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Survival and bioturbation of the amphipod *Monoporeia affinis* in sulphide-rich sediments

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Abstract Laboratory experiments were conducted to investigate the survival rate of *Monoporeia affinis* in sulphide-rich sediment with oxic overlying water, and the effect of amphipod bioturbation on sulphide and oxygen profiles. As long as the oxygen content in the water is high, the amphipods seem to avoid quite high concentrations ($> 200 \mu\text{mol l}^{-1}$) of sulphide in the sediment by creating microhabitats where sulphide is rapidly oxidised. In cores with amphipods, a decrease of sulphide concentration was found in upper layers, while an increase of sulphide was found in deeper layers. Aggregation of amphipods generated pockets of light-brown sediment, characterised by high oxygen concentrations and no sulphide, and their depth was clearly dependent on amphipod density. This indicates that *M. affinis* has a potential to recolonise sulphide-rich sediments, devoid of macroscopic life, after the overlying water column has become oxygenated.

Introduction

The response of benthic organisms and ecological implications of sulphide have been reviewed by Vismann (1991), Bagarinao (1992) and Giere (1992). Sulphides are highly toxic, and consequently animals have adopted several mechanisms of avoidance. The mechanisms to avoid sulphide toxicity can be of behavioural, physiological and/or biochemical character. Escape behaviour, exclusion of sulphide from the body, sulphide-resistant enzymes and a shift to anaerobic metabolism are examples of strategies employed by benthic animals to cope with sulphide (Bagarinao 1992; Hagerman 1998). Sulphide

exposure can result in a dramatic reduction of macrobenthic species diversity (Andersin et al. 1978; Włodarska-Kowalczyk et al. 1996; Laine et al. 1997). The response to sulphide exposure is generally species specific but may also differ with life stages (Jahn et al. 1997).

Sediment heterogeneity is often induced by animal disturbance, which can be of different intensity in space and time (Hall 1994 and references therein). Bioturbation, the burrowing and sediment reworking of benthic animals, may enhance oxygen content in deep sediment layers (Meyers et al. 1987; Wetzel et al. 1995) and influence the biogeochemical fluxes in the sediment (Aller and Aller 1992, 1998; Pelegrí and Blackburn 1994; Tuominen et al. 1999). In sulphidic sediments bioturbation can thus result in a mosaic of patches with higher concentrations of oxygen around burrows and consequently lower concentrations of sulphide, since sulphide readily oxidises in the presence of oxygen. But bioturbation can also increase the sulphide content in deeper sediment layers, through vertical transportation of sulphate down to deep sediment layers where sulphate reduction may otherwise be limited, due to low concentrations of sulphate (Andersen and Kristensen 1991).

In the Baltic Sea, vast areas under the halocline (60–80 m) are hypoxic for long periods, due to the lack of mixing in the water column. During long, stagnant periods, oxygen concentrations often decrease to the point of anoxia, whereby sulphide may accumulate in the bottom sediment and reach high concentrations (Fonselius 1981). Inflows of saline and oxygenated water, which occur with varying intensity and duration (Matthäus and Franck 1992), allow recolonisation of the macrozoobenthos (Laine et al. 1997). Sulphide can also accumulate in the sediment when oxic conditions exist in the water column, especially under high loads of organic material (e.g. Giordani et al. 1996).

Monoporeia affinis (Crustacea) is one of the most abundant and widespread macrofaunal species in deep (> 10 m), soft bottom habitats in the Baltic Sea, and their general biology has been a matter of extensive studies (e.g. Segerstråle 1937; Sarvala 1986; Ólafsson

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and Elmgren 1991; Lehtonen and Andersin 1998). Their burrowing and feeding behaviour affects the sediment structure (Tuominen et al. 1999; authors' personal observations) and can, for instance, influence nitrogen fluxes in the sediment, mainly due to improved oxygen conditions (Tuominen et al. 1999). *M. affinis* has a relatively low tolerance to hypoxic conditions (Johansson 1997; Modig and Ólafsson 1998; Sandberg-Kilpi et al. 1999) and has been classified as a species not tolerant to sulphide exposure (Sandberg-Kilpi et al. 1999).

The aim of the present study was to investigate whether *M. affinis* can survive in sulphide-rich sediments when the overlying water is oxic and whether *M. affinis* is able to increase oxygen penetration to the sediment and thereby oxidise sulphide in surface sediment layers.

Materials and methods

Field sampling

Brown sediment and amphipods were collected with a benthic sledge in the vicinity of the Askö laboratory in the north-western Baltic Sea and immediately placed in a 4 °C dark thermoconstant room. Black sediment (smelling sulphide) was collected with a benthic sledge and a Kajak core sampler (50 cm²) at Landsort (58°43'N; 17°50'E) at 80 m, where the near bottom water was severely hypoxic (< 1% O₂). All amphipods used in the experiments were 1-year-old adults.

Survival experiments

Sulphide-rich sediment (SRS) was homogenised and added to ten plastic jars (internal diameter 8.5 cm, height 12 cm) forming a 5 cm bottom layer. Similarly, sieved (500 µm sieve) sulphide-free sediment (SFS) was added to ten jars. Brackish water, filtered through a sandfilter, was added to the upper edge of all jars. The average sulphide concentration at 10 mm was 248 ± 143 (SE) µmol l⁻¹ in SRS jars (*n* = 3) before addition of amphipods. In two of the SFS jars the sulphide concentrations were measured; concentrations of sulphide were below the detection limit at 10 mm depth.

Monoporeia affinis (4718 ind. m⁻²) were added to each microcosm, and they immediately started to burrow into the sediment. The survival was estimated after 1 week in ten jars (five SFS and five SRS) and after 7 weeks in ten other jars (five SFS and five SRS). All jars were kept in a 4 °C and bubbled with air.

The same microcosm set-up was used to investigate the effects of SRS on survival of amphipods at low and high densities. Four treatments of five replicates each were established: SRS with a low (1573 ind. m⁻²) or high (9436 ind. m⁻²) density of *M. affinis* and SFS with a low or high amphipod density. Before addition of the amphipods, the jars were air-bubbled for 24 h. The density experiment was conducted for 4 weeks.

pH, sulphide and oxygen profiles

Immediately after sampling, air pumps were connected to ten Kajak cores (SRS), which were aerated for 24 h. Twenty amphipods, corresponding to medium field densities (4000 ind. m⁻²), were added to five cores. Sulphide/oxygen and pH profiles were measured in two cores, with and without amphipods, on a daily basis for 5 days. After measuring sulphide/oxygen and pH profiles, the cores were sacrificed and the survival rate of amphipods measured.

Sixteen Kajak cores (SRS) were randomly chosen for four treatments. In eight cores the water column was aerated and no animals added. Oxygen/sulphide profiles were measured after 1 week

in four of them and after 3 weeks in the remaining four cores. The eight other cores were aerated 1 week before the addition of amphipods. Two amphipod densities were used (four replicates each), i.e. medium density (4000 ind. m⁻²) and high density (8000 ind. m⁻²). Two weeks after addition of the amphipods, oxygen/sulphide and pH profiles were measured as well as the survival rate.

Sulphide/oxygen measurements

A combined polarographic, 20 cm long, oxygen and ion-selective sulphide electrode in a stainless steel needle was used to determine sulphide/oxygen content in the sediment (described in Visscher et al. 1991). The equilibrium of the three forms of sulphide (S²⁻, HS⁻ and H₂S) is pH dependent, whereas the calibration took place in a well-buffered system of known pH and devoid of oxygen, to avoid oxidation of sulphide. The electrode was fastened to a micro-manipulator, which allows stepwise vertical measurements on a millimetre scale. Measurements in the cores were done in the water column 10 mm above the sediment surface, at the sediment surface and in the sediment at 1 mm intervals down to at least 10 mm. The pH was measured at each depth layer with a PHR-146B, micro-combination pH electrode (Lazar Research Labs). Sulphide in the text refers to the total concentration of all three forms of sulphide: S²⁻, HS⁻ and H₂S. All oxygen/sulphide and pH profiles in cores with amphipods were done in light-brown pocket formations.

Statistics

Differences in survival rates were investigated by means of one-way analysis of variance (ANOVA). Paired a posteriori comparisons of survival estimates were carried out with a Tukey's test, using 95% confidence limits. Prior to the analysis of variance all data were arcsine transformed, and Cochran's *C*-test was used to check the assumption of homoscedasticity.

Results

Monoporeia affinis survival rate

The amphipod survival rate ranged between 67% and 99% in the tolerance experiment conducted for 1 week and 7 weeks (Fig. 1a). Significantly fewer animals survived in SRS compared with brown SFS after 1 week (ANOVA *P* < 0.001, Fig. 1a), while there was no significant difference in survival rate between SFS and SRS after 7 weeks. However, the experimental time affected the survival rate; the amphipod survival rate was lower in both sediment types after 7 weeks compared with 1 week (ANOVA *P* < 0.001, Fig. 1a).

The survival rate was 78–91% in jars with different amphipod densities (Fig. 1b). There was no significant difference in survival rate between SRS and SFS in low- and high-density jars (ANOVA *P* > 0.05, Fig. 1b).

pH, sulphide and oxygen profiles

pH increased generally from on average 7.1 at the sediment surface down to 8.2–8.9 at 10 mm depth. The lowest pH values at 10 mm depth were found in cores with 40 amphipods, and the highest values, in cores air-bubbled 1 week.

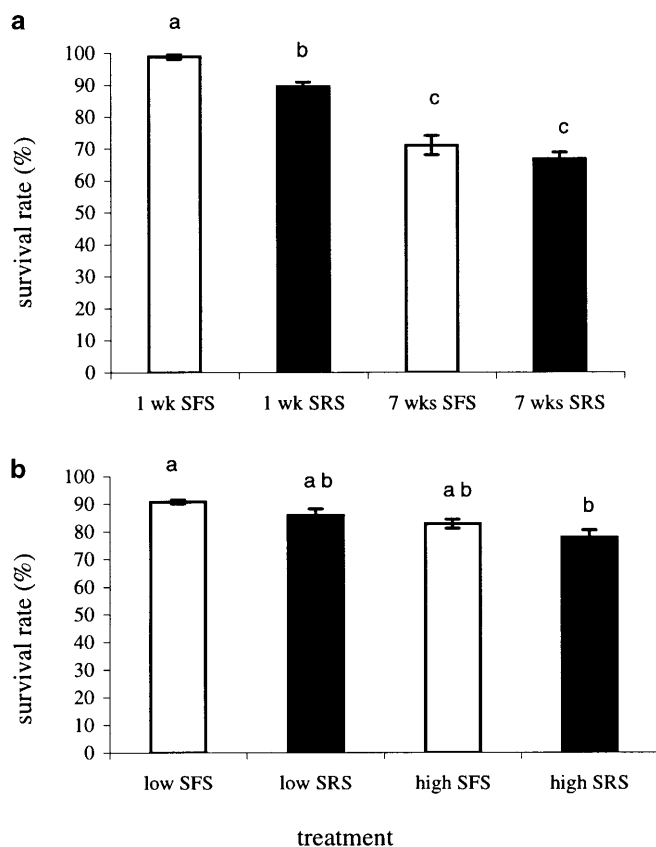


Fig. 1a, b *Monoporeia affinis*. Average survival rate (%) in treatments of amphipods: **a** in sulphide-free and sulphide-rich sediment for one (1 wk SFS, 1 wk SRS) and seven weeks (7 wks SFS, 7 wks SRS); and **b** in sulphide-free and sulphide-rich sediment for 4 weeks at low (low SFS, low SRS) and high amphipod densities (high SFS, high SRS). Error bars: SE. Common letter codes indicate no significant difference (Tukey test)

The sulphide concentration generally increased with depth from the sediment surface down to the 10 mm depth layer. In cores where *Monoporeia affinis* was present no sulphide was detected in the first 2 mm of the sediment from day 1 to day 5, while in cores without animals the concentration was 1–17 $\mu\text{mol l}^{-1}$. In deeper sediment layers, the sulphide concentration tended to be higher in cores with amphipods (Fig. 2). The highest total sulphide concentration (from sediment surface down to 10 mm) was found the third day in the core with amphipods (Fig. 2).

The rate of oxygen diffusion into the sediment was quicker in cores with *M. affinis* (Fig. 2). The oxygen concentration was higher in the core with amphipods already on the second day, but the largest differences were found the fourth and fifth day; oxygen concentrations were higher in the cores with amphipods at each depth down to 3 mm depth (Fig. 2).

Formation of microniches

In the cores where amphipods had been present for 2 weeks, “pockets” containing light-brown sediment

had developed. Adjacent to the pockets, the sediment was light brown only in the upper 1 or 2 mm but black underneath. The pockets were on average 15 mm deep (12–20 mm) in the high-density cores and on average 6 mm deep (2–8 mm) in the medium-density cores. Approximately 25% of the sediment surface consisted of pockets.

In one of the high-density cores, oxygen and sulphide concentrations were measured in a pocket formation and beside it (Fig. 3). In the pocket, oxygen was measurable down to 20 mm, and sulphide was only detected below that depth (239 $\mu\text{mol l}^{-1}$ at 25 mm depth). In the sediment next to the pocket, oxygen had a much shallower distribution, i.e. at 3 mm depth it was practically depleted, while the sulphide concentration was over 300 $\mu\text{mol l}^{-1}$.

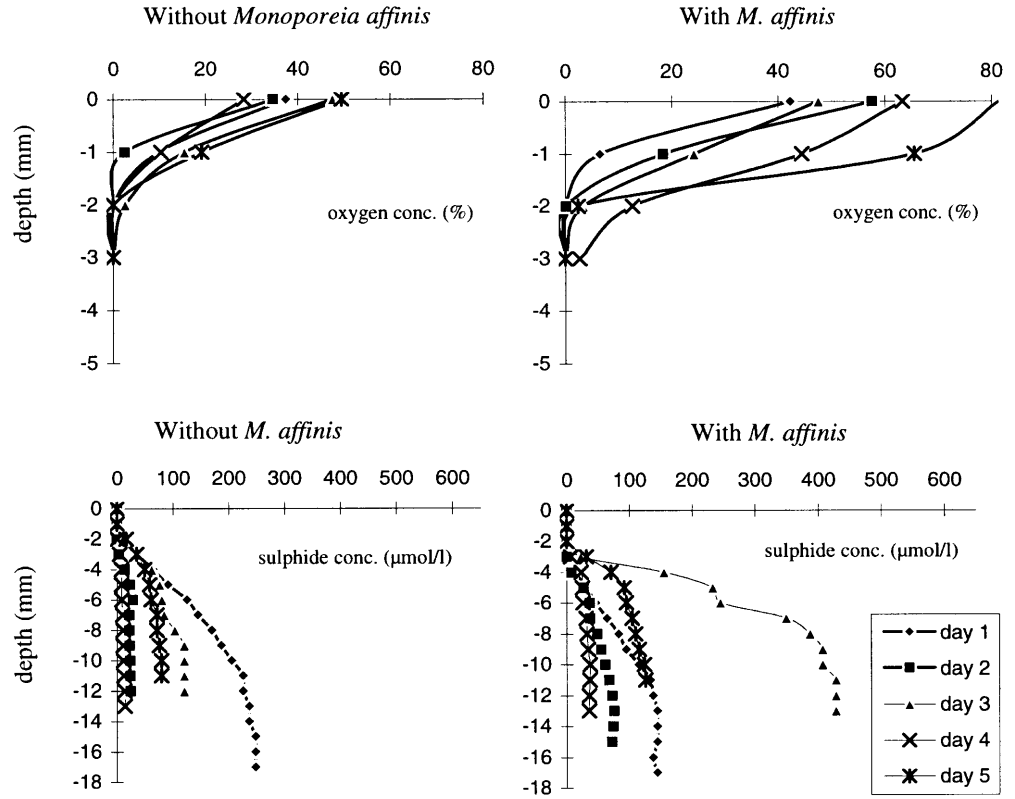
The reduction of sulphide in the sediment surface layers was density dependent in cores with amphipods after 2 weeks. In high-density cores, sulphide concentrations were below the detection limit in the first 8 mm, and measured on average 1 $\mu\text{mol l}^{-1}$ in the sediment layer 9–10 mm. In cores with amphipods at medium densities, the sulphide concentration was below the detection limit in the first couple of millimetres, but deeper down it increased from on average 76 at 4 mm to 242 $\mu\text{mol l}^{-1}$ in the 10 mm depth layer (Fig. 4a). Similarly, the oxygen distribution was deeper in cores with amphipods compared to cores without amphipods (Fig. 4b). The effect of amphipod bioturbation on the oxygen penetration was also density dependent; at 10 mm depth, oxygen concentration was on average 10% in amphipod high-density cores and 3% in medium-density cores.

In treatments without amphipods (1 and 3 weeks air-bubbling), sulphide was detectable close to the sediment surface or at 1 mm depth, and oxygen had a shallow distribution compared to cores with animals (Fig. 4a, b). Generally, the sulphide concentrations were higher in cores bubbled with air for 3 weeks compared to cores air-bubbled for 1 week (Fig. 4a). Oxygen penetrated the first 4 mm of the sediment in cores air-bubbled for 3 weeks and the first millimetres in cores bubbled with air for 1 week (Fig. 4b).

Discussion

The amphipod survival rate was in general high, independent of sediment type. The lowest survival rate was found after 7 weeks, both in SFS and SRS, possibly due to lack of food or accumulation of excretion products. Survival was significantly lower in sulphidic sediments after 1 week, presumably because already weak individuals were killed quicker in SRS than in SFS. We expected that under “sulphide stress” high densities of amphipods would result in lower survival rates, as they would have to cope with more intense individual interactions, plus higher concentrations of metabolites in the water.

Fig. 2 Oxygen (*upper panels*) and sulphide (*lower panels*) profiles performed each day for 5 days in one core with and one without amphipods (*Monoporeia affinis*)



However, we found no density effects on amphipod survival in sulphide-rich sediments. The positive effects of amphipod aggregations in the sediment, i.e. higher oxygen penetration and no measurable sulphides, may have counteracted the negative effects mentioned above. As long as the oxygen content in the water is high, the amphipods seem to avoid quite high concentrations of sulphide in the sediment by creating microhabitats where sulphide is rapidly oxidised. Other experiments (Ólafsson and Modig, unpublished) and field observations (Eriksson, personal communication) show that *Monoporeia affinis* burrow into the sediment even if it contains high concentrations of sulphide.

Sandberg-Kilpi et al. (1999) conducted tolerance experiments on *M. affinis* with sulphide concentrations

of 25 and 50 µmol l⁻¹. They concluded that *M. affinis* is a sulphide non-tolerant organism. Several studies indicate that *M. affinis* is very sensitive to low oxygen levels (Johansson 1997; Modig and Ólafsson 1998), and hypoxia in combination with sulphide exposure clearly increases the negative effect on the amphipod survival rate (Sandberg-Kilpi et al. 1999). However, the tolerance test conducted by Sandberg-Kilpi et al. (1999) is difficult to apply to natural conditions, as sulphide was added to the water column whereas in nature sulphide builds up in the sediment.

In our experiment, we tried to simulate a natural situation, in which the water column above a previously anoxic sediment, with high sulphide concentrations, turns oxic. Oxygen concentrations in the water column

Fig. 3 Oxygen (*left panel*) and sulphide (*right panel*) profiles from an amphipod (*Monoporeia affinis*) high-density core. Profiles were measured both in and beside a “pocket”

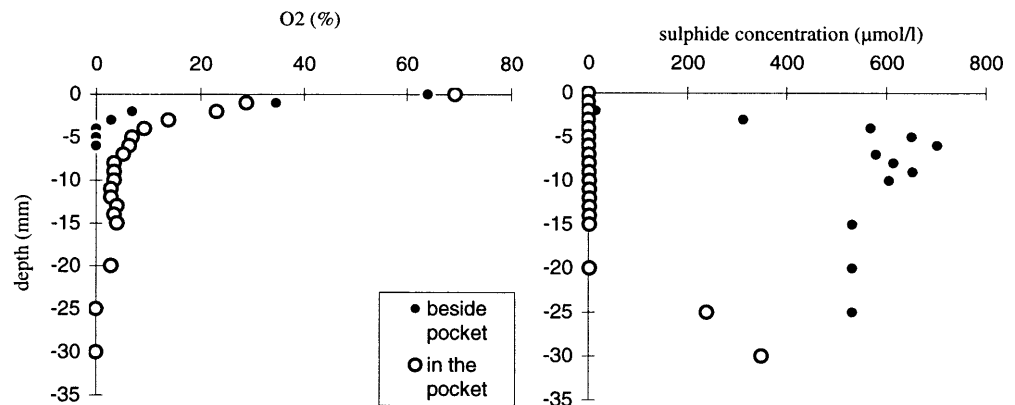
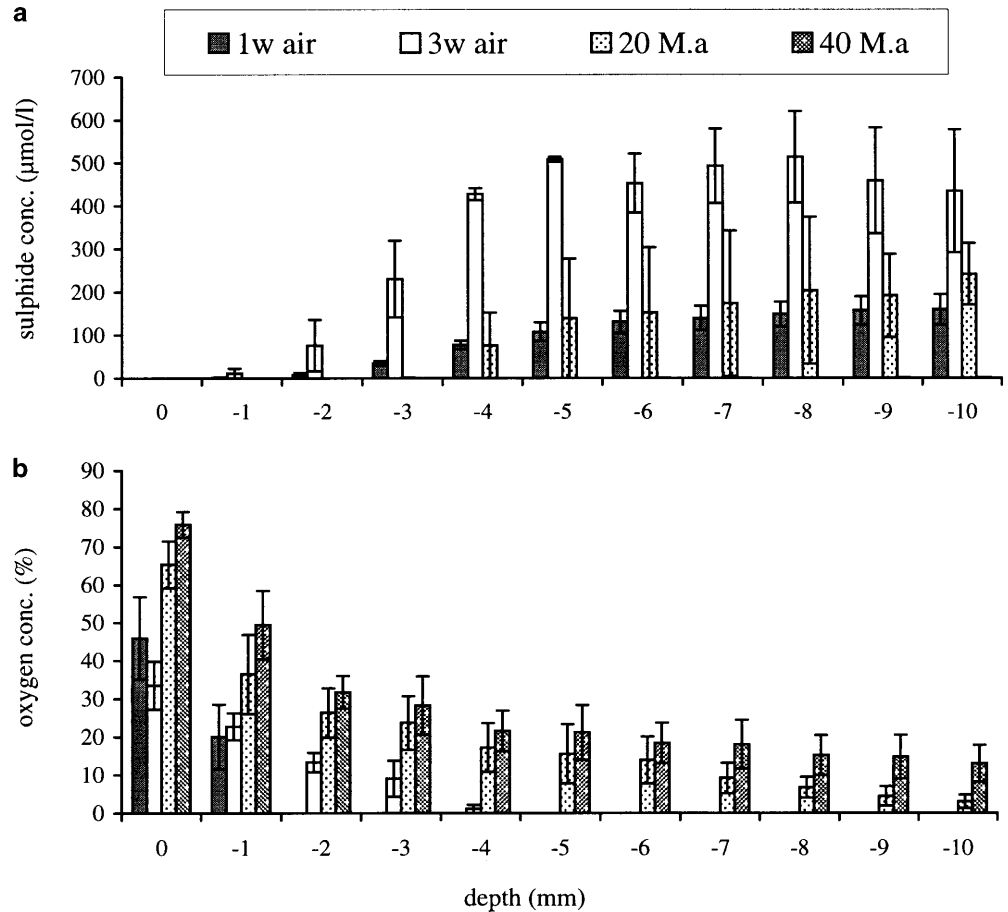


Fig. 4 Average **a** sulphide concentration ($\mu\text{mol l}^{-1}$) and **b** oxygen concentration (%) in different depth layers in all treatments. *Error bars: SE.* Depth layer 0 means sediment surface and negative values indicate distance (mm) from the surface into the sediment. Treatments: 1 and 3 weeks air-bubbling (*1w air*, *3w air*), and amphipods (*Monoporeia affinis*) at medium and high density (*20 M.a*, *40 M.a*) incubated for 2 weeks



ranged between 73 and 94% (normoxia), and the sulphide concentrations in the sediment were high, $248 \mu\text{mol l}^{-1}$ at 10 mm depth. The amphipods started to burrow into the sediment quickly after addition to the jars, and were thus exposed to high sulphide concentrations at least during a short period. But during burrowing they also reduced sulphide concentrations as they increased the oxygen diffusion rate into the sediment. It is clear from our results that the amphipod bioturbation ameliorated oxygen conditions and reduced sulphide concentrations in the upper sediment layers. Amphipod bioturbation also rendered the sediment heterogeneous; “pockets” of light-brown, oxygenated sediment had evolved after 2 weeks. One explanation for the pocket formation could be that amphipods detected where oxygen conditions were improved and/or sulphide oxidised, which lead to an aggregation to these areas. The attraction of fauna to tubes and burrows where the oxygen conditions are favourable has been demonstrated in a number of investigations (Reise and Ax 1979; Meyers et al. 1987, 1988; Wetzel et al. 1995). The formation of microniches with enhanced oxygen conditions seems to be a strategy to avoid exposure of sulphide.

Amphipod bioturbation caused a reduction of sulphides in the upper layers of the sediment, but in deeper layers the reverse situation tended to occur in the

short-term experiment; an increase of sulphide was found in bioturbated cores compared with cores without amphipods. The increase of sulphide in deeper layers may be due to an increased flux of sulphide from deeper parts up in the sediment due to the burrowing activity of the amphipods. Another likely explanation is that the amphipod bioturbation stimulated sulphate reduction, i.e. sulphate was transported into deeper anoxic sediment layers where sulphate reduction may be limited due to low concentrations of sulphate. Bioturbation can stimulate both aerobic and anaerobic bacterial activity (Andersen and Kristensen 1991 and references therein). During the first 5 days, the rate of oxygenation in the upper 2 mm of the sediment was quicker in cores with amphipods compared to cores without amphipods. The largest differences were found the fourth and fifth days. Oxygen and sulphide profiles were measured only once for each treatment the first 5 days and should be looked upon as indications. However, all five measurements in each treatment show a distinct pattern; the increase of oxygen levels in the upper 2 mm was quicker in cores with amphipods, and, in the same cores, the sulphide content was reduced in the upper layers while an increase was found in deeper layers.

To our surprise much higher concentrations of sulphide were found in sediment cores, without animals, that had been bubbled with air for 3 weeks compared

with 1 week. Oxygen penetration was notably deeper after 3 weeks or down to 4 mm, whereas only to 1 mm after 1 week. Obviously one would expect increased sulphide oxidation with deeper penetration of oxygen and therefore lower concentration of sulphide. However, like oxygen, sulphate might have been transported down from the water column and then fuelled the sulphate-reducing bacteria, causing increased levels of sulphide. Animal irrigation can result in increased fluxes of sulphate into deeper layers of the sediment (Andersen and Kristensen 1991), whether the water-bubbling could have similar effects, however, remains speculative.

In conclusion, the amphipod survival rate was high in sulphidic sediment when the water column was oxic. The amphipod bioturbation affected the oxygen and sulphide content in the sediment; oxygen conditions in the upper sediment layers were improved, and simultaneously the concentrations of sulphide were reduced. In the Baltic Sea, previously anoxic bottoms with sulphidic sediment may turn oxic after an inflow of oxygenated water from the North Sea. Amphipods seem to have the capability to quickly invade such areas, and their burrowing and reworking of the sediment may play an important role in "preparing" the sediment for further recolonisation.

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References

- Aller RC, Aller JY (1992) Meiofauna and solute transport in marine muds. *Limnol Oceanogr* 37: 1018–1033
- Aller RC, Aller JY (1998) The effect of biogenic irrigations intensity and solute exchange on diagenetic reaction rates in marine sediments. *J Mar Res* 56: 905–936
- Andersen FØ, Kristensen E (1991) Effects of burrowing macrofauna on organic matter decomposition in coastal marine sediments. *Symp Zool Soc Lond* 63: 69–88
- Andersin A-B, Lassig J, Parkkonen L, Sandler H (1978) The decline of macrofauna in the deeper parts of the Baltic proper and the Gulf of Finland. *Kiel Meeresforsch* 4: 23–52
- Bagarinao T (1992) Sulfide as an environmental factor and toxicant: tolerance and adaptations in aquatic organisms. *Aquat Toxicol (Amst)* 24: 21–62
- Fonselius SH (1981) Oxygen and hydrogen sulphide conditions in the Baltic Sea. *Mar Pollut Bull* 12: 187–194
- Giere O (1992) Benthic life in sulfidic zones of the sea – ecological and structural adaptations to a toxic environment. *Verh Dtsch Zool Ges* 85: 77–93
- Giordani G, Bartoli M, Cattadori M, Viaroli M (1996) Sulphide release from anoxic sediments in relation to iron availability and organic matter recalcitrance and its effects on inorganic phosphorus recycling. *Hydrobiologia* 329: 211–222
- Hagerman L (1998) Physiological flexibility; a necessity for life in anoxic and sulphidic habitats. *Hydrobiologia* 375/376: 241–254
- Hall SJ (1994) Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanogr Mar Biol Annu Rev* 32: 179–239
- Jahn A, Janas U, Theede H, Szaniawska A (1997) Significance of body size in sulphide detoxification in the Baltic clam *Macoma balthica* (Bivalvia, Tellinidae) in the Gulf of Gdansk. *Mar Ecol Prog Ser* 154: 175–183
- Johansson B (1997) Tolerance of the deposit-feeding Baltic amphipods *Monoporeia affinis* and *Pontoporeia femorata* to oxygen deficiency. *Mar Ecol Prog Ser* 151: 135–141
- Laine AO, Sandler H, Andersin A-B, Stigzelius J (1997) Long-term changes of macrozoobenthos in the eastern Gotland Basin and the Gulf of Finland (Baltic Sea) in relation to the hydrographical regime. *J Sea Res* 38: 135–159
- Lehtonen KK, Andersin A-B (1998) Population dynamics, response to sedimentation and role in benthic metabolism of the amphipod *Monoporeia affinis* in an open-sea area of the northern Baltic Sea. *Mar Ecol Prog Ser* 168: 71–85
- Matthäus W, Franck H (1992) Characteristics of major Baltic inflows – a statistical analysis. *Cont Shelf Res* 12: 1375–1400
- Meyers MB, Fossing H, Powell EN (1987) Microdistribution of interstitial meiofauna, oxygen and sulfide gradients, and the tubes of macro-infauna. *Mar Ecol Prog Ser* 35: 223–241
- Meyers MB, Powell EN, Fossing H (1988) Movement of oxybiotic and thiobiotic meiofauna in response to changes in pore-water oxygen and sulphide gradients around macro-infaunal tubes. *Mar Biol* 98: 395–414
- Modig H, Ólafsson E (1998) Responses of Baltic benthic invertebrates to hypoxic events. *J Exp Mar Biol Ecol* 229: 133–148
- Ólafsson E, Elmgren R (1991) Effects of biological disturbance by benthic amphipods *Monoporeia affinis* on meiobenthic community structure: a laboratory approach. *Mar Ecol Prog Ser* 74: 99–107
- Pelegri SP, Blackburn TH (1994) Bioturbation effects of the amphipod *Corophium volutator* on microbial nitrogen transformations in marine sediments. *Mar Biol* 121: 253–258
- Reise K, Ax P (1979) A meiofaunal "thiobios" limited to the anaerobic sulphide system of marine sand does not exist. *Mar Biol* 54: 225–237
- Sandberg-Kilpi E, Vismann B, Hagerman L (1999) Tolerance of the Baltic amphipod *Monoporeia affinis* to hypoxia, anoxia and hydrogen sulfide. *Ophelia* 50: 61–68
- Sarvala J (1986) Interannual variation of growth and recruitment in *Pontoporeia affinis* (Lindström) (Crustacea: Amphipoda) in relation to abundance fluctuations. *J Exp Mar Biol Ecol* 101: 41–59
- Segerstråle SG (1937) Studien über die Bodentierwelt in südfinnländischen Küstengewässern. III. Zur Morphologie und Biologie des Amphipoden *Pontoporeia affinis*, nebst einer Revision der *Pontoporeia*-Systematik. *Commentat Biol Soc Sci Fenn* 7(1): 1–183
- Tuominen L, Mäkelä K, Lehtonen KK, Haahti H, Hietanen S, Kuparinen J (1999) Nutrient fluxes, porewater profiles and denitrification in sediment influenced by algal sedimentation and bioturbation by *Monoporeia affinis*. *Estuar Coast Shelf Sci* 49: 83–97
- Vismann B (1991) Sulfide tolerance: physiological mechanisms and ecological implications. *Ophelia* 34: 1–27
- Visscher PT, Beukema J, Van Gernerden H (1991) In situ characterisation of sediments: measurements of oxygen and sulfide profiles with a novel combined needle electrode. *Limnol Oceanogr* 36: 1476–1480
- Wetzel MA, Jensen P, Giere O (1995) Oxygen/sulfide regime and nematode fauna associated with *Arenicola marina* burrows: new insights in the thiobios case. *Mar Biol* 124: 301–312
- Włodarska-Kowalczyk M, Janas U, Szaniawska A (1996) Hydrogen sulphide and other factors influencing the macrobenthic community structure in the Gulf of Gdansk. *Oceanologia* 38: 379–394