yes	0.397	6.334	0.006	Yes

Overall significance level = 0.05

Monoporeia, and 0.98 ± 0.09 mmol m^{-2} day^{-1} in Control (Fig. 2).

On day 65, the sulfide flux in the control was 23% lower compared to day 13. However, the difference between the faunated treatments and the control expanded even further, and was 82% and 68% lower in the *Marenzelleria* and *Monoporeia* treatments, respectively, compared to Control. Fluxes were still lower in *Marenzelleria* (0.13 ± 0.03 mmol m^{-2} day^{-1}) and in *Monoporeia* (0.24 ± 0.03 mmol m^{-2} day^{-1}) than in Control (0.75 ± 0.11 mmol m^{-2} day^{-1}). Throughout the course of the experiment, there was no significant difference in fluxes between *Monoporeia* and *Marenzelleria* ($p = 0.063$), but both *Marenzelleria* ($p = 0.003$) and *Monoporeia* ($p = 0.006$) were significantly lower than Control (Table 2).

Discussion

More than thirty oxygen profiles were carried out in this study and most of them in visibly bioturbated sediment. However, we did not record any burrow sign as oxygen concentration anomalies in our treatments, which is interesting to note. Our observations are in line with those of Karlson et al. (2005) who worked on a similar setting with recently oxygenated and colonized sediment, showing that the amphipod *Monoporeia affinis* is mainly living in the top 2 cm of the sediment. Here burrows cannot consolidate because of the non-cohesive nature of the sediment, which is characterized by a very high water content (92%) and porosity (0.97). The stability of the oxygen penetration depth in the *M. affinis* treatment aligns with a previous study by Tuominen et al. (1999) showing no significant increase in the oxygen penetration in highly porous (0.95) sediment colonized by *M. affinis* compared to bare sediment. These results together indicate that the colonization of previously hypoxic sediments by *M. affinis* does not expand the oxic portion of the sediment. We cannot exclude, however, that this species also renders the surficial sediment organic matter more reactive and degradable by digging and reworking the very top part of the sediment (Karlson et al. 2005), and may favor the contact between organic particles and meiofauna and microorganisms.

Contrary to *M. affinis*, the invasive polychaete *M. arctia* makes consolidated burrows and permanently lives inside the sediment (Renz and Forster 2013; Quintana et al. 2018). Genetic analyses demonstrated three sibling species of *Marenzelleria* coexist in the Baltic Sea, namely *M. arctia*, *M. neglecta* and *M. viridis* (Blank et al. 2008; Renz and Forster 2013). We did not apply genetic tools to identify the *Marenzelleria* species, but three lines of evidence indicate that our mesocosm was virtually exclusively colonized by *M. arctia*. First, in the sampling location, *M. viridis* has never been reported, whereas *M. neglecta* has been found only sporadically (Bastrop and Blank 2006; Blank et al. 2008; Ekeroth et al. 2016a). Second, the relatively shallow burrows (extending to 6–7 cm depth) were U shaped, which is a typical signature of *M. arctia* bioturbation (Quintana et al. 2018). Third, *M. arctia* is generally the sole species found at deep Baltic Sea sites (below 20 m) (Kauppi et al. 2018b). This is important to note as recent studies have highlighted that *M. arctia* has different bioirrigation activity compared to its sibling species and thus may affect porewater profiles differently (Renz and Forster 2013, 2014; Quintana et al. 2018).

A previous study using shallow well-oxidized muddy sediments showed that *M. arctia* has higher burrow ventilation and irrigation efficiencies compared to its two siblings (Quintana et al. 2018). The high irrigation activity by *M. arctia* may cause enhanced nonlocal transport of oxygen increasing, in turn, benthic phosphate retention (Quintana et al. 2018). A companion study, which worked on the same setup as the one used here (i.e., previously anoxic Baltic Sea deep sediments), showed that *M. arctia* had much lower irrigation potential compared to findings by Quintana et al. (2018), leading to insignificant effects for phosphate retention (Ekeroth et al. 2016a). The weak effect of *M. arctia* on phosphate along with mobilization of reduced compounds (e.g., ammonium) was recently confirmed (Kauppi et al. 2018a). Our results, which indicate that *M. arctia* did not substantially increase the oxygenation of the sediment, are in line with those from these previous studies (Ekeroth et al. 2016a; Kauppi et al. 2018a), and corroborate the idea that after sediment oxygenation and recolonization, *M.*

arctia maintains low activity at least in the first weeks of colonization.

As it was described previously, *M. arctia* by living and burrowing several centimeters inside the sediment substantially increases rates of total benthic oxygen uptake (Bonaglia et al. 2013). Also in the *M. arctia* treatment we did not record any burrow sign as oxygen concentration subsurface peaks. We cannot exclude that we might have profiled too far away from the burrows. However, considering that our sediment was visibly bioturbated—as the one in Fig. 1 of Norkko et al. (2012)—we rather believe that *M. arctia* burrows were generally not well ventilated and that oxygen was absent most of the time. This is supported by the fact that most of the enhanced benthic oxygen uptake by *M. arctia* activity is actually due to polychaete respiration (68%), while the contribution of new burrow structures is minor (32%) (Bonaglia et al. 2013).

About 2 weeks after the experiment started, the oxygen and sulfide profiles slightly overlapped indicating that sulfide was primarily oxidized by oxygen diffusing from the overlying water in the fauna-free sediment. By the end of the experiment, *M. arctia* decreased porewater sulfide pool by > 50%. Our observation contrasts with previous studies indicating that *M. arctia* temporally enhances sulfide concentrations in the porewater because its high irrigation potential mobilizes both oxidized and reduced compounds in sediment burrows (Bonaglia et al. 2013; Quintana et al. 2018). It is interesting to note that our results, valid for *M. arctia*, are apparently in contrast with those from the sibling species *M. viridis*, which can burrow much deeper (> 20 cm) and double sedimentary sulfate reduction rates in coastal sediments (Kristensen et al. 2011). Moreover, most of the studies on *M. viridis* have been carried out with sandy sediments, which are preferred by this larger species (Kristensen et al. 2011; Renz and Forster 2013; Quintana et al. 2018), while studies on *M. arctia* have been conducted almost exclusively on soft mud (Hietanen et al. 2007; Bonaglia et al. 2013; Quintana et al. 2018). Thus, different results may also be explained by the different degree of sediment cohesiveness.

Two weeks after colonization, *Marenzelleria* did not significantly extend the suboxic zone—the zone devoid of both oxygen and sulfide—while in the sediment with *Monoporeia* a distinct separation between the oxic and sulfidic zones could already be measured. Two months after sediment colonization, there were 0.5-cm- and 1.5-cm-thick suboxic zones in the *Marenzelleria* and *Monoporeia* treatments, respectively. We exclude that internal sulfide detoxification by the animals played a significant role, and we mainly attribute these expansions of the suboxic zone to the bioturbation activity of the animals. *M. arctia* was not actively burrowing during our measurements, but its activity was mainly limited to radial diffusion (bioirrigation), which mobilizes oxygen, sulfate and sulfide (Bonaglia et al. 2013; Quintana et al. 2018). This might have enhanced remineralization—including sulfate reduction—locally and have had an effect, although not significant, on oxygen penetration. The effect of sulfide re-oxidation by this species is probably ineffective when oxygenation is only a transient phenomenon (up to a few weeks), but may become significant after long-term oxygenation events (2 months on). *M. affinis* actively mixes the upper sediment layer and creates sulfide-free “pockets” inside the sediment (Modig and Olafsson 2001). Its activity resulted very effective in voiding the upper sediment from hydrogen sulfide both after short- and long-term oxygenation. Following oxygenation, the stronger sulfide removal induced by *M. affinis* might thus lead to faster recolonization by aerobic bacteria and opportunistic polychaetes as earlier suggested for a whole-fjord oxygenation experiment (Stigebrandt et al. 2015).

The 0.5–1.5-cm-thick suboxic zone induced by macrofauna bioturbation indicates that the sediment mixing by the amphipod and sediment irrigation by the polychaete activated Fe, Mn and nitrate cycling and with them the oxidation of acid volatile sulfide (AVS) and iron sulfide minerals (FeS_2). In the *Monoporeia* treatment, the pH minimum coincided with the depth where sulfide started appearing and not with the depth where O_2 disappeared. This might be symptomatic of the intense processes of re-oxidation of reduced metabolites and sulfide minerals (Boudreau and Canfield 1988), and indicate that the dominant process generating the pH minimum was sulfide oxidation and not aerobic respiration. In the presence of *M. affinis*, due to the larger separation between the O_2 and H_2S zones, the upward free sulfide was oxidized with something else than oxygen, likely Fe and/or Mn oxyhydroxides, or nitrate. Thus, *M. affinis* bioturbation activity may have facilitated the formation and recycling of Fe and/or Mn oxyhydroxides, which then likely generated this gap between the oxygenated and sulfidic zones. Mesocosm experiments with previously anoxic sediments collected in a 100-m-deep Baltic fjord showed indeed that especially Mn plays an important role in porewater geochemistry and that reduction of Mn oxides may account for a large fraction of carbon mineralization in these seasonally hypoxic, deep coastal sediments (Bonaglia et al. 2013; Danielsson et al. 2018). Besides oxidation of minerals by physical mixing, bioturbation by the amphipods might have favored oxidative nitrogen cycling processes such as nitrification (Ekeroth et al. 2016a), which in turn might promote nitrogen removal through denitrification (Tuominen et al. 1999).

Other organisms that can contribute to the separation between the oxic and sulfidic zones are sulfide-oxidizing bacteria, i.e., *Beggiatoaceae* and cable bacteria (filamentous *Desulfobulbaceae*). *Beggiatoaceae* can store nitrate intracellularly and migrate vertically in the sediment to oxidize sulfide (Sayama et al. 2005), whereas cable bacteria can couple sulfide oxidation with oxygen or nitrate reduction over distances of centimeters by conducting electric currents (Pfeffer et al. 2012; Marzocchi et al. 2014). *Beggiatoaceae* and cable bacteria both have been reported from Baltic sediment overlain by transient oxic water (Yucel et al. 2017; Marzocchi et al. 2018). However, these organisms leave characteristic pH signatures in the sediment (Sayama et al. 2005; Nielsen et al. 2010). Due to the systematic absence of such pH signatures in our profiles as well as the absence of a clear suboxic zone in the control mesocosm, we exclude that *Beggiatoaceae* and cable bacteria played a significant role in the buildup of the separation between the oxic and sulfidic zones observed in our mesocosms.

An earlier experiment carried out with similar deep Baltic Sea sediments showed that *M. affinis* actively dig into sulfidic sediments, perhaps in search for food (Modig and Olafsson 2001). Except for the short time following algal blooms, Baltic Sea sediments are limited in terms of fresh food for macrofauna (Elmgren 1978). When phytoplankton and other organic detritus are not available as main food source, *M. affinis* tend to feed on bacteria, meiofauna and juveniles of the tellinid bivalve *Macoma balthica* (Elmgren 1978; Goedkoop and Johnson 1994; Ejdung et al. 2000). Thus, it can be that the amphipods were actively seeking for bacteria and meiofaunal organisms, mostly nematodes, that have been shown to live in hypoxic and anoxic Baltic sediments (Elmgren 1975). Furthermore, we cannot exclude that the reactive organic carbon pool was getting more and more depleted in our mesocosms (Ekeroth et al. 2016a), due to a limited import of fresh organic particles with the inflowing water, and as a consequence the main product of heterotrophic anaerobic metabolism—hydrogen sulfide—was reduced. The decrease in sulfide fluxes from day 13 to day 65 in bare sediment confirms a general decrease in sediment metabolism (e.g., sulfate reduction activity) with time. The simple decrease in sulfate reduction alone is not expected to generate a suboxic zone, which is rather diagnostic of the activation of mineral cycling via sediment mixing possibly by meiofaunal nematodes. It is indeed well known that nematodes can survive anoxia (anoxybiosis) and even sulfidic conditions (thiobiosis) for years in aquatic sediments as reviewed by Tahseen (2012). However, the organisms that generated the suboxic zone in the control treatment did it to an extent that was significantly minor compared to the larger separation in the macrofauna treatments. We recommend that the influence of meiofauna bioturbation on sulfide oxidation be addressed in future experiments.

Conclusions

Baltic Sea bottom water and surface sediments are affected by temporal or long-term hypoxia and anoxia, which make large parts of the central Baltic azoic. Long-term studies of Baltic Sea water quality conditions show significant improvements in the eutrophication status in recent decades (Andersen et al. 2017). When oxygenation happens, macrofauna recolonize these previously anoxic sediments causing drastic effects in porewater geochemistry and benthic fluxes of solutes (Norkko et al. 2012; Bonaglia et al. 2013; Ekeroth et al. 2016a, b; Danielsson et al. 2018). Our results show that colonization by macrofauna did not significantly increase oxygen penetration inside the sediment. We ran our experiment for more than 2 months to understand the long-term effects of macrofauna bioturbation on porewater sulfide distribution. On the one hand, long-term responses could be appreciated, but on the other hand, the animals might have reduced their metabolism with time as input of fresh organic material became more limiting. However, our results show that *M. affinis* increased the volume of oxidized, sulfide-free sediments by 87% compared to the Control treatment and by 38% compared to the *M. arctia* treatment, respectively. When upscaled to a hectare of sea floor, it results that *M. affinis* leads to an increase of 98 m^3 and 58 m^3 of oxidized, sulfide-free sediment compared to non-bioturbated sediment and *M. arctia*, respectively. Thus, an important implication is that epifaunal amphipods colonizing previously hypoxic and anoxic sediments would make the sediment surface more hospitable for other benthic organisms that benefit from sulfide-free conditions. In contrast, we showed that *M. arctia* does not lead to a similarly clear sulfide removal. These latter results are in line with those of several modeling and experimental studies indicating that *M. arctia* (1) might increase the upward advective flux of anoxic and sulfidic waters; (2) stimulate sulfate reduction rates; (3) regenerate pools of reduced metabolites (Bonaglia et al. 2013; Danielsson et al. 2018; Kauppi et al. 2018a; Quintana et al. 2018). We conclude that colonization of previously anoxic sediment by the amphipod *M. affinis* stimulates the oxidation of a larger volume of sediment and is more favorable for the establishment of later colonizers than colonization by the invasive polychaete *M. arctia*.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable national and/or institutional guidelines for the use of collection material were followed. Only invertebrates were used in this study.

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