

Sediment sulfur dynamics related to biomass-density patterns in *Zostera marina* (eelgrass) beds

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ABSTRACT: Rates of sulfate reduction and the cycling of sulfur were measured in estuarine sediments vegetated with *Zostera marina* L. (eelgrass), and in adjacent bare sediment, in summer during the intensive period of the growth season. Sulfate reduction rates were determined along a shoot density gradient (210 to 1026 shoots m⁻²). There was a positive linear correlation between shoot density and depth-integrated sulfate reduction rates, and rates were 5-fold higher at the dense station (59.1 mmol m⁻² d⁻¹) than at the bare site (12.2 mmol m⁻² d⁻¹). The accumulation of particulate organic matter was low in the vegetated sediments, and there was no correlation between the organic content and microbial activity. The accumulation of dissolved organic carbon (DOC) was higher in the vegetated sediments, whereas pools of short chain fatty acids were low (<5 µM) at all stations. There was a positive relationship between the depth-integrated DOC pool and sulfate reduction rates along the shoot density gradient, indicating a direct plant effect probably from a production of labile organic matter within the eelgrass bed. Sulfate reduction rates were primarily enhanced in the rooted zone. The cycling of sulfur compounds was rapid, as there was an accumulation of dissolved sulfides in the pore waters throughout the examined sediment layer (0 to 8 cm) in the vegetated sediments. Burial of precipitated reduced sulfides increased with increasing shoot density, but the pools were low when related to the sulfate reduction rates, indicating a rapid reoxidation of sulfides at the location.

KEY WORDS: Eelgrass · Sediments · Sulfate reduction · DOC · Sulfides

INTRODUCTION

The role of seagrass meadows in the cycling of essential elements (i.e. nitrogen and phosphorus) is important owing to their ability to produce and accumulate organic matter including major nutrients (Kenworthy et al. 1982). Organic matter cycling is enhanced in vegetated sediments by: (1) entrapment and decomposition of allochthonous particulate organic material within the seagrass bed (Kemp et al. 1984); (2) microbial breakdown of dissolved organic compounds excreted from plant roots (Smith et al. 1988); (3) decomposition of senescent plant material (Barko et al. 1991).

As seagrasses are situated in sediments with high microbial activity, the highly reducing conditions could stress the macrophytes due to accumulation of reduced

metabolites. However, seagrasses have adapted to these reducing conditions by developing a system of internal lacunae for downward transport of O₂ to support root respiration (Sand-Jensen et al. 1982, Smith et al. 1984, Caffrey & Kemp 1991). Release of O₂ from seagrass roots has the potential to alter both sediment microbiology and chemistry, and rhizosphere oxidation may result in elevated rates of nitrification and denitrification (Caffrey & Kemp 1991). Furthermore, seagrasses may excrete labile photosynthetic compounds from the roots and rhizomes (Moriarty et al. 1985), resulting in increased concentrations of dissolved organic compounds in vegetated sediments (Koepller et al. 1993). The activity of benthic bacteria in seagrass ecosystems is believed to be closely controlled by the production of overlying plants and the availability of nutrients in the sediments (Danovaro & Fabiano 1995). López et al. (1995) found high bacterial activity in the sediments under *Posidonia oceanica*

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meadows, and attributed this to the plants' high supply of organic matter to the sediments, which were organically enriched relative to unvegetated sites.

Bacterial sulfate reduction is the predominant pathway of anaerobic mineralization of organic matter in coastal marine sediments, and accounts for more than half of the microbial decomposition in salt-marsh sediments, where rates of sulfate reduction are among the highest recorded (Howarth 1984). The pool of acid-volatile sulfides (dissolved sulfides and iron-monosulfides) is generally of minor importance in salt-marshes and mangrove sediments, whereas the burial of pyrite is high (Howarth 1984, Holmer et al. 1994). Oxidation of the sediments through root excretion has been suggested to aid the precipitation of pyrite. The accumulation of sulfides decreases the oxidation of the sediments and may cause the sediment environment to deteriorate, e.g. affecting the growth conditions for eelgrass and reducing benthic faunal activity. Sulfur cycling has been described in e.g. salt marshes and mangroves (Howarth 1984, Holmer et al. 1994), but is less well known in other types of vegetated sediments (Blackburn et al. 1994, Isaksen & Finster 1996).

In northern Europe and North America the dominant seagrass *Zostera marina* L. has declined significantly since the 1970s (Orth & Moore 1983, Giesen et al. 1990). Increased nutrient enrichment leading to decreased light availability has been linked to this decline. In their investigation on the effect of sediment conditions on photosynthetic response, Goodman et al. (1995) found a decrease in maximum rate of photosynthesis and an increase in light intensity needed to obtain net photosynthesis with increasing sulfide concentration in the sediment. *Z. marina* often inhabits light-limited environments, and is adapted to tolerate anoxia and the presence of sulfides by using anaerobic fermentation for energy generation (Smith et al. 1988). In most plants, protein synthesis is disrupted upon transition from aerobiosis to anaerobiosis, and prolonged anoxia in combination with light-limitation may reduce the growth of plants. Elevated sulfide levels may, therefore, contribute to seagrass loss in stressed areas where the potential for light utilization is reduced, but *Z. marina* is uniquely tolerant of even severe anoxia (Kraemer & Alberte 1995).

In the present study we measured pools of organic matter, reduced sulfides and rates of sulfate reduction along a gradient of increasing shoot density in a *Zostera marina* bed in Roskilde Fjord, Denmark, to evaluate the impact of seagrasses on sulfur cycling in sediments. Measurements of particulate and dissolved organic carbon pools within the eelgrass bed allowed assessment of the microbial substrates present for sulfate-reducing bacteria. Time course incubations were performed to determine sulfate reduction rates

for evaluation of the core injection technique in vegetated sediments.

MATERIALS AND METHODS

Study area and sampling procedures. The study was conducted in a heterogenous *Zostera marina* stand at Ølsted Strand, Roskilde Fjord, Denmark, in June 1995. One unvegetated station (Stn 1) and 4 vegetated stations with increasing shoot density (Stns 2 to 5) were sampled at a water depth of 1.5 m. The water temperature was 21°C and the salinity 13‰. Eelgrass density and biomass were determined by harvesting all plant material within 2 randomly chosen quadrats (0.25 m² each) at each station. Plant material was washed on a 1 mm sieve, and transported back to the laboratory, where the shoot density was quantified. The plant material was then separated into shoot, root-rhizome and dead biomass. Dry weight (DW) was determined by drying to constant weight at 105°C.

Sediment cores were collected immediately before harvesting the eelgrass. From each station 6 to 8 cores were taken (i.d. = 26 mm) for determination of sulfate reduction rates and 3 cores (i.d. = 80 mm) for pore water extraction and sediment characteristics. Cores were taken between the plants to avoid direct collection of shoots and root-rhizomes. Cores containing roots or rhizomes were discarded before analysis.

Pore water and sediment characteristics. Sediment cores (i.d. = 80 mm) were brought back to the laboratory and kept at 5°C during a processing time of maximum 8 h. The cores were sliced at 1 cm intervals down to 4 cm and then at 2 cm intervals down to 8 cm depth. Pore water was obtained by centrifugation (10 min, 1250 × *g*) in double centrifuge tubes through pre-combusted GF/F filters. Pore water was sampled for total CO₂ (TCO₂) (2 ml sample preserved with 10 µl of 125 mM HgCl₂ which also precipitates sulfides), sulfate (SO₄²⁻) (400 µl sample with 50 µl of 0.1 M HCl added to liberate sulfides), dissolved sulfides (DS) (1 ml sample fixed with 10 µl of 1 M zinc acetate), dissolved organic carbon (DOC) and short chain fatty acids (SCFA) (1 ml sample added 50 µl of 0.1 M HCl to prevent precipitation). Samples for TCO₂ were analysed within 4 d, and SO₄²⁻, DOC and SCFA were kept frozen until analysis within 2 mo. Sediment characteristics (density, water content, organic content) were determined concurrently with the pore water extraction.

Sulfate reduction rates. Sulfate reduction rates were measured by the core-injection technique (Jørgensen 1978), where 2 µl of carrier-free ³⁵S-SO₄²⁻ (70 kBq) was injected at 1 cm intervals down to 10 cm. Injections were done immediately after sampling, and cores were incubated for 1, 2, 4, or 6 to 8 h (only 3 incubation times

at Stns 1 to 3) at *in situ* temperature. The incubation was terminated by slicing the sediment at 1 cm intervals down to 4 cm and 2 cm intervals down to 8 cm depth directly into 1 M zinc acetate. The sediment was kept frozen until analysis. Background contamination of ^{35}S was determined by slicing and fixing one core from Stn 5 before the addition of radioisotope (Fossing pers. comm.).

The sediment was distilled according to the 2-step procedure of Fossing & Jørgensen (1989). Briefly, 3 to 5 g of centrifuged sediment (5 min, $2500 \times g$) was transferred to a reaction flask and 10 ml of 50% ethanol was added. After degassing with N_2 for 10 min, 8 ml 12 M HCl was added before the slurry was distilled at room temperature for 30 min to obtain the acid-volatile fraction (AVS). The reducible sulfur compounds were released as H_2S and trapped as ZnS in 10 ml of 250 mM zinc acetate. A new trap was inserted, 16 ml of 1 M Cr^{2+} in 0.5 M HCl was added to the reaction flask, and the mixture was distilled by boiling for 30 min to obtain the chromium reducible sulfur (CRS). Subsamples from supernatants and suspended ZnS from the traps were mixed with Ultima Gold scintillation cocktail, and radioactivity was counted on a Packard TriCarb 2000 scintillation counter. The total sulfate reduction rate (SRR_{tot}) was calculated by addition of sulfate reduction rates based on the AVS (SRR_{AVS}) and the CRS (SRR_{CRS}) fractions. The pools of reduced inorganic sulfur (P_{AVS} and P_{CRS}) were determined as total amount of sulfide trapped by the spectrophotometric method of Cline (1969).

Analysis. TCO_2 was measured by the flow injection technique of Hall & Aller (1992). SO_4^{2-} was measured by ion-chromatography with a Dionex auto-suppressed anion-system (IonPac AS4A-SC column and ASRS suppressor). Dissolved sulfides were determined by the method of Cline (1969). DOC was measured with a Shimadzu TOC-5000 total organic carbon analyzer on acidified samples and SCFA with a Dionex chemical-suppressed ion-exclusion principle using a IonPac ICE-AS6 column (Dionex Corp.) and 0.4 mM HCl as eluent followed by an Anion-MicroMembrane Suppressor (AMMS-ICE, Dionex) with 5.00 mM tetrabutylammonium hydroxide as regenerant (Bøtte & Jørgensen 1992, Holmer & Kristensen 1994).

Sediment density was obtained by weight of known sediment volume and water content was measured as weight loss after drying overnight at 105°C and used in calculations of sulfate reduction rates. Particulate organic carbon (POC) and nitrogen (PON) were determined (1 core from each station) on pre-dried (105°C) sediment after subtraction of the inor-

ganic carbon and nitrogen measured on ignited (520°C) sediment according to Kristensen & Andersen (1987) using a Carlo Erba 1100EA elemental analyzer.

RESULTS

Eelgrass and sediment data

Eelgrass density increased with a factor of 5 from Stn 2 (210 shoots m^{-2}) to Stn 5 (1026 shoots m^{-2}) (Table 1). A positive, significant relationship between shoot density and both shoot biomass ($y = 0.02x^{1.32}$, $R^2 = 0.801$, $p = 0.003$) and root-rhizome biomass ($y = 0.07x^{1.16}$, $R^2 = 0.814$, $p = 0.002$) could be described with a power function: $y = Ax^B$. The exponent (B) was >1 indicating a relative increase in individual plant weight from Stn 2 towards Stn 5. The root-rhizome fraction accounted for 54 to 63% of the total living biomass with the highest fraction at the lowest density. There was no significant correlation between shoot density and dead biomass ($R^2 = 0.077$, $p = 0.506$). Dead biomass varied at Stn 2 where 1 of the 2 samples showed a very high value (114.0 g dry wt m^{-2}); otherwise the relative fraction of dead biomass (dead:total) was negatively related to shoot density, reaching 14.2% of the total biomass at Stn 2 (high value at Stn 2 omitted).

The POC and PON content in the sediment was low at all 5 stations (POC $< 0.206\%$ dry wt, PON $< 0.010\%$ dry wt) with an erratic depth pattern (data not shown). The depth-integrated POC content (0 to 8 cm) increased from the unvegetated site (10.9 mol C m^{-2}) along the density gradient to a maximum at Stn 3 (19.6 mol C m^{-2}) and decreased again at Stns 4 and 5 (12.6 to 15.1 mol C m^{-2}). There was no significant relationship between POC and dead biomass (least-squares regression: $R^2 = 0.056$, $p = 0.574$). PON content was generally close to the detection limit of the analysis, and the presented data are probably maximum values.

Table 1. Eelgrass data at the 4 vegetated stations. Shoot density and shoot, rhizome+root and dead biomass are given as mean (\pm range) of 2 collections. Rhizome-root biomass is given as percentage of the total living biomass ($\text{RR:tot} = \text{rhizome+root}/\text{shoot+rhizome+root}$). The dead biomass is calculated similarly ($\text{Dead:tot} = \text{dead}/\text{shoot+rhizome+root}$)

Stn	Shoot density (shoot m^{-2})	Shoot biomass (g DW m^{-2})	Rhizome+ root biomass (g DW m^{-2})	Dead biomass (g DW m^{-2})	RR:tot (%)	Dead:tot (%)
2	210 \pm 34	19.0 \pm 2.3	29.6 \pm 0.4	4.2	60.8	14.2
3	336 \pm 156	29.6 \pm 1.1	49.4 \pm 10.5	3.7 \pm 3.0	62.5	4.5
4	696 \pm 8	145.1 \pm 55.5	169.2 \pm 60.7	1.8 \pm 0.4	53.8	0.6
5	1026 \pm 94	194.8 \pm 3.7	238.0 \pm 123.6	5.2 \pm 0.5	55.0	1.2

Dissolved carbon pools

The DOC attained concentrations between 0.9 and 4.5 mM with highest values in the deep layers at the vegetated sites (Fig. 1). The depth profiles were separated into a rooted layer (0 to 4 cm) and a non-rooted zone (4 to 8 cm). The effect of increasing shoot density in each layer was tested with a regression analysis. There was a significant increase with shoot density in both the rooted layer and below, which was linearly correlated with shoot density (Fig. 2). The depth-integrated DOC pool (0 to 8 cm) (IDOC) showed a significant positive relationship with shoot density (least-squares regression: $y = 0.024x + 6.717$, $R^2 = 0.857$, $p < 0.001$). Despite the elevated pools of DOC in the vegetated sediments, the concentration of SCFA was below detection limit ($<5 \mu\text{M}$) at all sites (data not shown). The concentration of TCO_2 was almost constant with

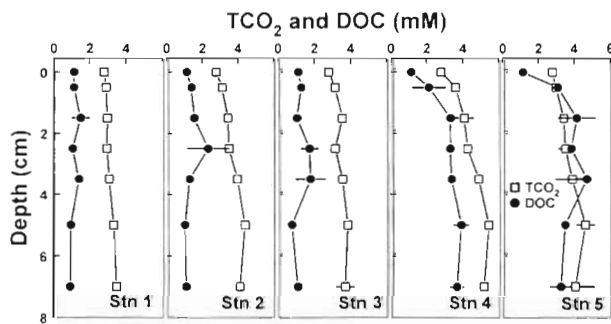


Fig. 1. Depth profiles of TCO_2 and dissolved organic carbon (DOC) at the 5 examined stations. Each point is the average of 2 sediment cores (\pm range)

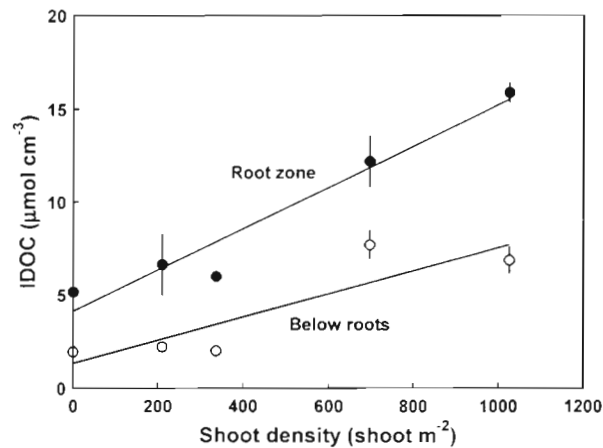


Fig. 2. Depth-integrated DOC pools in the root zone (●) and below roots (○) plotted against shoot density. Each point is the average of 2 cores (\pm range). The best fit with linear least squares analysis is given (root zone: $y = 0.011x + 4.104$, $R^2 = 0.893$, $p < 0.001$; below roots: $y = 0.006x + 1.306$, $R^2 = 0.749$, $p = 0.001$)

depth at the unvegetated site (2.8 to 3.5 mM) (Fig. 1), whereas it increased with depth at the vegetated sites. There was, however, no significant relation between TCO_2 concentration and shoot density in the 2 layers (least-squares regression: root zone: $R^2 = 0.242$, $p = 0.149$; below roots $R^2 = 0.306$, $p = 0.097$)

Sulfate reduction rates (SRR)

Regression analysis of the depth-integrated sulfate reduction rate (ISRR_{tot}) showed that ISRR_{tot} was independent of incubation time at all stations (Table 2). By relating ISRR_{tot} with shoot density, a positive linear relation was evident (least-squares regression: $R^2 = 0.902$, $p = 0.013$) (Fig. 3), showing a 5-fold increase from Stn 1, the unvegetated site ($12.2 \text{ mmol m}^{-2} \text{ d}^{-1}$), to Stn 5 ($59.1 \text{ mmol m}^{-2} \text{ d}^{-1}$) with highest shoot density. There was no linear correlation between ISRR_{tot} and dead biomass ($R^2 = 0.127$, $p = 0.073$).

The depth profile of SRR_{tot} generally showed decreasing activity with sediment depth at all stations (Fig. 4) and SRR_{CRS} was the larger component at all

Table 2. Results of least-squares regression analysis of depth-integrated sulfate reduction rates versus incubation time. n: number of cores; R^2 and p values of the regression are given

Stn	n	R^2	p
1	6	<0.001	0.989
2	6	0.449	0.145
3	6	0.218	0.350
4	8	0.343	0.127
5	8	0.218	0.243

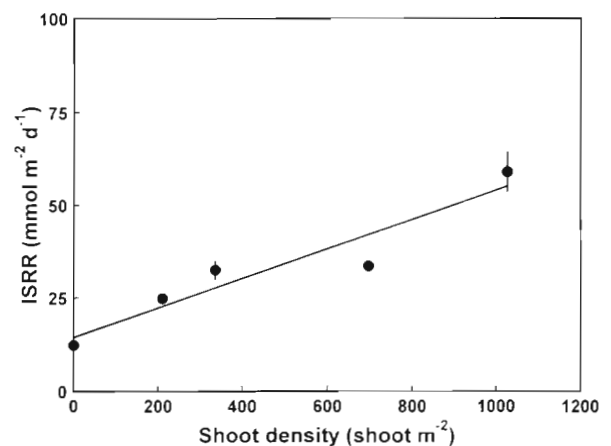


Fig. 3. Depth-integrated sulfate reduction rates (ISRR) plotted against shoot density. Each point is the average of 6 to 8 sediment cores (\pm SE). The best fit with linear least squares analysis is given: $y = 0.036x + 15.055$, $R^2 = 0.902$, $p = 0.013$

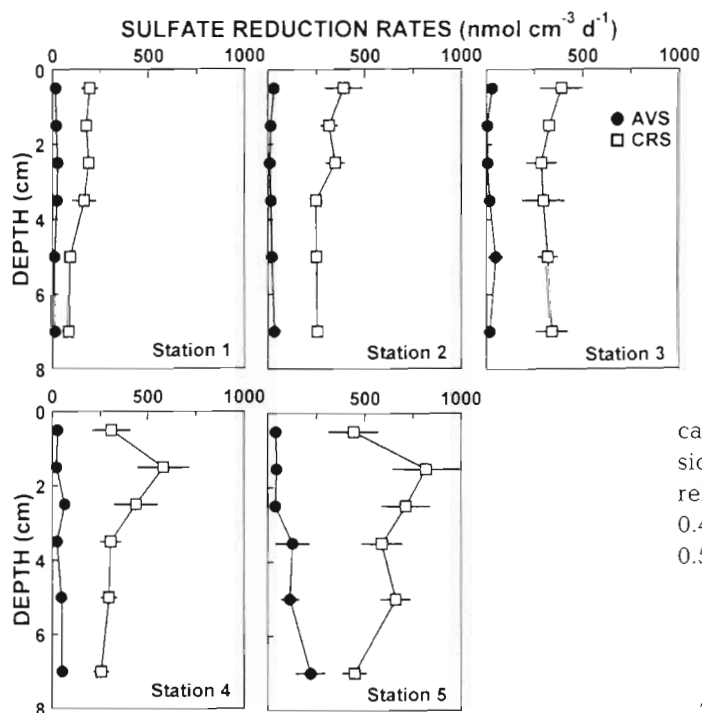


Fig. 4. Depth profiles of sulfate reduction rates at the 5 stations. Rates are shown as SRR_{AVS} (AVS) and SRR_{CRS} (CRS). Each point is the average of 6 to 8 sediment cores (\pm SE)

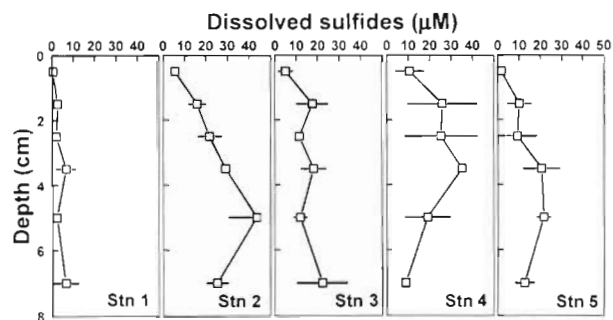


Fig. 5. Depth profiles of dissolved sulfides at the 5 examined stations. Each point is the average of 2 sediment cores (\pm range)

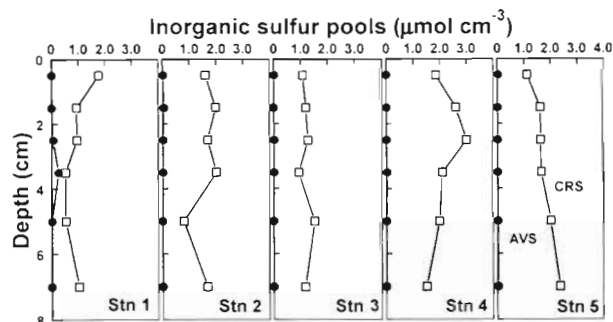


Fig. 6. Depth profiles of reduced sulfur pools at the 5 examined stations. Pools are separated into acid-volatile (AVS) and chromium reducible sulfur (CRS) pools. Each point is the average of 3 sediment cores

depths ($SRR_{CRS} > 69\%$ of SRR_{tot}). SRR_{AVS} was low in the surface layer (1 to 2% of SRR_{tot}) and increased with depth (5 to 31% of SRR_{tot}). At the unvegetated site SRR_{tot} decreased from the surface ($211 \text{ nmol cm}^{-3} \text{ d}^{-1}$) down to 6–8 cm ($95 \text{ nmol cm}^{-3} \text{ d}^{-1}$). At the 2 stations with the highest shoot density SRR_{tot} attained a subsurface maximum at 1 to 2 cm depth (613 and $862 \text{ nmol cm}^{-3} \text{ d}^{-1}$ at Stns 4 and 5, respectively). At Stns 2 and 3 SRR_{tot} had a pattern similar to the unvegetated site, although the overall rates were higher (up to $479 \text{ nmol cm}^{-3} \text{ d}^{-1}$). SRR_{tot} increased with shoot density with the most significant increase in the surface layers (1 to 4 cm). Regression analysis showed a significant positive linear relationship with shoot density in both zones (root: $y = 0.481x + 207.9$, $R^2 = 0.939$, $p = 0.006$; below roots: $y = 0.504x + 136.5$, $R^2 = 0.819$, $p = 0.035$).

Sulfur pools

The inorganic sulfur pools were measured as dissolved sulfides (DS) (Fig. 5) and as particulate pools separated into acid-volatile (P_{AVS}) and chromium reducible sulfur (P_{CRS}) (Fig. 6). At the unvegetated site the concentration of dissolved sulfides was below detection limit in the surface layer and increased with depth (to $6.5 \mu\text{M}$). At the vegetated sites DS were present (1.1 to $10.5 \mu\text{M}$) in the surface layer (0 to 1 cm) but showed highest concentrations at 2 to 6 cm depth (up to $43 \mu\text{M}$). This corresponds to the sediment depth where maximal SRR was found. There was a significant difference among the stations (2-way ANOVA: $F_{4,20} = 3.222$, $p = 0.045$), whereas there was no difference between the rooted layer and below ($F_{1,20} = 2.957$, $p = 0.108$). P_{AVS} was low at all stations ($< 70 \text{ nmol cm}^{-3}$), and P_{CRS} accounted for $> 93\%$ of the total sulfide pool (0.6 to $3.2 \mu\text{mol cm}^{-3}$). P_{CRS} was generally higher at the vegetated stations, except for the 0 to 1 cm layer. There was no significant trend with shoot density in the rooted layer (least-squares regression: root zone: $R^2 = 0.194$, $p = 0.458$), whereas there was a positive linear relationship below the roots ($y = 0.003x + 1.738$, $R^2 = 0.981$, $p = 0.001$). The depth-integrated P_{CRS} also showed a positive trend with increasing shoot density (Fig. 7).

DISCUSSION

Eelgrass location

The 4 vegetated stations examined here were situated at a location with many small ($< 200 \text{ m}^2$) *Zostera*

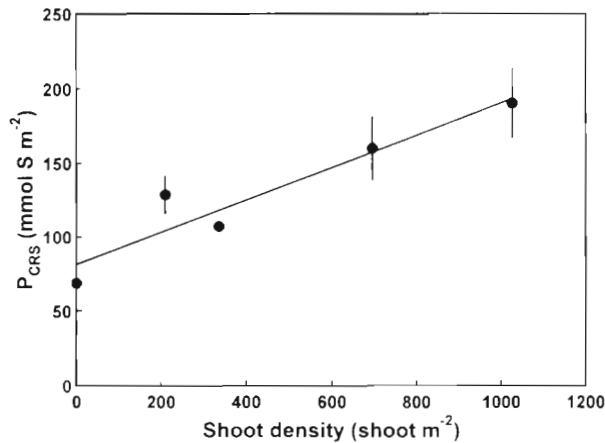


Fig. 7 Depth-integrated chromium reducible sulfur pools plotted against shoot density. Each point is the average of 3 sediment cores (\pm SE). The best fit with linear least squares analysis is given: $y = 0.109x + 81.343$, $R^2 = 0.900$, $p < 0.001$

marina patches, and due to the shallow water depth, the eelgrass patches are exposed to high physical disturbance and resuspension. The examined eelgrass population is important in stabilizing the sediments, but may also experience a high degree of seasonal and annual variability. The shoot density and the living biomass of shoots and rhizomes fall in the range of those found in other eelgrass patches (Sand-Jensen 1975, Jacobs 1979, Wium-Andersen & Borum 1984, Olesen & Sand-Jensen 1994). The observed shoot:root (including rhizome) ratio which is lower than 1 is in accordance with Olesen & Sand-Jensen (1994), and the high percentage of below-ground allocation indicated perennial eelgrass populations (Sand-Jensen 1975, Robertson & Mann 1984).

Sulfate reduction within the eelgrass bed

There was no effect of increasing incubation time in the determination of depth-integrated sulfate reduction rates, indicating that the sulfate reduction activity was constant during the incubation and that reoxidation of reduced label was insignificant. Isaksen & Finster (1996) suggested shorter incubation times (<0.5 h) to avoid reoxidation in the sediments with oxidized root zones. In this study dissolved sulfides were present throughout the examined depth interval, and the sediments were reduced, limiting reoxidation (Moeslund et al. 1994).

Sulfate reduction rates were stimulated by the presence of eelgrass, and there was a strong correlation between the density of living plants and the depth-integrated sulfate reduction rate (ISRR_{tot}) (Fig. 3), whereas there was no correlation with dead biomass.

The obtained rates of sulfate reduction were high in the vegetated sediments compared to most coastal sediments (Thode-Andersen & Jørgensen 1989, Moeslund et al. 1994), but similar high sulfate reduction rates have been measured in *Spartina* sp. marsh sediments (Hines et al. 1994) and in sediments vegetated with *Zostera noltii* (Isaksen & Finster 1996) and *Halodule beaudetti* (Blackburn et al. 1994). Stimulation of microbial activity measured as aerobic respiration, nitrification and denitrification has also been observed in eelgrass beds (Caffrey & Kemp 1990), indicating that the entire sediment metabolism is enhanced, and not only sulfate reduction as measured here. Smith et al. (1984) found a release of O₂ from the roots, and in accordance with the O₂ release Caffrey & Kemp (1991) found that aerobic respiration and nitrification was enhanced. Denitrification, in turn, is stimulated by the release of nitrate from nitrification.

Sulfate reduction in coastal sediments is primarily controlled by temperature and input of organic substrates (Moeslund et al. 1994). Temperature was similar at all 5 sites during measurements, whereas sedimentation of organic debris probably is density dependent, as the denser eelgrass stands hamper water movement and thus increase the sedimentation rate to a higher degree than scattered stands. Seagrass beds have been shown to act as sinks of allochthonous organic matter in the form of phytoplanktonic detritus, land run-off and resuspended matter (Velimirov 1987, Pérez-Lloréns & Niell 1993, Dauby et al. 1995). The sediment organic content was low at all sites, and there was no correlation between organic content and shoot density, indicating that either the deposition of organic matter was low or that the turnover was high. External sources are possibly more important during spring bloom sedimentation and winter organic inputs (Danovaro & Fabiano 1995). Autochthonous sources of organic matter may relate directly to the shoot density. Blum & Mills (1991) found that fresh eelgrass detritus loses 20% of its original dry weight within 1 d, and an additional 20% within the following 20 d due to leaching. Leached material is often labile and may be rapidly utilized by bacteria. The poor correlation between dead biomass and ISRR, on the other hand, is probably due to the fact that the labile pool only accounts for a low and variable fraction of the total organic pool. López et al. (1995) suggested that the enhanced input of organic matter from the seagrasses explains a positive correlation between the production of *Posidonia oceanica* and bacterial activity, and Blackburn et al. (1994) propose that excretion of organic matter directly from the plants supports a high sulfate reduction rate in rooted depths. Isaksen & Finster (1996), however, found no difference in sulfate reduction

rates during illumination and darkness, and they suggest that organic molecules that fuel sulfate reducers are produced by microbial hydrolysis of macromolecules within the sediment. Release of organic matter from the rhizome and roots of *Zostera marina* has been found during photosynthesis and growth (Smith et al. 1988), and in this study pore water DOC pools increased with increasing plant density. Sulfate reduction rates were higher in the rooted layers compared to the layers below, and showed a positive relation with the shoot density, with the steepest increase in rates in the rooted layers. The depth-integrated SRR and the depth-integrated DOC pool show a weak positive correlation ($y = 1.171x + 11.224$, $R^2 = 0.602$, $p = 0.008$). Koepfler et al. (1993) also found higher DOC concentrations in sediments vegetated with *Halodule wrightii* compared to a bare site, and they found a positive correlation between sediment oxygen uptake and pore water DOC concentration, suggesting that the total sediment metabolism is related to the DOC concentration. Kristensen & Hansen (1995) found high accumulation of DOC and stimulated microbial activity during decomposition of macrophyte detritus (*Ruppia maritima*) within the sediment. SCFA may be important components of the DOC pool, as alcohols are excreted from the roots of *Z. marina* (Smith et al. 1988). Alcohols may rapidly be degraded to SCFA, but concentrations were low in the vegetated sites, indicating a low production or rapid turnover of these substrates. SCFA are considered important microbial substrates to sulfate-reducing bacteria (Parkes et al. 1989). Hines et al. (1994) found high concentrations of acetate in salt-marsh sediments with stands of *Spartina* sp. They measured acetate oxidation rates lower than the sulfate reduction rates, and suggested that sulfate-reducing bacteria may utilize other compounds than acetate in vegetated sediments.

Sulfur pools in vegetated sediments

The high sulfate reduction activity in the vegetated sediments resulted in enhanced pools of reduced sulfur compared to the unvegetated site. The increase was most noticeable for dissolved sulfides. Isaksen & Finster (1996), on the other hand, did not detect dissolved sulfides despite high rates of sulfate reduction in sediments with *Zostera noltii*, and Blackburn et al. (1994) found low pools of reduced sulfides (dissolved and precipitated) in sediments vegetated by *Halodule beaudetti* roots. They suggested that sulfides are rapidly reoxidized by the excretion of O_2 from the roots. Dissolved sulfides are usually not found close to the surface in low-organic sandy coastal sediments,

where the reoxidation with e.g. oxidized Fe and Mn is rapid (Moeslund et al. 1994, Thamdrup et al. 1994). A high reoxidation was also expected in eelgrass sediments due to excretion of oxidized compounds through the roots (Smith et al. 1984, Caffrey & Kemp 1990), but the high sulfate reduction activity may have exceeded the reoxidation capacity. The dissolved sulfides can affect the growth of the plants, as Goodman et al. (1995) found reduced rates of photosynthesis at similar sulfide concentrations.

The pools of precipitated reduced sulfides (P_{AVS} and P_{CRS}) showed no significant increase with depth, indicating that the burial of reduced sulfides was low. P_{AVS} was very low at all sites, implying that the formation of pyrite (CRS) was rapid in accordance with the SRR_{CRS} measured at the site, and suggesting that the route for burial of sulfides is similar to salt marshes and mangrove sediments with pyrite as the main sulfide precipitant (Howarth 1984, Holmer et al. 1994). The pools of pyrite were low when compared to salt marshes and mangrove sediments, probably due to reoxidation of the buried sulfides during autumn and winter storms where the sediments are physically disturbed. The depth-integrated pools of P_{CRS} showed a positive correlation with shoot density, indicating that the higher sulfate reduction activity resulted in increased burial of reduced sulfides despite the high degree of reoxidation. The accumulation of sulfides cause a reduced sediment environment, which may limit the floral and faunal activity, and visual inspections at the location showed almost no faunal activity inside the eelgrass patches. As no historical records are available for the examined eelgrass bed, the smallness of the difference in sulfide burial between the bare and the vegetated sediments could also be due to recent eelgrass colonization.

CONCLUSIONS

Our results suggest a strong positive relationship between plant abundance and sediment bacterial activity in eelgrass beds. The relationship may involve a direct plant effect resulting from the production of autochthonous labile organic matter within the eelgrass bed as indicated by an accumulation of dissolved organic carbon in the pore waters. The high sulfate reduction results in a rapid sulfur cycling with dissolved sulfides present in the pore waters and an elevated pool of precipitated reduced sulfides within the eelgrass bed. We conclude that the sulfur and organic matter cycling is directly related to the density of the seagrass population in Roskilde Fjord, probably because of enhanced inputs of organic matter by the seagrasses.

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