

## BLACK SPOTS PRODUCED BY BURIED MACROALGAE IN INTERTIDAL SANDY SEDIMENTS OF THE WADDEN SEA: EFFECTS ON THE MEIOBENTHOS

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### ABSTRACT

The effects of buried decaying macroalgae on meiobenthos were examined in intertidal sandy sediments of the Wadden Sea of Lower Saxony. *In situ* experiments confirmed that one of the principal causes of the formation of reduced surface sediments or 'black spots' on the tidal flats is the increasing occurrence and subsequent decomposition of filamentous green algae (*Enteromorpha* spp.) buried in the sediment. Five to fifteen days after algal material had been buried, the sediment surface turned black. The impact of these black spots on meiobenthos was dramatic: the changed chemical conditions in the sediment resulted in long and drastic reductions in meiofaunal abundance and number of taxa. A multi-dimensional scaling (MDS) analysis of data on meiobenthic abundances revealed that samples from black-spot areas were clearly separated from those of control and reference areas. Re-oxidized black spots showed recolonization by meiofaunal animals, with numbers of individuals and taxa similar to those of oxidized surface sediments. The use of abundances of members of higher meiobenthic taxa to monitor changes in the sediment's chemistry, especially those caused by biomass overload, is discussed.

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Keywords: black spots, meiofauna, buried macroalgae, tidal flats

### 1. INTRODUCTION

Since 1989, the tidal flats of the German Wadden Sea have been affected by increasing growth of green macroalgae, particularly *Ulva* spp. and *Enteromorpha* spp. (Reise *et al.*, 1994; Reise & Siebert, 1994), which is possibly due to large-scale man-induced changes of the environment, e.g. eutrophication (De Jonge & Essink, 1991; Beukema, 1992; Brockmann *et al.*, 1994; Asmus *et al.*, 1994; Michaelis & Reise, 1994; Kolbe *et al.*, 1995). Eutrophication in estuaries and coastal waters is well documented and may explain the increased growth of certain species of epibenthic macroalgae that take advantage of such conditions (Schories & Reise, 1993; Reise *et al.*, 1994). Increasing degradable organic matter may strongly affect the biogeochemical cycling and nutrient processes (Conley & Johnstone, 1995) and lead to oxygen depletion (Kelly & Nixon, 1984), as well as to accumulation of toxic sulphide (Holmer & Kristensen, 1994; Osinga *et al.*,

1995) even at the surface sediment layer. Increasing organic matter may also cause long-term changes in the zoobenthic community (Beukema, 1991, 1992; Michaelis & Reise, 1994) and even massive death of benthic fauna (Reise, 1983; Reise *et al.*, 1994; Schories, 1991; Heip, 1995).

Since 1987, black sandy surface sediments (later called 'black spots', Michaelis *et al.*, 1992; Philippart & Brinkman, 1992) have been observed to increase in the German Wadden Sea. Early investigations indicated a close connection between the appearance of masses of green macroalgae and the formation of black spots: after having been dislodged by tidal flow and storms, the dense algal mats formed compact rolls which were covered by sand and thus seemed to vanish without leaving a trace. Some days later, however, black spots would appear precisely at such sites (Höpner & Michaelis, 1994; own obs.). Studies carried out on the dynamics of these black spots indicated a marked variability in appearance, size, and lifetime (Kolbe, 1991; Thiessen, 1992; own obs.). Fur-

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ther observations revealed that black spots may also originate from decaying clams (Eversberg *et al.*, 1994; Suppes, 1995; own obs.), from local erosion, or from black pore water seeping out at the slopes of tidal channels (Höpner & Michaelis, 1994; own obs.). Black spots do not only appear in summer, when the oxidized sediment layer is thinner than in winter, but they also occur in winter (Michaelis *et al.*, 1992; own obs.).

Recently, studies conducted by our working group on artificial black spots (generated by buried macroalgal biomass) have revealed dramatic changes in the sediment chemistry (Höpner & Michaelis, 1994). Such changes may turn the sediment into an unfavourable habitat for benthic organisms, including meiobenthos. The effects of organic enrichment on the meiobenthos have been treated frequently in the literature (Coull & Chandler, 1992), but most of the publications refer to sewage rather than decaying macroalgae. In addition, most of the studies dealing with macroalgal decomposition in shallow sandy beaches and its effects on the benthic environment are based on macroalgal biomass deposited on top of the sediment after being uprooted and transported by wave action (McComb *et al.*, 1979; Koop *et al.*, 1982; McLachlan, 1985; Reise, 1983; Rosenberg, 1985; McGwynne *et al.*, 1988; Rieper-Kirchner, 1989, 1990; Sundbäck *et al.*, 1990; Enoksson, 1993; Villano & Warwick, 1995). These studies do not treat buried macroalgae. The present investigation focuses on the effects that algal biomass buried in the sediment has on the meiobenthos.

## 2. MATERIALS AND METHODS

### 2.1. STUDY SITE

The study site 'Gröninger Plate' is a sandy tidal flat between the mainland and Spiekeroog island (North Sea, Germany). It is subject to a semi-diurnal tidal regime. The selected experimental site (about 25 m<sup>2</sup>) is located in the northwestern part of the Plate (53°43'57"N and 07°45'27"E). It is far away from tidal channels and is emersed for four hours during low tide.

When the experiment took place the area was inhabited by the polychaetes *Arenicola marina* and *Lanice conchilega* at relatively low densities. The sediment consisted of well-sorted fine sand (92%) with a medium particle size of 0.12 mm (Röhring pers. comm.) mixed with 8% (by weight) of silt-clay (<63 µm). Loss on ignition was 1.2% of dry weight. The water content amounted to 20% (W/W).

### 2.2. EXPERIMENTAL DESIGN

To induce the formation of black spots by burying macroalgae and to assess the effects on meiobenthos and sediment chemistry, parts of the selected

site were treated as follows: on 20 July 1994, three areas of 1 x 1 m were delimited. The sediment of two areas was excavated to a depth of about 16 cm. Fifty kg of *Enteromorpha* spp. freshly collected in the vicinity were put inside the first area ('algal load') and covered with the removed sediment. We chose *Enteromorpha* because this type of algae was observed naturally buried in the summer of 1993 and 1994. The algal mat formed a layer about 6 cm thick. In the second area ('control'), the removed sediment was replaced without addition of algae in order to determine whether the observed effects were actually caused by the buried biomass and not by mechanical disturbance. The third area ('reference') remained untreated. To obtain a picture characterizing the initial situation of the study site, about 1 h before the start of the experiment sediment cores of 14.5 mm in diameter and 2 cm thick were taken for meiofauna, using cut-off plastic syringes. Likewise, cores (inner diameter 5 cm; length 30 cm) were taken to characterize the sediment chemistry.

For meiobenthos monitoring, nine parallel cores (diameter 14.5 mm; area 1.65 cm<sup>2</sup>) of the top 2-cm layer were taken approximately every week until 15 August 1994. Later sampling was done on a monthly basis until the end of the experiment (13 October 1994). The plunger of the cut-off syringe was withdrawn as the syringe cylinder was pushed into the sediment so that core compression was avoided. The sediment samples were treated with a solution of magnesium chloride (75 g·dm<sup>-3</sup>) to remove strongly attached animals from the particles (Pfannkuche & Thiel, 1988). They were fixed with a 7% formaldehyde solution containing rose bengal (1 g·dm<sup>-3</sup>). The sediment was sieved once through a 500-µm mesh with tap water to exclude macrofauna and larger particles. The sediment which passed was resuspended in a 500-cm<sup>3</sup> cylinder and the meiofauna was poured through a 63-µm sieve by successive shaking, decanting and sieving (Wieser, 1960). Meiofaunal taxa were defined as metazoans that passed through a 0.5-mm sieve and were retained on a 0.063-mm sieve (Giere, 1993). Meiofaunal animals were sorted into major taxa and the individuals were counted under a dissecting microscope. To assess the effects of black spots on the vertical distribution of meiobenthos, sediment cores were taken and immediately sliced at depth intervals of 0.5 cm up to a depth of 4 cm. The slices were treated as before. In order to describe the meiofauna distribution along the horizontal transition zone from an oxidized surface to a reduced one (black spot) and back to oxidized surface sediment, an array of ten square cores (2 x 2 cm each), forming a linear transect, were used. Samples were collected by pushing the tubes into the sediment to a depth of 2 cm and by treating them as before. Meiobenthic densities are expressed as number of individuals (N) per 10 cm<sup>2</sup>.

### 2.3. SEDIMENT CHEMISTRY

For chemical analysis, sediment cores (inner diameter 5 cm; length 30 cm) were taken at the same time as meiofauna samples. Cores were sliced at 2-cm intervals, except for the top 2-cm layer which was cut at 1-cm intervals. Some of the sediment slices were dried at 105°C to estimate the water content. The remaining sediment was lyophilized, homogenized and analysed for total organic matter (TOM) as loss on ignition at 500°C for four hours. Vertical profiles of the redox potential (Eh) in the sediment were measured *in situ* with multi-electrode lances (Forster & Graf, 1992), modified to enable simultaneous measurements at 2-cm intervals down to a depth of 30 cm. For hydrogen sulphide, pore water was sucked out of the sediment with a pore-water lance. Samples were stabilized with zinc acetate and analysed for sulphide by applying a modified methylene blue method (Cline, 1969).

Chlorophyll *a* (Chl *a*, used for an estimate of living algal biomass) and phaeopigments (phe, used for an estimate of degraded plant material) were determined in the lyophilized sediment samples, according to Stal *et al.* (1984).

### 2.4. STATISTICAL ANALYSIS

Significance tests for differences in mean total meiofaunal abundances between black spots, control, reference and reoxidized black spots were performed by using the Mann-Whitney U-tests with the aid of a SYSTAT's Npar module (Wilkinson, 1990).

## 3. RESULTS

### 3.1. DEVELOPMENT OF BLACK SPOTS

The algae-loaded area showed a black surface one week after the start of the experiment. The sediment was slimy and the sediment cores smelled strongly of sulphide. On 2 August 1994, a visual examination of undisturbed sediment cores from the algae-loaded area revealed a compact blackish-green layer without recognizable algal structures. All sediment cores from the control and reference areas exhibited a well-delimited oxidized brown top zone 1 to 3 cm thick, overlying black anoxic sediment. A typical redox potential profile within a black spot is shown in Fig. 1. Even the top 1-cm layer exhibited a redox potential of about -200 mV which became only slightly more negative with increasing depth. A redox potential discontinuity layer (RPD) was not distinguished. Redox potentials from the control and reference areas showed a distinct RPD layer. Values beyond +200 mV, even +300 mV were measured in the top layers (Eversberg, pers. comm.).

Sulphide in the pore water of the algae-loaded area increased strongly after one and a half weeks, up to

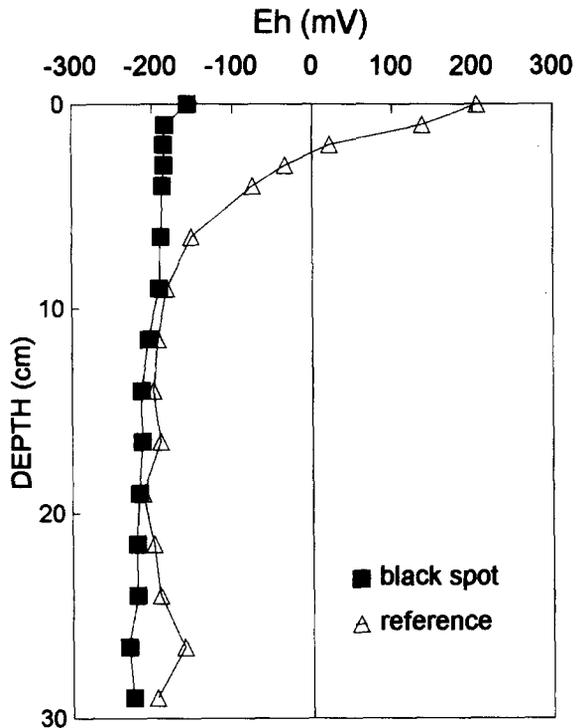


Fig. 1. Typical vertical profile of redox potentials (Eh) of surface sediment that turned black, compared with an adjacent oxidized reference sediment.

14 mmol·dm<sup>-3</sup> in the algal biomass layer, with a mean concentration of 5.7 mmol·dm<sup>-3</sup> for the whole sediment column. After three weeks the maximum concentration reached 18 mmol·dm<sup>-3</sup>, with a mean of 7.2 mmol·dm<sup>-3</sup> for the sediment column. Almost two months later, 13 mmol·dm<sup>-3</sup> were recorded in the top layers. Finally, almost three months after the beginning of the experiment, the concentration decreased to 4 mmol·dm<sup>-3</sup> with a vertical mean concentration of 2.2 mmol·dm<sup>-3</sup> (Fig. 2). Values in the control and reference areas never exceeded 2 mmol·dm<sup>-3</sup>.

Shortly before the start of the experiment TOM was about 1.2% DW (Fig. 3). TOM depth profiles were also recorded 12, 55 and 84 days later (Fig. 4). For the algae-loaded area it can be seen that the layer between 10 and 16 cm depth was richest in TOM (highest value observed: 62.7% DW) which corresponded to the algal layer. After 55 days (14 September 1994), TOM in the algal area had decreased to one tenth. Three months later (13 October 1994), TOM had attained 1.4%, almost the value measured before the start of the experiment. Visual examination showed that the algal layer was no longer the same. It had been replaced by a very fine, strongly black slimy sediment mixture with some small black fibrous algal remains. The TOM content of the unloaded areas at the equivalent depth layers remained almost constant at 1.2% DW.

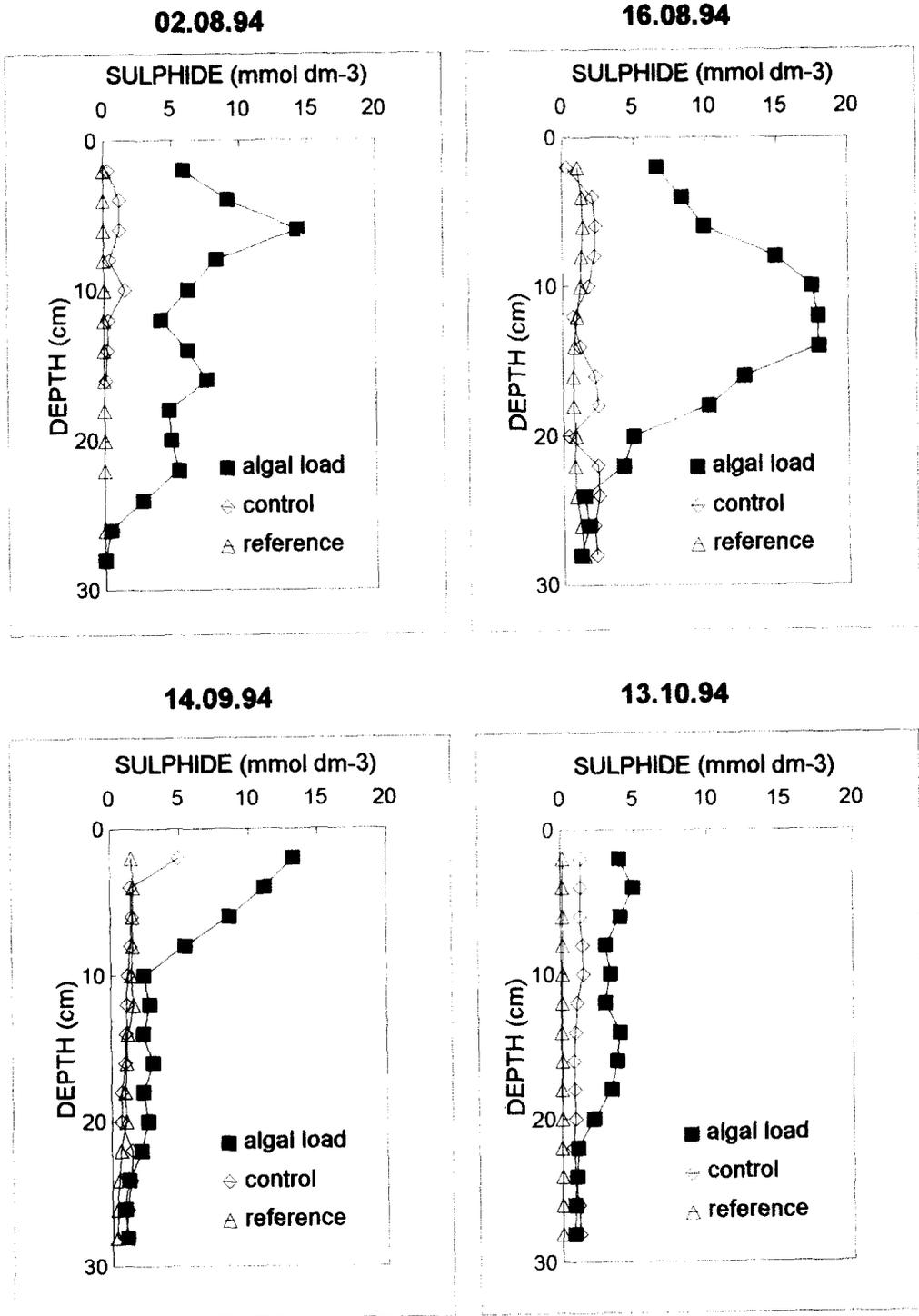


Fig. 2. Depth profiles of sulphide in the interstitial water of the sampling areas, a) algal load: area loaded with buried macroalgae; b) control: disturbed area through digging sediment but without addition of algae; c) reference: unloaded and undisturbed area.

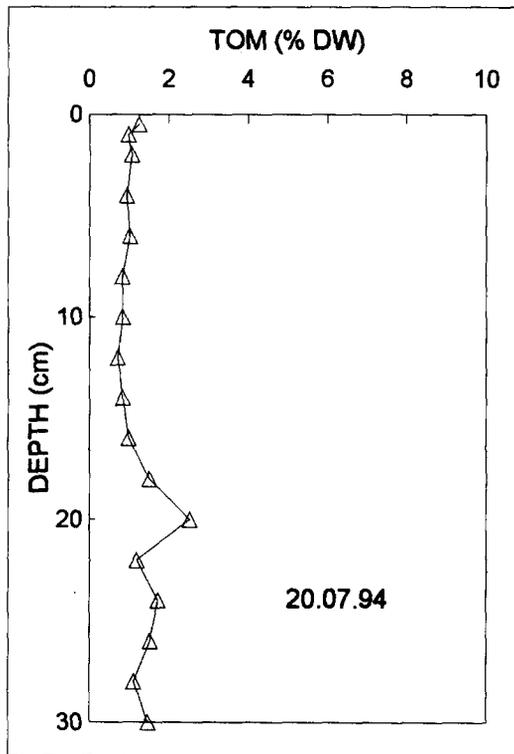


Fig. 3. Depth profile of total organic matter (TOM), in the sediment of the study site just before the start of the experiment.

Vertical profiles of Chl *a* and phaeopigments in the sediment of the study site just before the start of the experiment are shown in Fig. 5. It has been observed that the top 0.5-cm layer contained higher concentrations of Chl *a* and of its phaeopigment. Changes in Chl *a* concentrations in the sediment during the algal loading experiment are summarized in Fig. 6. Already after twelve days, most of the buried Chl *a* was converted to phaeopigment, which attained  $208 \mu\text{g}\cdot\text{g}^{-1}$ . Fifty-five days later the Chl *a* concentration had dropped by half and its phaeopigment reached  $310 \mu\text{g}\cdot\text{g}^{-1}$ . Finally, 84 days after the start, no peak of Chl *a* was detected and the phaeopigment content dropped to  $57 \mu\text{g}\cdot\text{g}^{-1}$  at the depth where algae had been buried.

### 3.2. MEIOFAUNA IN BLACK SPOT AREAS

Eight higher meiobenthic taxa were identified during the study: Nematoda, Harpacticoida (adults, copepodids and nauplii), Ostracoda, Tardigrada, Turbellaria, Gastrotricha, Polychaeta, Bivalvia. The polychaetes and bivalves belonged to the temporary meiofauna, *i.e.* juvenile macrofauna that passed through the  $500\text{-}\mu\text{m}$  sieve but was retained by the finer sieve

( $63\mu\text{m}$ ) (Coull & Bell, 1979). The other groups belong to the permanent meiofauna.

Meiofaunal abundances obtained from the top 2-cm sediment layer within the black spots were drastically reduced ( $P < 0.001$ ) throughout the experiment. The mean total abundance in the unloaded areas (control and reference) amounted to 1748 and 1640 ind per  $10 \text{ cm}^2$ , respectively. By contrast within the black spot (loaded area) it amounted to only 65 ind per  $10 \text{ cm}^2$ , *i.e.* about 3.8% of the abundance found in the unloaded areas. In addition, only nematodes and occasionally some nauplii were found. Throughout the experiment, vertical profiles of total meiofaunal abundances showed that within the black spot meiobenthic animals were either absent or strongly reduced, and mostly restricted to a few nematodes and nauplii in the top 5-mm layer. Fig. 7 typically shows the vertical profile of total abundances at the end of the experiment on 13 October 1994. In normal sediments, *i.e.* with an oxidized surface layer, the meiofauna was found deeper in the sediment, although the abundances and the number of taxa decreased with increasing depth. Specimens of nematodes were found deepest in the sediment layers. Harpacticoids (adults) and nauplii, polychaetes, turbellarians, and bivalves were concentrated in the top layers.

Spatial and temporal meiofauna patterns during the experiment were analysed by Multi-Dimensional Scaling (MDS) (Field *et al.*, 1982), by applying the SYSTAT's MDS module (Wilkinson, 1990). Similarities of higher taxa compositions among treatments are graphically presented, on the basis of Euclidean normalized distances computed from standardized abundance data of the eight meiofaunal taxa (Fig. 8). It showed a clear separation between the samples of the black-spot area and the others (control and reference) throughout the sampling period.

### 3.3. RECOVERY OF MEIOFAUNA AFTER RE-ESTABLISHMENT OF OXIDIZED SEDIMENT

Distinctly re-oxidized areas in the algae-induced black spots were observed during sampling on 15 August 1994. On the following two sampling days (14 September and 13 October) the re-oxidized areas were larger, but inhomogeneously distributed. The redox horizon, *i.e.* the thickness of the oxidized layer with its characteristic brown colour, ranged from 0.7 to 1.0 cm. The redox horizon of the control and reference areas ranged from 1.5 to 3.0 cm. Differences in mean total abundances between black spots and reoxidized black spots were highly significant ( $P < 0.001$ ). Total meiofaunal abundances of re-oxidized areas reached about 1000 ind per  $10 \text{ cm}^2$  comparable to reference and control squares ( $P > 0.5$ ). An MDS analysis separated samples of black spots quite well from those of re-oxidized black spots, reference, and control (Fig. 9).

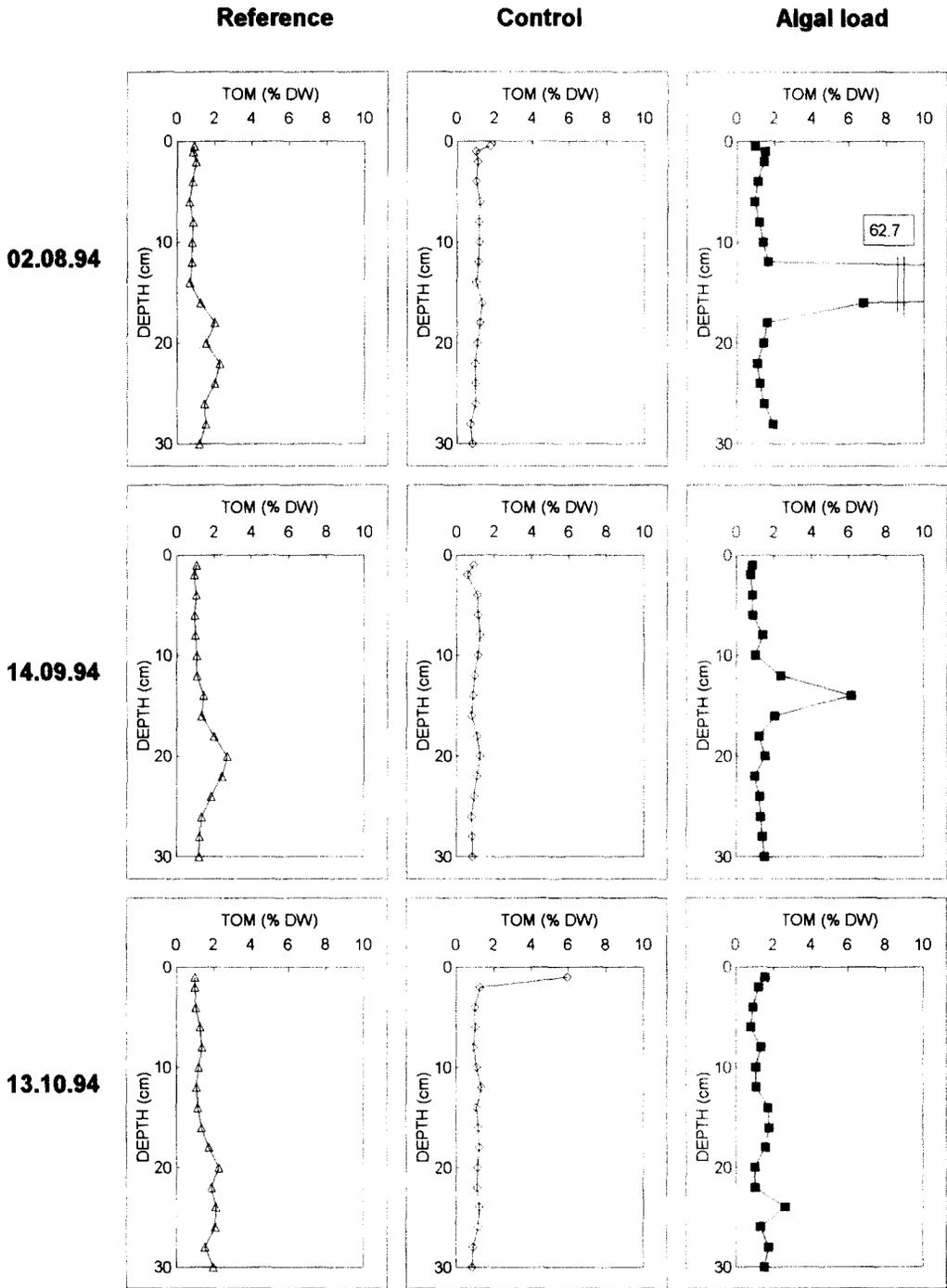


Fig. 4. Depth profiles of total organic matter (TOM), 12, 55 and 84 days after the start of the experiment. The three sampling areas are described in the legend of Fig. 2.

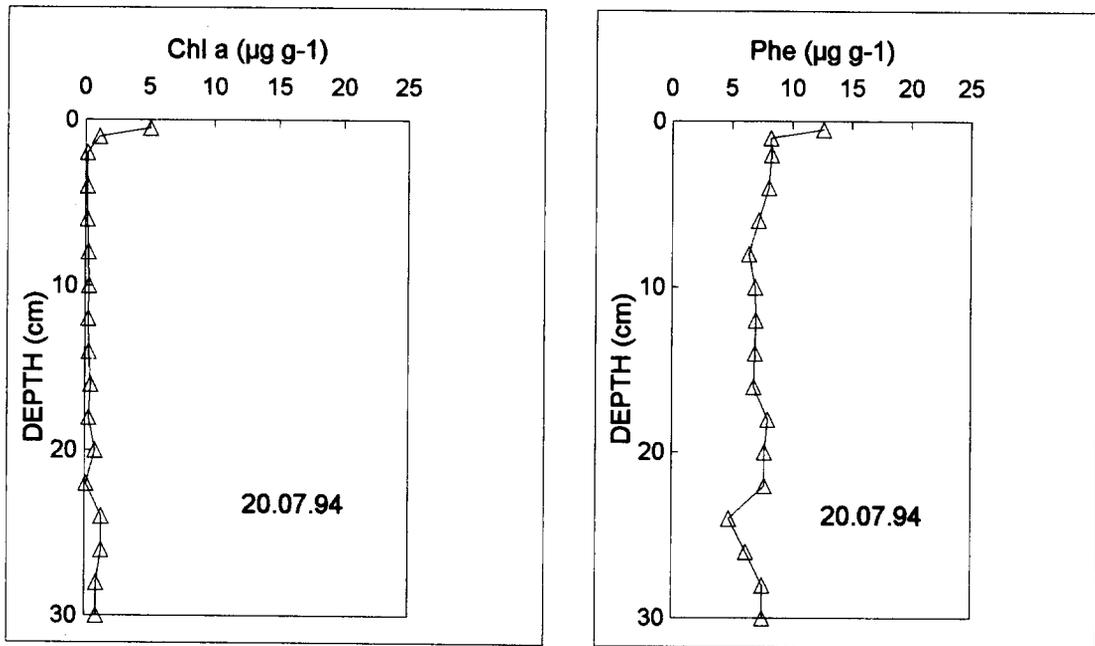


Fig. 5. Depth profiles of Chl a and phaeopigment content in the sediment of the study site just before the start of the experiment (20 July 1994).

#### 4. DISCUSSION

##### 4.1. NATURAL BURYING PROCESS OF MACROALGAE AT THE GRÖNINGER PLATE

Between May and September 1993 and 1994 large intertidal areas south of Spiekeroog island were covered by green macroalgal mats, largely dominated by *Enteromorpha* spp. After germination in early spring (Schories, 1991), algae attach to solid substrates such as worm tubes, mollusc shells and stones (Reise, 1983; Schories & Reise, 1993). In May a rapid growth starts due to higher temperatures and longer light periods. In summer, because of nutrient exhaustion, self-shading and higher temperatures, the decay begins. Waves and tidal currents uproot the algae from the substrates and cause larger assemblages that drift and roll with the tidal current. 'Parcels' of sediment containing algal biomass are deposited and do not float during the next high tide. Finally, they are covered with sediment so that they seem to have disappeared. However, some days later a black spot marks the place of such a natural burial.

The rapid decomposition of the macroalgae buried in the sediment caused severe changes in the chemical environment (Höpner & Michaelis, 1994): very low redox potentials and extremely high concentrations of sulphide were measured even in the top layers. The

Eh gradients showed the decrease of the oxidized and the increase of the reduced zone in the sediment. In an unloaded area, redox potentials around +200 mV and higher were found in the top 1-cm layer, typical of oxidized sediments (Jørgensen, 1977a). By contrast, redox potentials below -150 mV, which are normally found only in deeper layers, were found at the sediment surface in an algae-loaded area. Pore-water concentrations of sulphide in the range of 4-9 mmol·dm<sup>-3</sup> in deep layers and occasionally in the top layers are among the highest ones reported for marine sediments (Goldhaber & Kaplan, 1975; Jørgensen 1977b). We found concentrations of 17 mmol·dm<sup>-3</sup> and more in natural black spots, and 23 mmol·dm<sup>-3</sup> after experimental simulation of the observed natural burying process (Höpner & Michaelis, 1994; Oelschläger, 1994). This means that the pore-water sulphate had been completely reduced to sulphide. One week after the 'burial' the concentration of sulphide increased in the algal layer. Three weeks later a wide peak with a characteristic 'belly' form was built around and above the buried algae. Two months later the belly form had disappeared and the concentration peak moved to the surface. After three months, sulphide concentrations decreased. A similar dynamic was observed for dissolved organic carbon (DOC) which attained concentrations of up to 800 mg·dm<sup>-3</sup> (Kellner-Gross, 1994; Höpner & Michaelis, 1994). The apparent upward movement cannot only

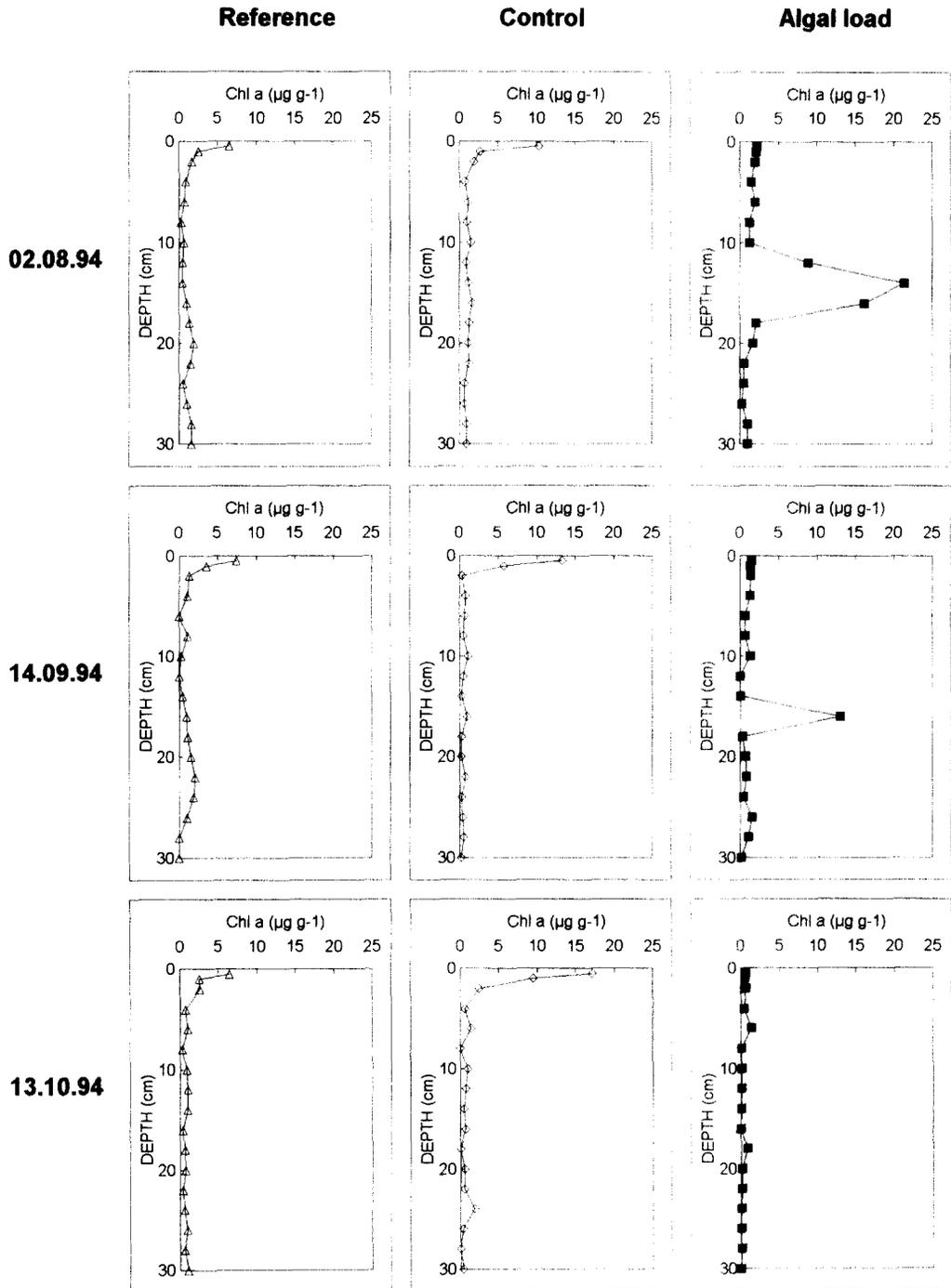


Fig. 6. Depth profiles of Chl a concentrations in the sediment of the three sampling areas, 12, 55 and 84 days after the start of the experiment. The sampling areas are described in the legend of Fig. 2.

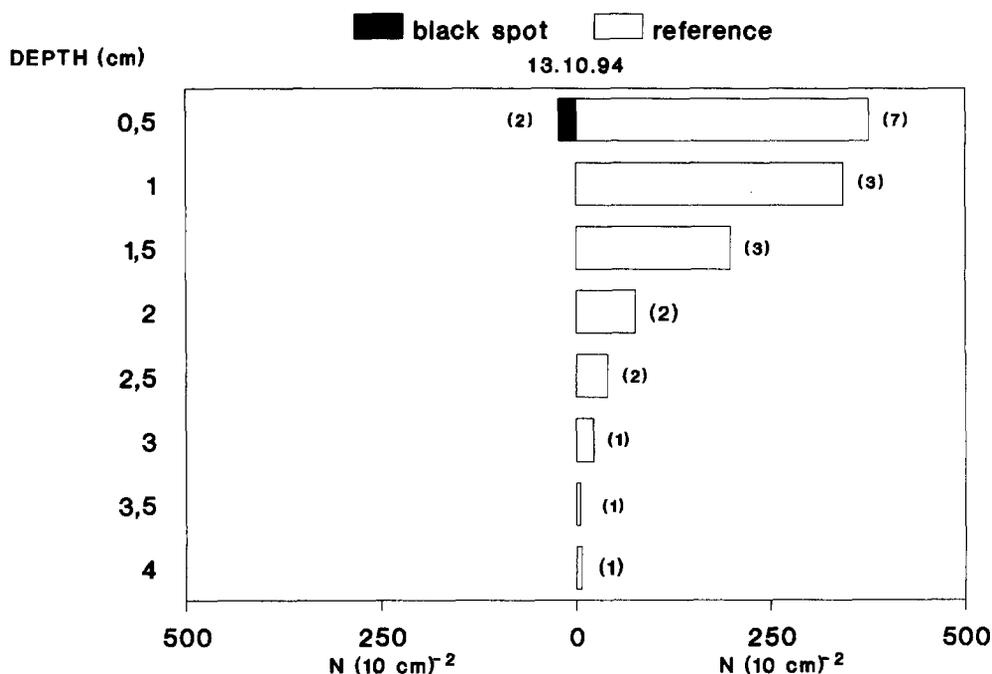


Fig. 7. Depth profiles of total meiofaunal abundances at the end of the experiment (13 October 1994) Left: black surface sediment (black spot). Right: oxidized surface reference sediment. In brackets, the number of taxa.

be explained by diffusion. Postma (1988) stated that the rate of interstitial water renewal and removal of dissolved end products may be very fast in sand flats since part of the water percolates out of the sediment at low tide. Another mechanism which may contribute to the upward transport of pore water is the formation of methane gas bubbles and the enlargement of the bubbles by hydrostatic decompression during ebb (Langner-Van Voorst, pers. comm.). Normally, anaerobic decomposition does not go beyond sulphate reduction (Postma, 1988). However, with the extremely high supply of organic matter, methane gas is readily formed, coincidentally with sulphate reduction (Höpner & Michaelis, 1994).

Rapid exchange of interstitial water should prevent long persistence of black spots, but in most cases this is not true. The most probable explanation is that the degradation of such a quantity of organic matter favours the growth of anaerobic bacteria, which, in spite of the oxygen-rich seawater (90% saturation) and wind ventilation during low tide, may form a barrier to oxygen diffusion into the sediment (Jørgensen & Fenchel, 1974). Additionally, the upward advection of pore water may cause a depression of the downward transport of oxygen and nitrate. Finally, because macro- and meiofauna were practically absent, there was no bioturbation, a natural process which accelerates the transport of solutes (Postma, 1988; Aller & Aller, 1992).

The dynamics of the vertical gradients of TOM, Chl *a*, phaeopigment, sulphide and other dissolved substances in the sediment, indicated a rapid degradation of the macroalgae. A first step is the release of large amounts of DOC into the pore water within a few weeks (Höpner & Michaelis, 1994). More than 90% of this DOC was composed of small degradable substances such as sugars, amino acids and short-chain fatty acids (Roback, 1995). The mineralization of these metabolites sometimes led to both exhaustion of sulphate and sulphide production. In the algal layer pH values dropped to 6.5-7 within a few days, while in the reference and control areas pH ranged from 7.2 to 8.1. In strongly reduced sediments pH values can drop to approximately 6 (Giere *et al.*, 1988) because of the production of carbon dioxide, organic acids and hydrogen sulphide (Foree & McCarty, 1970; Berner 1980). This acidic environment may favour the breaking up of chlorophyll into phaeopigments (Sun *et al.*, 1993) which has been considered an indication of chloropigment diagenesis (Sun *et al.*, 1991). Chl *a* of algae is degraded over a period of several weeks (Bianchi *et al.*, 1988), a process which results in the release of their molecular components into the interstitial milieu. Successive steps are the loss of magnesium, the loss of phytol, the modification of the side chains and the cleavage of the tetrapyrrolic ring (Brown *et al.*, 1991).

On the tidal flats of the Wadden Sea, the microphy-

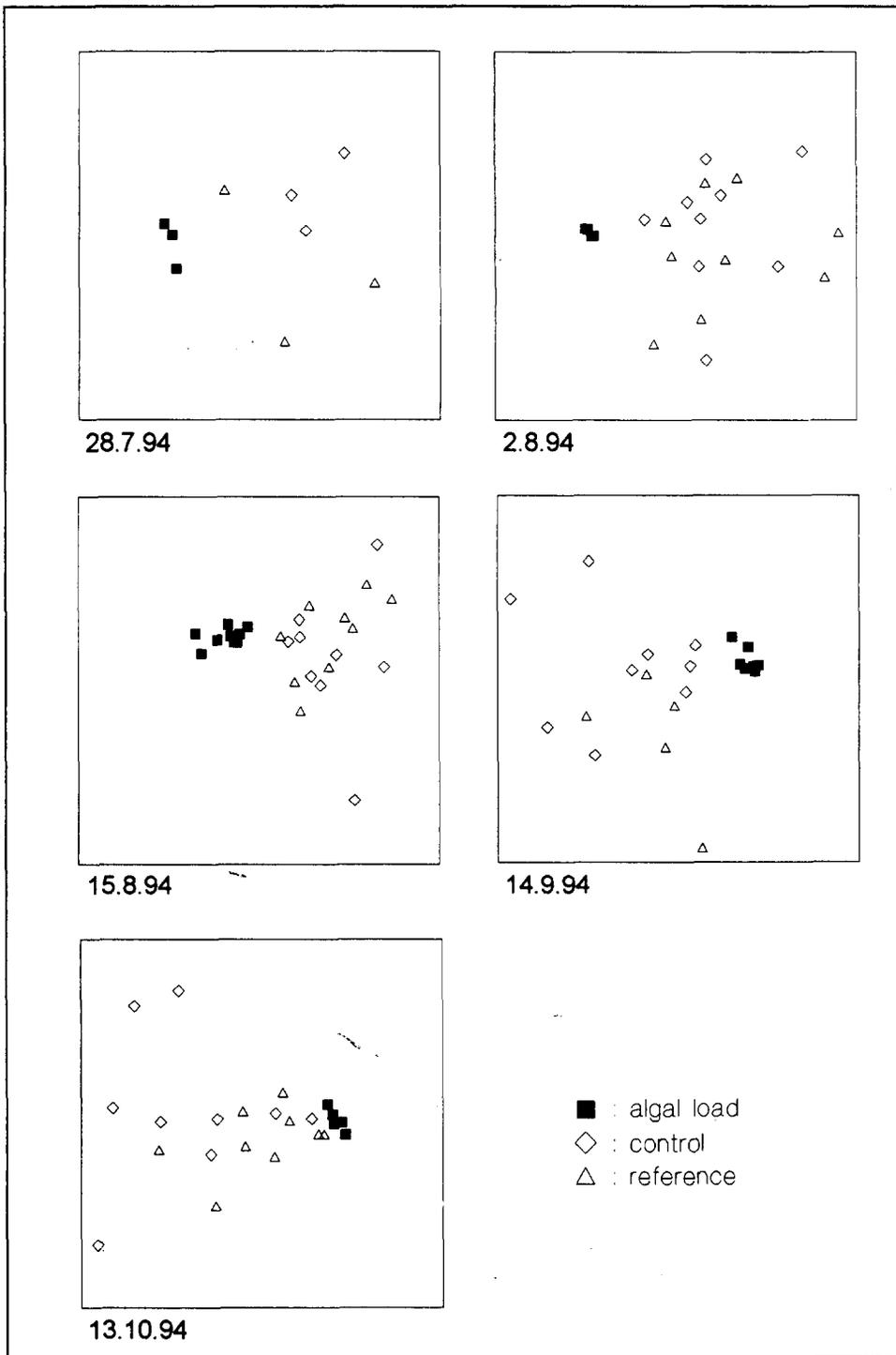


Fig. 8. Results of MDS analysis of meiofauna taxa abundance data showing the marked separation of the points representing black spot from those of reference and control areas. (Stress values: 0.06; 0.14; 0.15; 0.11; 0.10).

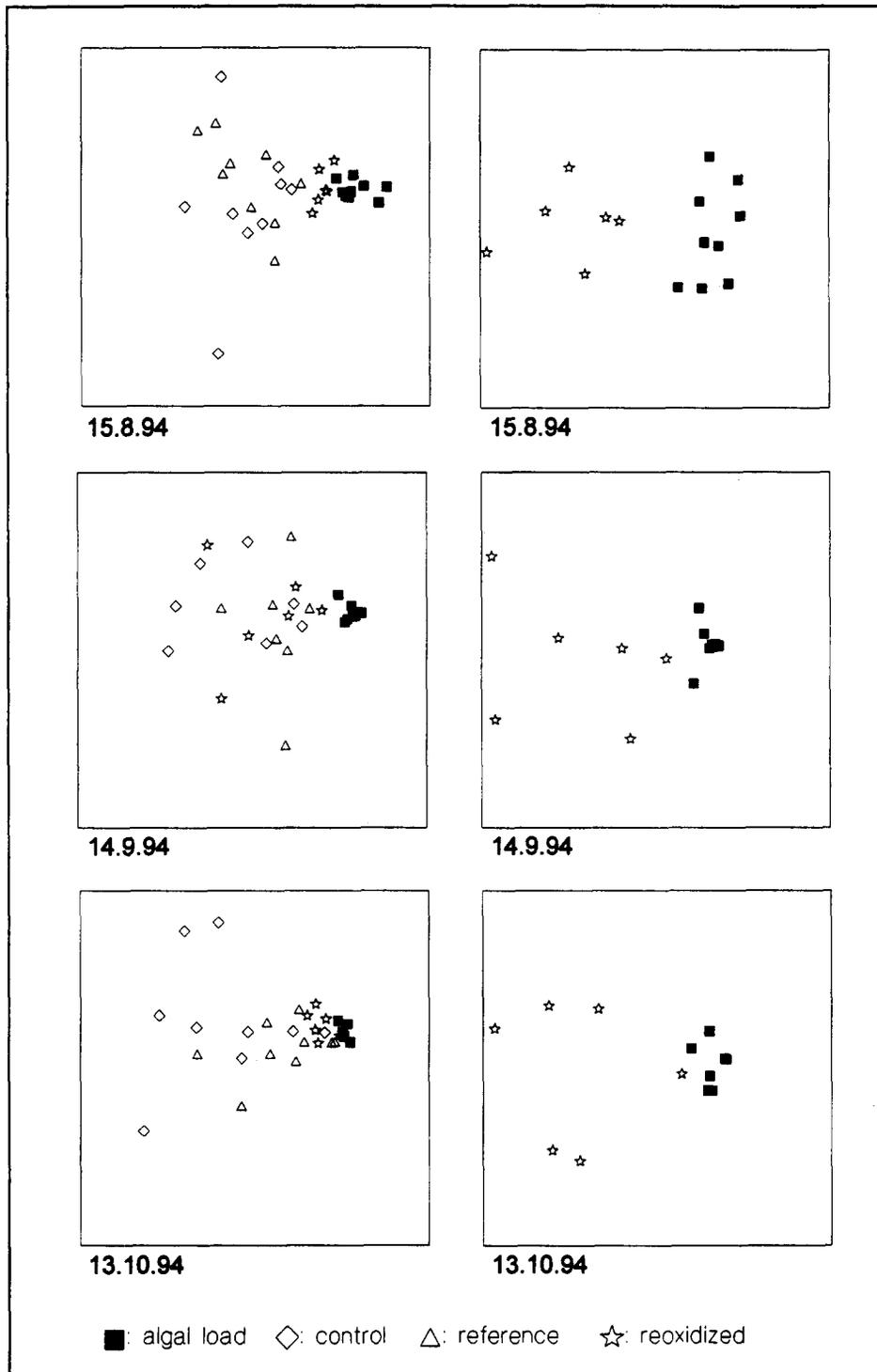


Fig. 9. Results of MDS analysis of meiofauna taxa abundance data. Left column: separation of re-oxidized black spot from those of black spots, including reference and control. (Stress values: 0.15; 0.16; 0.10). Right column: the same, reference and control omitted. (Stress values: 0.07; 0.05; 0.05).

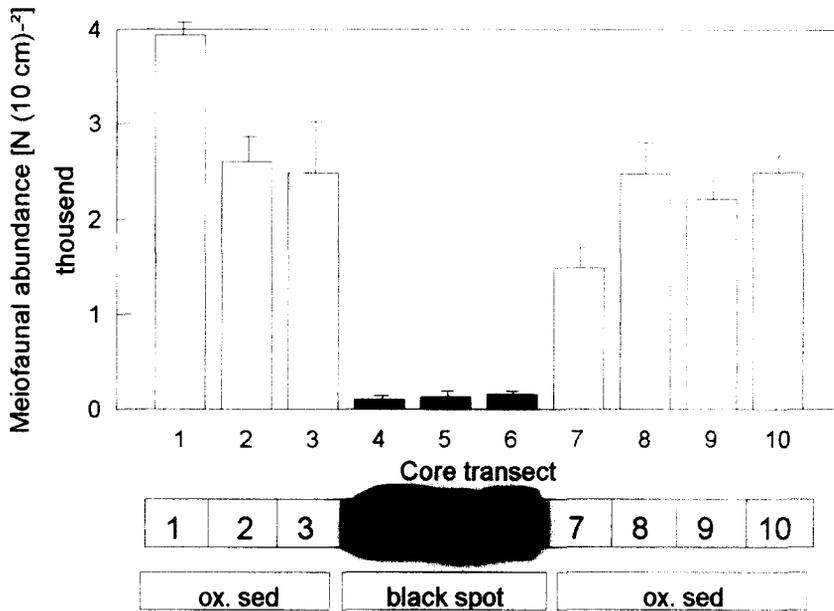


Fig. 10. Horizontal transect of 10 cores across a black spot and the adjacent oxidized surface sediment, showing that the sharp boundaries of the black spots are reflected in the total meiofaunal abundances.

tobenthos is predominantly composed of benthic diatoms (Asmus *et al.*, 1994). Besides contributing considerably to primary productivity, these diatoms stabilize the sediments by excretion of polymeric substances that hold particles together (Grant *et al.*, 1986; Hoagland *et al.*, 1993). This microphytobenthic biomass was reflected by the increased Chl *a* content in the top sediment layer of the control and reference areas. In the algae-loaded area (black spot), however, no peak of Chl *a* was found in the top sediment layer. Kolbe (1991) found a decrease of microphytobenthos in terms of Chl *a* in black spots of the East Frisian Wadden Sea. We suggest that the high concentrations of sulphide are responsible for the reduced microphytobenthos. Free sulphide is detrimental to many sensitive benthic diatom populations due to loss of photosynthetic capacity (Admiraal & Peletier, 1979; Kennet & Hargraves, 1985). It is possible that the occurrence of diatoms in the black-spot bottom is limited to a relatively tolerant species. Such aspects of the black spots require further investigation.

Recently, Nixon (1995) defined the term eutrophication as an 'increase in the rate of supply of organic matter to an ecosystem'. This process may be triggered by an increase in input of inorganic nutrients, a decrease in water turbidity, and a decline in grazing pressure. The Pearson-Rosenberg model (Pearson & Rosenberg, 1978) describes three successive steps of the effects of organic enrichment on qualitative characteristics of benthic communities, depending on the organic input: 1) if organic loading increases only slightly, species abundances and biomass values

also increase; 2) further increase favours opportunistic organisms; 3) if organic loading continues, zoobenthic organisms disappear and 'azoic' sediments appear. According to our results, the black spots correspond to the third step of this model, i.e. strong reduction or disappearance of zoobenthos. From our observations and experimental results we conclude that the deterioration does not proceed homogeneously within an area affected by eutrophication. Because the underlying process was local biomass accumulation, as described above, the damages only occurred in small areas which become uninhabitable for macro- and meiobenthos (Pearson & Rosenberg, 1978; McGwynne *et al.*, 1988). The major part of the sediment surface was, however, hardly affected.

#### 4.2. IMPACT ON THE MEIOFAUNA

Since most of the benthic metabolism depends on the input of organic matter produced elsewhere, eutrophication is generally expected to lead to an increase in meiobenthic abundance. In black spots, however, this did not occur. An initial increase in meiobenthic abundance with the organic load was probably stopped as soon as the biogeochemical conditions changed from oxygen-dependent to sulphate-dependent, thus marking a drastic metabolic limitation for the meiofauna. It is known that the most abundant animals in reduced sediments are nematodes, although turbellarians and gastrotrichs have been found in deep sediments of various tidal flats (Powell, 1989). An examination of the vertical meiofauna distribution in

black spot sediments showed that meiobenthos and even nematodes almost disappeared. Rosenberg *et al.*, (1991) observed that infaunal animals moved away in search of oxygen or to escape from hydrogen sulphide. The ecological potential of habitats exposed to sulphide can only be utilized by those organisms that are physiologically adapted to such hostile conditions which means that they cannot only cope with exposition to lasting hypoxia or even anoxia, but also with exposition to toxic and highly permeable hydrogen sulphide (Powell, 1989; Ott *et al.*, 1991). In organically enriched (but not overloaded) sediments, biological activities of infauna can promote the decomposition of organic matter and the oxidation of sulphides (Chareonpanish *et al.*, 1993). Within a black spot, however, the benthic animals have no influence on the decomposition of organic matter, because they avoid this sulphide-rich area or die. Considering the important ecological roles attributed to meiofauna, e.g. bioturbation (Tenore, 1977), solute transport (Aller & Aller, 1992), initial burial (Webb & Montagna, 1993), gardening (Gerlach, 1978), mechanical destruction of biogenic structures (Cullen, 1973; Neira & Höpner, 1994) and detrital mineralization (Alkemade *et al.*, 1992), prolonged periods of absence or strong reduction of meiofauna as in black spots may result in a delay or even absence of these natural processes.

The visible sharp boundaries to the adjacent oxidized sediment are characteristic of black spots. These boundaries are reflected by the chemical and physico-chemical parameters, and also by the highly

significant reduction ( $P < 0.001$ ) of meiofaunal abundances and taxa. According to the results of the cores arrayed horizontally along an oxic-anoxic-oxic sediment surface, the meiobenthic abundances were reduced to about 5% in the cores located inside the black spot (Fig. 10), where the concentrations of dissolved compounds (DOC, ammonia, phosphate and sulphide) were 50 to 500 times higher than in the adjacent oxidized sediments (Höpner & Michaelis, 1994).

In contrast to macrofauna, meiofauna seems to be less sensitive to physical disturbance and destabilization of the sediment (Thistle, 1980; Austen *et al.*, 1989; Warwick *et al.*, 1990a and b; Hall *et al.*, 1991). This makes it possible to discriminate between mechanical and chemical impairment. At the time of the first sampling, i.e. eight days after the physical disturbance of our control area, the mean total meiofaunal abundances were not significantly ( $P > 0.5$ ) different from the undisturbed reference area. This situation was observed throughout the rest of the experiment. Even a slight increase was noted (Fig. 11). If there was an initial negative effect, it was overcome within eight days. This did not occur in the black-spot area, in which the meiofaunal abundance remained significantly reduced ( $P < 0.001$ ). This suggests that a change in the chemical environment had a greater impact than the physical disturbance. The high abundance after mechanical disturbance suggests that the meiobenthic animals responded positively to a favourable resource situation created by the disturbance (Thistle, 1981). Digging of the sediment

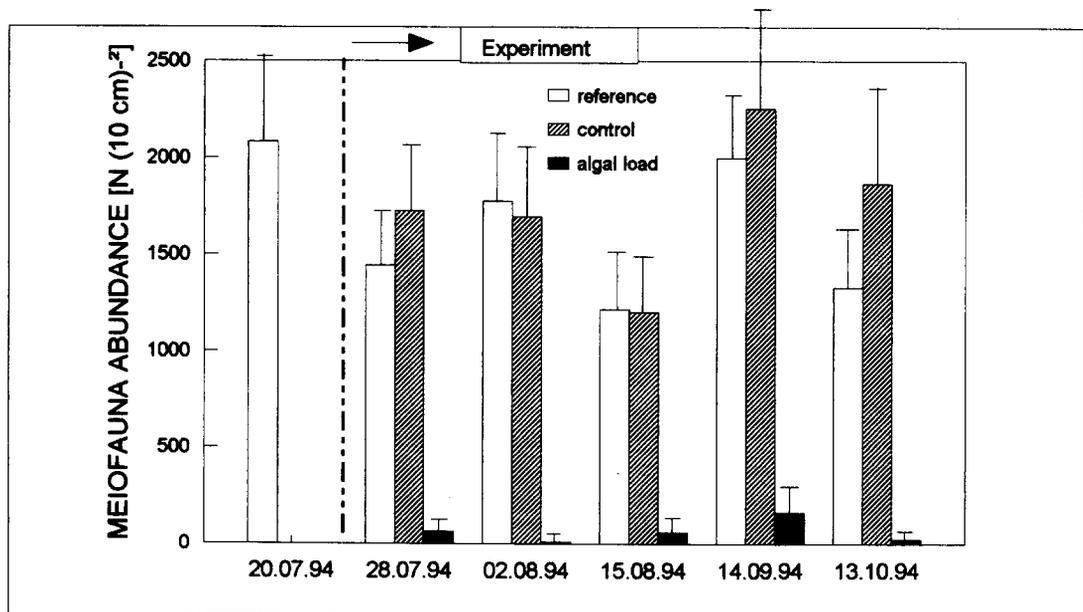


Fig. 11. Meiobenthic abundances in the top 2-cm sediment layer of the three sampling areas at six sampling dates. Reference, control, and algal load as in Fig. 2. The bar of 20 July 1994 shows the meiobenthic abundances of the whole study site just before the start of the experiment.

may have made organic material available to the meiofauna which otherwise would have remained buried. Disturbances create new patches that are recolonized. The responses may vary from hours to months, apparently reflecting different strategies of exploitation (Thistle, 1981).

4.3. RECOVERY OF THE MEIOFAUNA

Meiobenthos recolonized a black spot only after redevelopment of an oxidized sediment cover. Re-attained abundances were similar ( $P>0.5$ ) to those of the reference and control areas and the originally present eight major taxa were found again. However, it remains unknown whether or not there are changes in the species composition. In those places where the surface sediment remained black, the meiofauna did not re-establish or their abundances were very low for a long time. In fact, in an almost identical experiment carried out by our group from June 1993 to May 1994, only 50 m away from the study site, the effects on the meiofauna were noticeable over a period of almost one year (Fig. 12).

Several studies have demonstrated that the velocities and the extent of meiofaunal colonization of defaunated or azoic sediments vary greatly. Chandler

& Fleeger (1983) showed that copepods and nauplii recolonized azoic estuarine sediments in only two days, whereas nematodes required 29 days. Sherman & Coull (1980) found almost complete recolonization of a partially defaunated intertidal mud flat by copepods and nematodes after one tidal cycle (12 h). However, Alongi (1981) reported that in subtidally placed, azoic sediment trays, copepods required five days to reach background densities, while for nematodes it took seven days. Differences in colonizing modes of the meiobenthic animals may be attributed to their ability to become suspended as well as to differences in their vertical distribution in the sediment (Chandler & Fleeger 1983). The re-establishment of meiobenthic organisms in such re-oxidized black spots may be induced by a combination of passive re-transport with sediment particles, and a selective re-entry into the sediment (Butman, 1989), a process which is influenced by the physical and chemical characteristics of the substrate (Palmer, 1988; Fleeger *et al.*, 1990). It is not surprising that despite their general sensitivity copepods can rapidly recover due to their motility. If environmental deterioration occurs, meiofauna, especially copepods, ostracods, turbellarians, polychaetes and juvenile bivalves, can, in the absence of currents, easily respond to this by

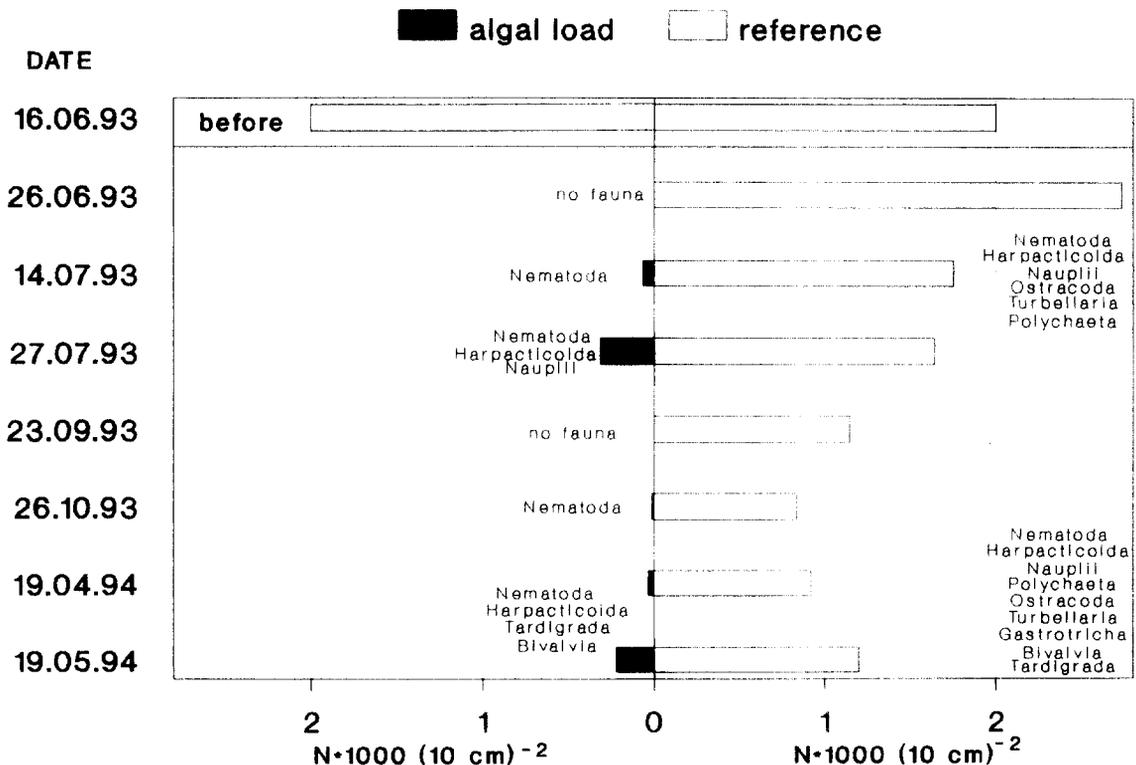


Fig. 12. Occurrence of meiofauna in the top 2-cm sediment layer over a period of 11 months. Left: algal-loaded area. Right: adjacent oxidized reference sediment. Upper bar represents meiofaunal abundance of the study site just before the start of the experiment.

active migration away from the sediment (Bell & Sherman, 1980; Armonies 1988). Nematodes are predominantly dispersed either by passive suspension by currents or waves or by locally restricted movements within the sediment. However, they are also able to swim actively (Hagerman & Rieger, 1981; Chandler & Fleeger, 1983; Decho & Fleeger, 1988; Walters, 1988; Armonies 1990, 1994). Recruitment of meiobenthos in the sediment from the water column is even more relevant than immigration from adjacent areas and can explain the rapid recolonization within a few days of the disturbance (Palmer, 1988, 1992). Meiofauna is not only considered to include important early colonists (Rhoads *et al.*, 1977) but are also thought to have a high resilience (Alongi *et al.*, 1983). Our results suggest that re-oxidation is a precondition of resettlement, and that after chemical recovery black-spot areas may be rapidly recolonized by immigrants from adjacent unaffected areas or from the overlying water. Besides *in situ* re-oxidation, there is a second explanation for the reappearance of oxidized covers on top of former black spots: the deposition of sediment from adjacent areas after resuspension. Due to complex interactions between hydrodynamic, morphological, biological, and sedimentological factors, tidal flat sediments are subject to continuous erosion and redeposition (Eitner & Ragutzki, 1994).

Black spots represent a highly stressed environment which may persist over a considerable period of time. This was reflected by the low number of taxa and the low abundance of meiobenthic organisms. The presence of some meiobenthic animals within a black spot over a long time span is probably due to their tolerance of an altered chemical milieu as well as to toxic substances such as sulphide and other reduced compounds. Meiobenthic organisms quickly respond to changes in their environment (Giere, 1993) and are therefore suitable candidates for monitoring the state of a marine ecosystem as tested in this experiment. Normally the identification of meiofaunal species is so complicated that it requires great expertise and so time-consuming that it is hardly compatible with monitoring schedules. Also, the knowledge on the ecology of individual species is so limited that the presence or absence of a species in a particular area cannot usually be fully explained. In conclusion, individual meiofaunal species do not seem to be suitable for the monitoring of ecosystems (Bouwman, 1987), whereas the abundances of higher meiofaunal taxa (Heip *et al.*, 1988; Herman & Heip, 1988) appear to be an effective indicator providing rapid results on the impact of disturbances by high organic loading in tidal-flat sediments.

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## 5. REFERENCES

- Aller, R.C. & J.Y. Aller, 1992. Meiofauna and solute transport in marine muds.—*Limnol. Oceanogr.* **37**: 1018-1033.
- Admiraal, W. & H. Peletier, 1979. Sulphide tolerance of benthic diatoms in relation to their distribution in an estuary.—*Br. phycol. J.* **14**: 185-196.
- Alkemade, R., A. Wielemaker, S.A. De Jong & J.J. Sandee, 1992. Experimental evidence for the role of bioturbation by the marine nematode *Diplolaimella dievengatensis* in stimulating the mineralization of *Spartina anglica* detritus.—*Mar. Ecol. Prog. Ser.* **90**: 149-155.
- Alongi, D.M., 1981. Recolonization of meiobenthos in oiled azoic subtidal muddy sands of the York River estuary, Virginia. M.A. thesis, College of William and Mary, Virginia: 1-96.
- Alongi, D.M., D.F. Boesch & R.J. Diaz, 1983. Colonization of meiobenthos in oil-contaminated subtidal sands in the lower Chesapeake bay.—*Mar. Biol.* **72**: 325-335.
- Armonies, W., 1988. Active emergence of meiofauna from intertidal sediments.—*Mar. Ecol. Prog. Ser.* **43**: 151-154.
- , 1990. Short-term changes of meiofaunal abundance in intertidal sediments.—*Helgoländer Meeresunters.* **44**: 375-386.
- , 1994. Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review.—*Helgoländer Meeresunters.* **48**: 299-320.
- Asmus, R., C. Gätje & V.N. De Jonge, 1994. Microphytobenthos - empfindliche Oberflächenhaut des Wattbodens. In: J. L. Lozán, E. Rachor, K. Reise, H. Von Westernhagen & W. Lenz. Warnsignale aus dem Wattenmeer. Blackwell Wissenschafts-Verlag, Berlin: 75-81.
- Austen, M.C., R.M. Warwick & M.C. Rosado, 1989. Meiobenthic and macrobenthic community structure along a putative pollution gradient in southern Portugal.—*Mar. Pollut. Bull.* **20**: 398-404.
- Bell, S.S. & K.M. Sherman, 1980. A field investigation of meiofaunal dispersal: tidal resuspension and implications.—*Mar. Ecol. Prog. Ser.* **3**: 245-249.
- Berner, R.A., 1980. Early diagenesis: a theoretical approach. Princeton University Press, Princeton, N.J.: 1-241.
- Beukema, J.J., 1991. Changes in composition of bottom fauna of a tidal-flat area during a period of eutrophication.—*Mar. Biol.* **111**: 293-301.
- , 1992. Long-term and recent changes in the benthic macrofauna living on tidal flats in the western part of the Wadden Sea.—*Neth. Inst. Sea Res. Publ Ser.* **20**: 135-141.
- Bianchi, T.S., R. Dawson & P. Sawangwong, 1988. The effects of chloropigments in sandy sediments.—*J. exp. mar. Biol. Ecol.* **122**: 243-255.
- Bouwman, L.A., 1987. Meiofauna. In: J.M. Baker & W.J. Wolff. Biological surveys of estuaries and coasts. Cambridge University Press: 140-156.

- Brockmann, U., V. De Jonge & K. Hesse, 1994. Zufuhr und Verteilung von Nährstoffen. In: J. L. Lozán, E. Rachor, K. Reise, H. Von Westernhagen & W. Lenz. Warnsignale aus dem Wattenmeer. Blackwell Wissenschafts-Verlag, Berlin: 23-30.
- Brown, S.B., J.D. Houghton & A.F. Hendry, 1991. Chlorophyll breakdown. In: H. Scheer. Chlorophylls. CRC Press: 465-489.
- Butman, C.A., 1989. Sediment-trap experiments on the importance of hydrodynamic processes in distributing settling larvae in near-bottom waters.—*J. exp. mar. Biol. Ecol.* **134**: 37-88.
- Buttermore, R.E., 1977. Eutrophication of an impounded estuarine lagoon.—*Mar. Pollut. Bull.* **8**: 13-15.
- Chandler, G.T. & J.W. Fleeger, 1983. Meiofaunal colonization of azoic estuarine sediment in Louisiana: mechanisms of dispersal.—*J. exp. mar. Biol. Ecol.* **69**: 175-188.
- Chareonpanich, C., S. Montani, H. Tsutsumi & S. Matsuoka, 1993. Modification of chemical characteristics of organically enriched sediment by *Capitella* sp. I.—*Mar. Pollut. Bull.* **26**: 375-379.
- Cline, J.D., 1969. Spectrophotometric determination of hydrogen sulfide in natural waters.—*Limnol. Oceanogr.* **14**: 454-485.
- Conley, D.J., R.W. Johnstone, 1995. Biogeochemistry of N, P, and Si in Baltic Sea sediments: response to simulated deposition of a spring diatom bloom.—*Mar. Ecol. Prog. Ser.* **122**: 265-276.
- Coull, B.C., S.S. Bell, 1979. Perspectives of marine meiofaunal ecology. In: R.J. Livingston. Ecological processes in coastal and marine systems. Plenum Press, New York: 189-216.
- Coull, B.C. & G.T. Chandler, 1992. Pollution and meiofauna: field, laboratory, and mesocosm studies.—*Oceanogr. mar. biol. ann. Rev.* **30**: 191-271.
- Cullen, D.J., 1973. Bioturbation of superficial marine sediments by interstitial meiobenthos.—*Nature* **242**: 323-324.
- Decho, A.W., J.W. Fleeger, 1988. Ontogenic feeding shifts in the meiobenthic harpacticoid copepod *Nitocra lacustris*.—*Mar. Biol.* **97**: 191-197.
- De Jonge, V.N. & K. Essink, 1991. Long-term changes in nutrient loads and primary and secondary production in the Dutch Wadden Sea. In: M. Elliott & J. P. Ducrotoy. Estuaries and coasts: spatial and temporal intercomparisons. Intern. Symp. Ser. Olsen & Olsen, Fredensborg: 307-316.
- Eitner, V. & G. Ragutzki, 1994. Temporal and spatial variability of tidal flats sediments: A case study.—*Senckenbergiana marit.* **25**: 1-9.
- Enoksson, V., 1993. Nutrient recycling by coastal sediments: effects of added algal material.—*Mar. Ecol. Prog. Ser.* **92**: 245-254.
- Eversberg, U., C. Suppes & H. Theede, 1994. Black spots above *Mya arenaria* - a model for reduced sediment surfaces. Umweltbundesamt. ökosystemforschung Niedersächsisches Wattenmeer - Zwischenbericht 1994. A2.3/1-A2.3/16.
- Fenchel, T., 1969. The ecology of marine microbenthos IV. Structure and function of the benthic ecosystem, its chemical and physical factors and the microfauna communities with special reference to the ciliated protozoa.—*Ophelia* **6**: 1-182.
- Field, J.G., K.R. Clarke & R.M. Warwick, 1982. A practical strategy for analysing multispecies distribution patterns.—*Mar. Ecol. Prog. Ser.* **8**: 37-52.
- Findlay, S.E.G., 1982. Influence of sampling scale on apparent distribution of meiofauna on a sand flat.—*Estuaries* **5**: 322-324.
- Fleeger, J.W., M.A. Palmer & E.B. Moser, 1990. On the scale aggregation of meiobenthic copepods on a tidal mudflat.—*PSZNI Mar. Ecol.* **11**: 227-237.
- Foree, E.G. & P.L. McCarty, 1970. Anaerobic decomposition of algae.—*Environ. Sci. Technol.* **4**: 842-949.
- Forster, S. & G. Graf, 1992. Continuously measured changes in redox potential influenced by oxygen penetrating from burrows of *Callinassa subterranea*.—*Hydrobiologia* **235/236**: 527-532.
- Gerlach, S.A., 1978. Food-chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity.—*Oecologia (Berlin)* **33**: 55-69.
- Giere, O., 1993. Meiobenthology. The microscopic fauna in aquatic sediments. Springer-Verlag, Berlin: 1-328.
- Giere, O., A. Eleftheriou & D.J. Murison, 1988. Abiotic factors. In: R.P. Higgins & H. Thiel. Introduction to the study of meiofauna. Smithsonian Inst. Press, Washington, D.C.: 1-488.
- Goldhaber, M.B. & I.R. Kaplan, 1975. Control and consequences of sulphate reduction rates in recent marine sediments.—*Soil Sci.* **119**: 42-55.
- Grant, J., U.V. Bathmann & E.L. Mills, 1986. The interaction between benthic diatom films and sediment transport.—*Estuar. coast Shelf Sci.* **23**: 225-238.
- Gray, J.S., 1984. Ökologie mariner Sedimente. Eine Einführung. Springer-Verlag, Berlin: 1-133.
- Hagermann, G.M. & R.M. Rieger, 1981. Dispersal of benthic meiofauna by wave and current action in Bogue South, North Carolina, USA.—*PSZNI Mar. Ecol.* **2**: 245-270.
- Hall, S.J., D. J. Basford, M. R. Robertson, D.G. Raffaelli & I. Tuck, 1991. Patterns of recolonization and the importance of pit-digging by the crab *Cancer pagurus* in a subtidal sand habitat.—*Mar. Ecol. Prog. Ser.* **72**: 93-102.
- Heip, C., 1995. Eutrophication and zoobenthos dynamics.—*Ophelia* **41**: 113-136.
- Heip, C., R.M. Warwick, M.R. Carr, P.M.J. Herman, R. Huys, N. Smol & K. Van Holsbeke, 1988. Analysis of community attributes of the benthic meiofauna of Frierfjord/Langesundfjord.—*Mar. Ecol. Prog. Ser.* **46**: 171-180.
- Herman, P.M.J. & C. Heip, 1988. On the use of meiofauna in ecological monitoring: Who needs taxonomy?—*Mar. Pollut. Bull.* **19**: 665-668.
- Hoagland, K.D., J.R. Rosowski, M.R. Gretz & S.C. Roemer, 1993. Diatom extracellular polymeric substances: function, fine structure, chemistry, and physiology.—*J. Phycol.* **29**: 537-566.
- Holmer, M. & E. Kristensen, 1994. Organic matter mineralization in an organic-rich sediment: experimental stimulation of sulfate reduction by fish food pellets.—*FEMS Microbiol. Ecol.* **14**: 33-44.
- Höpner, T. & H. Michaelis, 1994. Sogenannte 'schwarze Flecken' - ein Eutrophierungssymptom des Wattenmeeres. In: J. L. Lozán, E. Rachor, K. Reise, H. Von Westernhagen & W. Lenz. Warnsignale aus dem Wattenmeer. Blackwell Wissenschafts-Verlag, Berlin: 153-159.
- Jørgensen, B.B., 1977a. Bacterial sulfate reduction within reduced microniches of oxidized marine sediments.—*Mar. Biol.* **41**: 7-17.

- , 1977b. The sulfur cycle of a coastal marine sediment (Limfjorden, Denmark).—*Limnol. Oceanogr.* **22**: 814-832.
- , 1995. Die Mikrowelt der Meeresbakterien.—*Naturwissenschaften* **82**: 269-278.
- Jørgensen, B.B. & T. Fenchel, 1974. The sulfur cycle of a marine sediment model system.—*Mar. Biol.* **24**: 189-201.
- Kellner-Gross, I., 1994. Sedimentchemismus nach hoher Belastung mit Makroalgen Biomasse. Diplomarbeit, Universität Oldenburg, 49 pp. (unpublished).
- Kelly, J.R. & S.W. Nixon, 1984. Experimental studies of the effect of organic deposition on the metabolism of a coastal marine bottom community.—*Mar. Ecol. Prog. Ser.* **17**: 157-169.
- Kennet, D.M. & P.E. Hargraves, 1985. Benthic diatoms and sulfide fluctuations: upper Basin of Pettaquamscutt River, Rhode Island.—*Est. coast. Shelf Sci.* **21**: 577-586.
- Kolbe, K., 1991. Zum Auftreten 'schwarzer Flecken', oberflächlich anstehender, reduzierter Sedimente, im ostfriesischen Wattenmeer. Niedersächsisches Landesamt für Wasser und Abfall, Arbeiten Forschungsstelle Küste: 1-26.
- Kolbe, K., E. Kaminski, H. Michaelis, B. Obert & J. Rahmel, 1995. Macroalgal mass development in the Wadden Sea: first experiences with monitoring system.—*Helgoländer Meeresunters.* **49**: 519-528.
- Koop, K., R.C. Newell & M.I. Lucas, 1982. Microbial regeneration of nutrients from the decomposition of macrophyte debris on the shore.—*Mar. Ecol. Prog. Ser.* **9**: 91-96.
- McComb, A.J., P.B. Birch, D.M. Gordon & R.J. Lukatelich, 1979. Eutrophication in the Peel-Harvey estuarine system, western Australia. In: B.J. Neilson & L.E. Cronin. *Estuaries and nutrients*. Humana Press, Clifton, New Jersey: 323-342.
- McGwynne, L.E., A. McLachlan & J.P. Furstenberg, 1988. Wrack breakdown on sandy beaches - its impact on interstitial meiofauna.—*Mar. environ. Res.* **25**: 213-232.
- McLachlan, A., 1985. The biomass of macro- and interstitial fauna on clean and wrack-covered beaches in western Australia.—*Estuar. coast. Shelf Sci.* **21**: 587-599.
- Michaelis, H. & K. Reise, 1994. Langfristige Veränderungen des Zoobenthos im Wattenmeer. In: J. L. Lozán, E. Rachor, K. Reise, H. Von Westernhagen & W. Lenz. *Warnsignale aus dem Wattenmeer*. Blackwell Wissenschafts-Verlag, Berlin: 106-117.
- Michaelis, H., K. Kolbe & A. Thiessen, 1992. The 'black spot disease' (anaerobic surface sediments) of the Wadden Sea. *Contrib. ICES Statutory Meeting, Rostock 1992 Code Nr.E:36*.
- Neira, C. & T. Höpner, 1994. The role of *Heteromastus filiformis* (Capitellidae, Polychaeta) in organic carbon cycling.—*Ophelia* **39**: 55-73.
- Nixon, S.W., 1995. Coastal marine eutrophication: a definition, social causes, and future concerns.—*Ophelia* **41**: 199-219.
- Oelschläger, B., 1994. Fleckenhaftigkeit von Stoffkonzentrationen im Kohlenstoffbelasteten Wattsediment. Sulfat, Sulfid, Methan. Diplomarbeit, Universität Oldenburg, 51pp. (unpublished).
- Osinga, R., W.E. Lewis, J.L.M. Wopereis, C. Vriezen & F.C. Van Duyl, 1995. Effects of the sea urchin *Echinocardium cordatum* on oxygen uptake and sulfate reduction in experimental benthic systems under increasing organic load.—*Ophelia* **41**: 221-236.
- Ott, J.A., R. Novak, F. Schiemer, U. Hentschel, M. Nebelsick & M. Polz, 1991. Tackling the sulfide gradient: a novel strategy involving marine nematodes and chemoautotrophic ectosymbionts.—*PSZNI Mar. Ecol.* **12**: 261-279.
- Palmer, M.A., 1988. Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment.—*Mar. Ecol. Prog. Ser.* **48**: 81-91.
- , 1992. Incorporating lotic meiofauna into our understanding of faunal transport processes.—*Limnol Oceanogr.* **37**: 329-341.
- Pearson, T.H. & R. Rosenberg, 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment.—*Oceanogr. mar. biol. ann. Rev.* **16**: 229-311.
- Pfannkuche, O. & H. Thiel, 1988. Sample processing. In: R.P. Higgins & H. Thiel. *Introduction to the study of meiofauna*. Smithsonian Inst. Press, Washington, D.C.: 134-145.
- Philippart, K. & B. Brinkman, 1992. Herkomst zwarte vlekken in de Waddenzee - Zwartkijkers?—*Waddenbulletin* **27**: 90-93.
- Postma, H., 1988. Tidal flats areas. In: B.-O. Jansson. *Coastal-offshore ecosystem interactions. Lecture Notes on Coastal and Estuaries studies*. Springer-Verlag, Berlin: 102-121.
- Powell, E.N., 1989. Oxygen, sulfide and diffusion: why thio-biotic meiofauna must be sulfide-insensitive first-order respirers.—*J. mar. Res.* **47**: 887-932.
- Rafaelli, D., S. Hull & H. Milne, 1989. Long-term changes in nutrients, weed mats and shore birds in a estuarine system.—*Cah. Biol. mar.* **30**: 259-270.
- Reise, K., 1983. Sewage, green algae mats anchored by lugworms, and the effects on Turbellaria and small Polychaeta.—*Helgoländer Meeresunters.* **36**: 151-162.
- Reise, K. & I. Siebert, 1994. Mass occurrence of green algae in the German Wadden Sea.—*Dt. Hydrogr. Z., (Suppl.)* **46**: 171-180.
- Reise, K., K. Kolbe & V. De Jonge, 1994. Makroalgen und Seegrasbestände im Wattenmeer. In: J.L. Lozán, E. Rachor, K. Reise, H. Von Westernhagen & W. Lenz. *Warnsignale aus dem Wattenmeer*. Blackwell Wissenschafts-Verlag, Berlin: 90-100.
- Rhoads, D.C., R.C. Aller & M.B. Goldhaber, 1977. The influence of colonizing benthos on physical properties and chemical diagenesis of the estuarine seafloor. In: B.C. Coull. *Ecology of marine benthos*. University of South Carolina Press, Columbia: 113-138.
- Rieper-Kirchner, M., 1989. Microbial degradation of North Sea macroalgae: field and laboratory studies.—*Botanica mar.* **32**: 241-252.
- , 1990. Macroalgal decomposition: laboratory studies with particular regard to microorganisms and meiofauna.—*Helgoländer Meeresunters.* **44**: 397-410.
- Robak, M., 1995. Teilcharakterisierung von 'jungem' Porenwasser-DOC aus Wattsedimenten und experimenteller Belastung mit Makroalgen-Biomasse. Diplomarbeit, Universität Oldenburg, 94 pp. (unpublished).
- Rosenberg, R., 1985. Eutrophication - the future marine coastal nuisance?—*Mar. Pollut. Bull.* **16**: 227-231.
- Rosenberg, R., B. Hellmann & B. Johansson, 1991. Hypoxic

- tolerance of marine benthic fauna.—Mar. Ecol. Prog. Ser. **79**: 127-131.
- Schories, D., 1991. Wechselwirkungen zwischen Grünanlagen und Bodenfauna im Wattenmeer. Thesis, Universität Kiel: 1-95.
- Schories, D. & K. Reise, 1993. Germination and anchorage of *Enteromorpha* spp. in sediments of the Wadden Sea.—Helgoländer Meeresunters. **47**: 275-285.
- Sherman, K.M. & B.C. Coull, 1980. The response of meiofauna to sediment disturbance.—J. exp. mar. Biol. Ecol. **46**: 59-71.
- Stal, L.J., H. Van Gemerden & W.E. Krumbein, 1984. The simultaneous assay of chlorophyll and bacteriochlorophyll in natural microbial communities.—J. microbiol. Meth. **2**: 295-306.
- Sun, M., R.C. Aller & C. Lee, 1991. Early diagenesis of chlorophyll-a in Long Island Sound sediments: a measure of carbon flux and particle reworking.—J. mar. Res. **49**: 379-401.
- Sun, M., C. Lee & R.C. Aller, 1993. Anoxic and oxic degradation of <sup>14</sup>C-labeled chloropigments and a <sup>14</sup>C-labeled diatom in Long Island Sound sediments.—Limnol. Oceanogr. **38**: 1438-1451.
- Sundbäck, K., B. Jönsson, P. Nilsson & I. Lindström, 1990. Impact of accumulating drifting macroalgae on a shallow-water sediment system: an experimental study.—Mar. Ecol. Prog. Ser. **58**: 261-274.
- Suppes, C., 1995. Die Dynamik 'Schwarzer Flecken' im Wattenmeer. Veränderungen im Sediment durch den Abbau organischer Substanz. Diplomarbeit, Universität Bremen, 95 pp. (unpublished).
- Tenore, K.R., 1977. Food chain pathways in detrital feeding benthic communities: a review, with new observations on sediment resuspension and detrital recycling. In: B.C. Coull. Ecology of marine benthos. Univ. of South Carolina Press, Columbia: 37-53.
- Thiessen, A., 1992. Anaerobe Bereiche der Wattoberfläche, deren Phaenomenologie sowie deren Auswirkungen auf die Bodenlebewelt - Eine Untersuchung im Rückseitenwatt der ostfriesischen Insel Norderney (Niedersachsen). Diplomarbeit, Universität Osnabrück, 103 pp. (unpublished).
- Thistle, D., 1980. The response of a harpacticoid copepod community to a small-scale natural disturbance.—J. mar. Res. **38**: 381-395.
- , 1981. Natural physical disturbances and communities of marine soft bottoms.—Mar. Ecol. Prog. Ser. **6**: 223-228.
- Villano, N. & R.M. Warwick, 1995. Meiobenthic communities associated with the seasonal cycle of growth and decay of *Ulva rigida* Agardh in the Palude Della Rosa, Lagoon of Venice.—Est. coast Shelf Sci. **41**: 181-194.
- Vismann, B., 1991. Sulfide tolerance: physiological mechanisms and ecological implications.—Ophelia **34**: 1-27.
- Walters, K., 1988. Diel vertical migration of sediment-associated meiofauna in subtropical sand and seagrass habitats.—J. exp. mar. Biol. Ecol. **117**: 169-186.
- Warwick, R.M., K.R. Clarke & J.M. Gee, 1990a. The effect of disturbance by soldier crabs *Mictyris platycheles* H. Milne Edwards on meiobenthic community structure.—J. exp. mar. Biol. Ecol. **135**: 19-33.
- Warwick, R.M., H.M. Platt, K.R. Clarke, J. Agard & J. Gobin, 1990b. Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda.—J. exp. mar. Biol. Ecol. **138**: 119-142.
- Webb, D.G. & P.A. Montagna, 1993. Initial burial and subsequent degradation of sedimented phytoplankton: relative impact of macro- and meiobenthos.—J. exp. mar. Biol. Ecol. **166**: 151-163.
- Wieser, W., 1960. Benthic studies in Buzzards bay II. The meiofauna.—Limnol. Oceanogr. **2**: 121-137.
- Wilkinson, L., 1990. SYSTAT: the system for statistics. Evanston, Ill: 1-822.

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