

Small-scale heterogeneity in the geochemistry of seagrass vegetated and non-vegetated estuarine sediments: causes and consequences

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Abstract In addition to nutrient and light availability, sedimentary biogeochemical processes can play an essential role in seagrass productivity. Previous investigations of the interactions between seagrasses and their underlying sediments have failed to clearly identify the spatio-temporal variability of the major geochemical parameters involved. Dissolved and solid phase chemical parameters in eelgrass vegetated and nearby non-vegetated sediments were investigated in this study to determine their vertical, lateral, and temporal distributions. Solid-state microelectrodes were used to investigate dissolved O_2 , ΣH_2S , Fe^{2+} , and Mn^{2+} on mm space scales. In this study, spatial heterogeneity was assessed and diurnal “ventilation” by seagrass productivity (i.e., the translocation of photosynthetically produced oxygen to the anoxic sedimentary environment) was not observed probably because benthic infaunal activity (bioturbation and bioirrigation) and microzones established by microbial processes led to highly heterogeneous sediment geochemistry where temporal variability was obscured by small-scale spatial variability. Non-vegetated sediments were less

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geochemically variable laterally than vegetated sediments, however, in some cases, they had similar vertical variability, possibly because they had been vegetated at an earlier time. This study demonstrates that in vegetated sediments where there is also substantial benthic macrofaunal activity it is difficult to separate the impacts of the two types of biota on sediment geochemistry and their spatial patterns, and it also raises the question of the applicability of traditional one-dimensional diagenetic models for such spatially–temporally complex sediments.

Keywords Seagrass · Sulfide · Light · Heterogeneity · Nutrients · Carbon · Voltammetry

1 Introduction

Sediment biogeochemistry associated with early diagenetic processes involves a complex and dynamic interplay among benthic biota, porewaters, sedimentary minerals, and organic matter. Since the pioneering work of Berner in the 1960s a vast amount of research has taken place in gathering and modeling data on early diagenesis. Many of these studies have focused largely on the role of bacteria in driving diagenetic reactions and macrofauna in influencing, and often dominating, transport processes near the sediment–water interface through bioturbation and bioirrigation.

However, there has been an increasing appreciation that in relatively shallow water sediments benthic vegetation, such as seagrasses, play an important role as well, and benthic vegetation in turn can be strongly influenced by sediment biogeochemistry (e.g., Pulich 1989; Goodman et al. 1995; Holmer and Nielsen 1997; Terrados et al. 1999; Erskine and Koch 2000; Lee and Dunton 2000; Holmer et al. 2001). These processes can vary on small spatial (<1 mm) and temporal (<1 h) scales (Harper et al. 1999; Shuttleworth et al. 1999; Hebert and Morse 2003; Morse et al. 2003). Geochemical processes in seagrass-vegetated sediments are generally not at steady state. Processes are spatially and temporally heterogeneous due to biological activity, including bacterial respiration, localized inputs of seagrass exudates, and bioturbation/bioirrigation. It is therefore important to know how biomediated and abiotic processes interact.

Because benthic photosynthetic activity is light dependent, diurnal cycles result in sediment biogeochemistry in response to photosynthetic oxygen input or increased mineralization of photosynthates exuded from roots (Blaabjerg and Finster 1998; Blaabjerg et al. 1998; Boschker et al. 2000; Hansen et al. 2000; Lee and Dunton 2000; Hebert and Morse 2003). The diurnal effects that seagrasses have on sediment may reach beyond changes in dissolved components and also change the concentration of solid phases such as sulfide and carbonate minerals.

Eldridge and Morse (2000) were successful in modeling the influence of three species of seagrasses on sediment biogeochemistry for sediments with relatively low densities of benthic infaunal organisms in Laguna Madre, Texas. Their model was based on porewater data gathered by the traditional method of slicing of cores and extraction of porewater by squeezer on 2 or greater cm depth intervals.

In this study, we have chosen seagrass vegetated and adjacent non-seagrass vegetated (unvegetated) sediments as well, however, these sediments have abundant infaunal organisms, which are more typical of many seagrass meadows (Ferraro and Cole 2004). Infaunal organisms may influence near-interfacial

sediment chemistry either directly through irrigation processes (Morse and Eldridge 2006) or indirectly by clearing the water column of particles enhancing seagrass production and thereby stabilizing sediments (Newell and Koch 2004). Because we expected considerable heterogeneity, solid-state microelectrodes were used to measure dissolved $\Sigma\text{H}_2\text{S}$ and Fe^{2+} (O_2 and Mn^{2+} were below detection limits) at millimeter scales so that fine-scale heterogeneity could be assessed. The results of these measurements are the primary focus of this paper. A wide variety of other sediment parameters were also measured by traditional methods on centimeter depth scales including NO_3^- , NH_4^+ , PO_4^{3-} , dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), and solid phase chemical parameters (acid volatile sulfides (AVS), total reduced sulfides (TRS), total organic carbon (TOC), reactive metals (Fe, Mn, Zn, Cu, Ni, Cr) (see for example, Morse and Rowe 1999; Arvidson et al. 2004). However, because of the large heterogeneity, concentrations of the aforementioned analytes within separate cores may not convincingly be comparable to the analytes of the incubated cores for micro-profiling. The methods and data for these components are nevertheless presented and will only be generally referred to in the Discussion portion of this paper.

2 Methods

2.1 Study area and sampling strategy

The study was conducted on subtidal sediments (1.5 m low tide water depth) vegetated with *Zostera marina* (eelgrass) at Idaho Point which is located on the south side of the Yaquina Bay estuary in Newport, OR (44°37.125' N, 124°01.847' W). Samples were taken during August 2003 from the middle of an eelgrass bed (>~50 shoots m^{-2}) and unvegetated (non-seagrass vegetated) sediments 10 m from the edge of the bed.

Cores were taken avoiding, as much as possible, obvious macrofaunal structures (e.g., burrows). Much of the unvegetated site was covered with benthic micro- and macroalgal mats. These were also avoided as reasonably achievable, and for the purposes of this paper, “unvegetated” sediments refer to non-seagrass vegetated sediments. Cores were taken at mid-day (~12:00 pm Pacific time) and at night (~4:00 am), to examine both light and dark conditions. At each time and for each sediment type, a variety of cores were taken for three different experiments (1) two Plexiglas cores (14 cm dia. \times 40 cm length) were taken for micropfiles incubations (72 profiles total), (2) two cores (3 cm \times 30 cm) with siliconed injection ports every five cm (2 cm depth intervals) were taken and processed for sulfate reduction rates, and (3) two core liners (7 cm \times 40 cm) were taken and processed for porewater and solid geochemical analyses (Table 1). In some cases, porewater had to be combined between replicate cores to obtain enough porewater volume for the determination of all the analytes.

2.2 Micropfiles

The micropfile cores were used for the determination of dissolved O_2 , Mn^{2+} , Fe^{2+} , $\Sigma\text{H}_2\text{S}$, and seagrass aboveground, root, and rhizome biomass. Intact cores were taken from the field, transported to the laboratory (<1 h), and incubated in

Table 1 Sampling strategy and core liner descriptions

Analytical purpose	Three core types for both vegetated and unvegetated sediments			
	Laboratory incubations for vertical and lateral microprofiles	Sediment geochemistry		³⁵ S radiotracer injections
Core dimensions (radius (i.d.) × length)	14 cm × 50 cm (Acrylic)	7 cm × 40 cm (Plexiglas)		3 cm × 40 cm (Acrylic with 5 cm siliconed injection ports)
Analytes	Dissolved O ₂ , Mn ²⁺ , Fe ²⁺ , ΣH ₂ S	Solids	Porewater	Sulfate reduction rates
	%Total sulfur plant biomass	TRS AVS TOC	NH ₄ ⁺ NO ₃ ⁻ PO ₄ ³⁻ DIC DOC	
Sampling regime	Replicate cores obtained for both vegetated and unvegetated sediments at night (4:00 am) and during the day (12:00 pm). All cores were taken back to the lab for processing			
	Three near-simultaneous profiles every four hours (12/12 h light/dark)	Sediments were sliced into 2-cm depth intervals		12-hour incubation period

mesocosm aquaria. The cores were submerged in the aquaria with ~20 cm of overlying water above the top of the core liner (Fig. 1). Filtered in situ seawater was continuously being replaced in the aquaria while under aeration and maintained at in situ temperature. Lighting was supplied by 1,000-watt metal halide bulbs with a measured irradiance of ca. 400 μmol photons m⁻² s⁻¹ with a 12/12 h on/off cycle. Aluminum foil covered the sides of the cores from the sediment–water interface down to the bottom of the core to avoid illuminating the sides of the sediments. Seagrass leaves were allowed to extend out of the core as they do during low tide exposure. Gold–mercury amalgam, solid-state voltammetric microelectrodes were used to measure porewater dissolved O₂, Mn²⁺, Fe²⁺, and ΣH₂S at 2 mm depth increments down to 50 mm, at which point 5 mm depth increments were made to a total depth of 150 mm. Microelectrodes were calibrated against reagent grade MnCl₂ (Aldrich) standard solutions with the pilot ion method (Brendel 1995; Brendel and Luther 1995). Sediments in both the seagrass (core identification SG1) and unvegetated (core identification UV1) cores were profiled every 4 h for a 24 h period. Three near-simultaneous (10 s lag) microelectrode profiles, spaced 1.5 cm apart horizontally from each other, were obtained for each time point for 2-dimensional profiles. Microelectrode conditioning was performed at -0.5 V for 5 s before every scan to remove any previously deposited ΣH₂S from the Hg amalgam

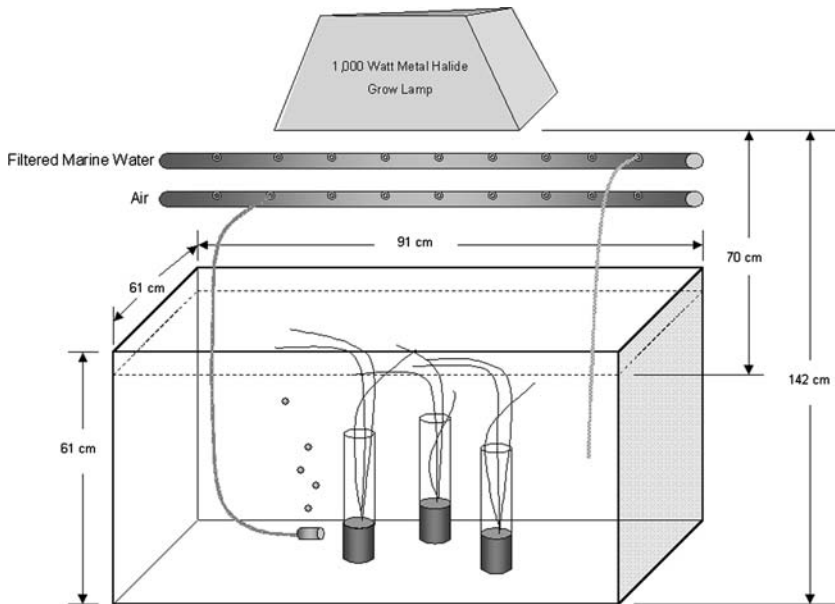


Fig. 1 Illustration of mesocosm aquarium with cores for microprofiling

surface. The experiment was replicated a week later with fresh cores from the same location (core identifications SG2 and UV2). Additional horizontal profiles were obtained by starting ~3 cm from the sidewall of the core liner (zero cm reference) and sampled every 5 cm laterally across the diameter of the core liner. This was done at the sediment–water interface, 5, 10, and 15 cm depth intervals.

Seagrass aboveground, root and rhizome biomass data were obtained from the microprofile cores at the end of the experiment. Sediments were rinsed with deionized water from the rhizome and roots and epiphytic algae were removed from seagrass leaves. The shoots and leaves were oven-dried at 60°C for 24 h and weighed as grams dry weight (gdw) of aboveground biomass normalized to core area. Roots and rhizomes were divided and dried separately. Percent total sulfur (%TS), assumed to be largely organic-S because of reduced sulfur oxidation and plant rinsing, was determined by combusting plant material in a UIC furnace-coulometer against sulfur standards (UIC, Inc.). Previous porosity data from earlier in the year from the site was used (obtained from percent water loss upon drying at 80°C for 24 h with salinity correction). Grain size analysis was determined by wet sieving the sand fraction and pipette analysis for silt and clay fractions.

2.3 Sulfate reduction rates

Sulfate reduction rates (SRR) were determined using the radiotracer ^{35}S method of Jørgensen (1978) and Canfield et al. (1986). Cores obtained in the field were processed immediately (<2 h) at the laboratory. Cores were injected with 10 μCi of $\text{Na}_2^{35}\text{SO}_4$ at 2 cm intervals through silicone injection ports, incubated for 12 h, quickly frozen, and shipped back to Texas A&M University on dry ice where they were processed and analyzed on a Rackbeta liquid scintillation counter.

2.4 Sediment porewater and solids geochemistry

Cores were sectioned at 2 cm intervals to a final depth of 20 cm under a nitrogen environment and porewater was extracted using Reeburgh (1967) squeezers. The porewater was syringe-filtered (0.45 μm) into separate glass vials with septa. Samples were poisoned with mercuric chloride and refrigerated or frozen where appropriate (e.g., DIC) until analysis. Solids were placed in whirl bags under nitrogen and frozen.

Dissolved inorganic carbon (DIC) was determined by coulometric titration (UIC Inc. CO₂ Coulometer). The instrument was standardized using solutions of primary standard Na₂CO₃ (Aldrich) (Dickson and Goyet 1994). A Shimadzu TOC-5000 analyzer was used to determine dissolved organic carbon (DOC) using potassium biphthalate (Fisher) standards. Ammonium-N (NH₄⁺) was determined spectrophotometrically by the phenol–hypochlorite method using nitroprusside as a catalyst according to Strickland and Parsons (1972). Nitrate (NO₃⁻) was determined as NO₃⁻ + NO₂⁻ using a Clark-type nitrate sensor and a picoameter PA2000 (Unisense). Phosphate was spectrophotometrically determined (Varian DMS 100S UV–visible spectrophotometer) as soluble reactive PO₄³⁻ using ammonium molybdate, ascorbic acid, and trivalent antimony (Strickland and Parsons 1972).

Modified procedures similar to those of Canfield et al. (1986) and Cornwell and Morse (1987) were used to determine TRS and AVS, respectively. A UIC sulfur coulometer was used to determine the $\Sigma\text{H}_2\text{S}$ concentration. Na₂S (Sigma) standards were used to verify accuracy and precision of the analysis and instrumentation. AVS was determined using a room temperature 6 N HCl + SnCl₂ for 1 h (Cornwell and Morse 1987). Total organic carbon (TOC) was calculated as weight percent total carbon by combusting acidified and unacidified dried sediment samples in a UIC furnace coupled to a UIC carbon coulometer (UIC, Inc.). Cold HCl and citrate dithionite extracted metals from the sediments (Raiswell et al. 1994) were analyzed using ICP-OES. Iron data reported will be distinguished by CDE-Fe (citrate dithionite extracted iron) and HCl-Fe (1 M HCl-extracted iron).

3 Results

3.1 Microprofile sediment porewater geochemistry

Dissolved oxygen and manganese (Mn²⁺) concentrations in the porewater were below detection (<5 μM) in all cases so these data are not presented. Overlying surface water was ~5.4 mg O₂ l⁻¹, $S = 34.2$, and $t = 15.4^\circ\text{C}$. Porosity was -0.72 ± 0.01 for all depths 0–20 cm. Grain size was determined in the top 2 cm for seagrass and unvegetated sediments. For the unvegetated sediments, the distribution was 79% sand (>63 μm), 21% silt (4–62 μm), and no clay (<4 μm). The seagrass sediment grain size distribution was 72% sand, 27% silt, and 1% clay.

The spatial heterogeneity of $\Sigma\text{H}_2\text{S}$ concentrations (as indicated by standard deviations) in seagrass vegetated sites was in most cases too large to resolve diurnal changes. Figure 2 is a representative of all profiles obtained (SG1 shown) during the study period. $\Sigma\text{H}_2\text{S}$ concentrations in unvegetated sediments were also laterally heterogeneous (Fig. 2, UV1–3), but were close to or below detection limits below throughout most of the profiles. In general, however, they did not show the same

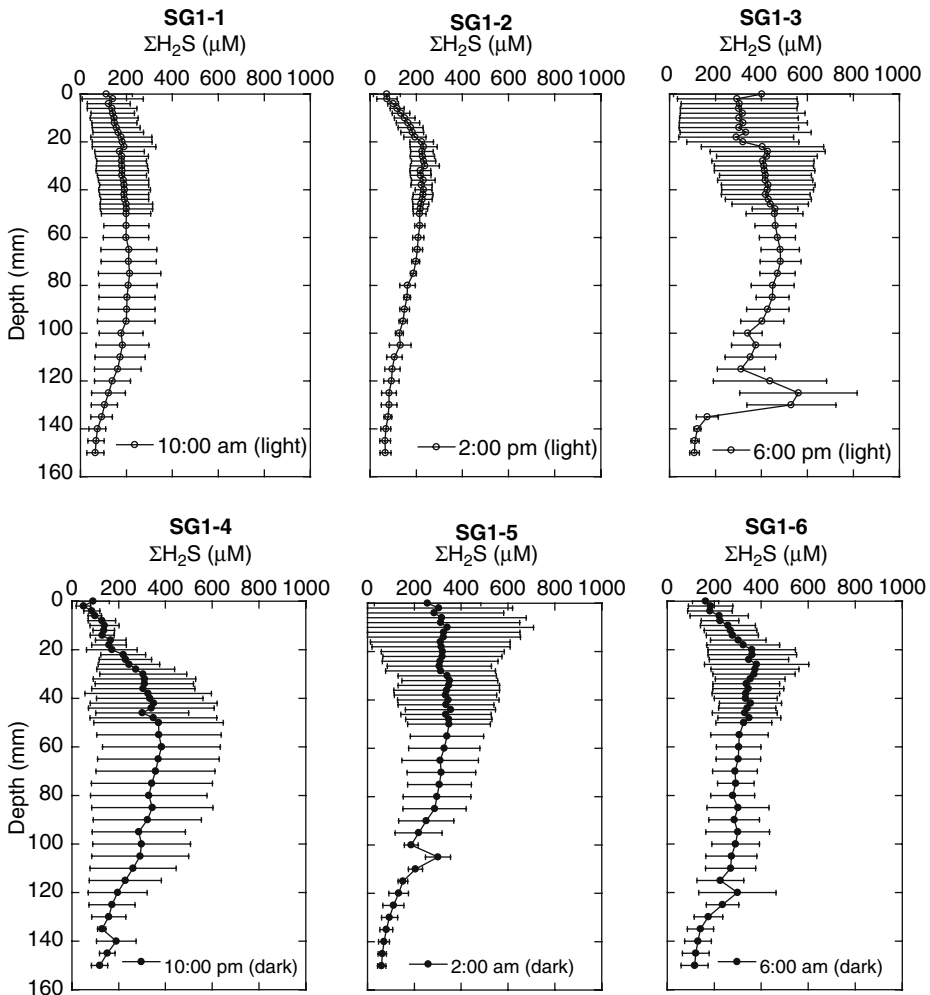


Fig. 2 Average dissolved porewater $\Sigma\text{H}_2\text{S}$ profiles for a seagrass core (SG1) in a 24 h period (bars represent \pm standard deviation for three profiles)

extent of heterogeneity as seagrass vegetated sediments (Fig. 3). Light and dark $\Sigma\text{H}_2\text{S}$ profiles of all cores were averaged separately into 5–10 cm depth bins (the depth which constitutes the majority of belowground biomass; Fig. 4). SG1 did not have any discernable temporal changes in $\Sigma\text{H}_2\text{S}$, but SG2 which had ~ 6 times less $\Sigma\text{H}_2\text{S}$ than SG1, appeared to exhibit diurnal changes in $\Sigma\text{H}_2\text{S}$ opposite of what was expected, with higher $\Sigma\text{H}_2\text{S}$ in light than dark (Fig. 4). $\Sigma\text{H}_2\text{S}$ concentrations in UV1 were much lower ($< 5 \mu\text{M}$) than seagrass vegetated cores and were not different between lights and dark. UV2 had higher ($> 40 \mu\text{M}$) $\Sigma\text{H}_2\text{S}$ and, like SG2, had higher concentrations in the light than in the dark.

Fe^{2+} was present in the first seagrass core (SG1) in high concentrations (up to $\sim 5 \text{ mM}$) but was not detected in the second seagrass core (SG2) (Fig. 5). Fe^{2+} concentrations up to $600 \mu\text{M}$ were observed in patchy distributions in the first

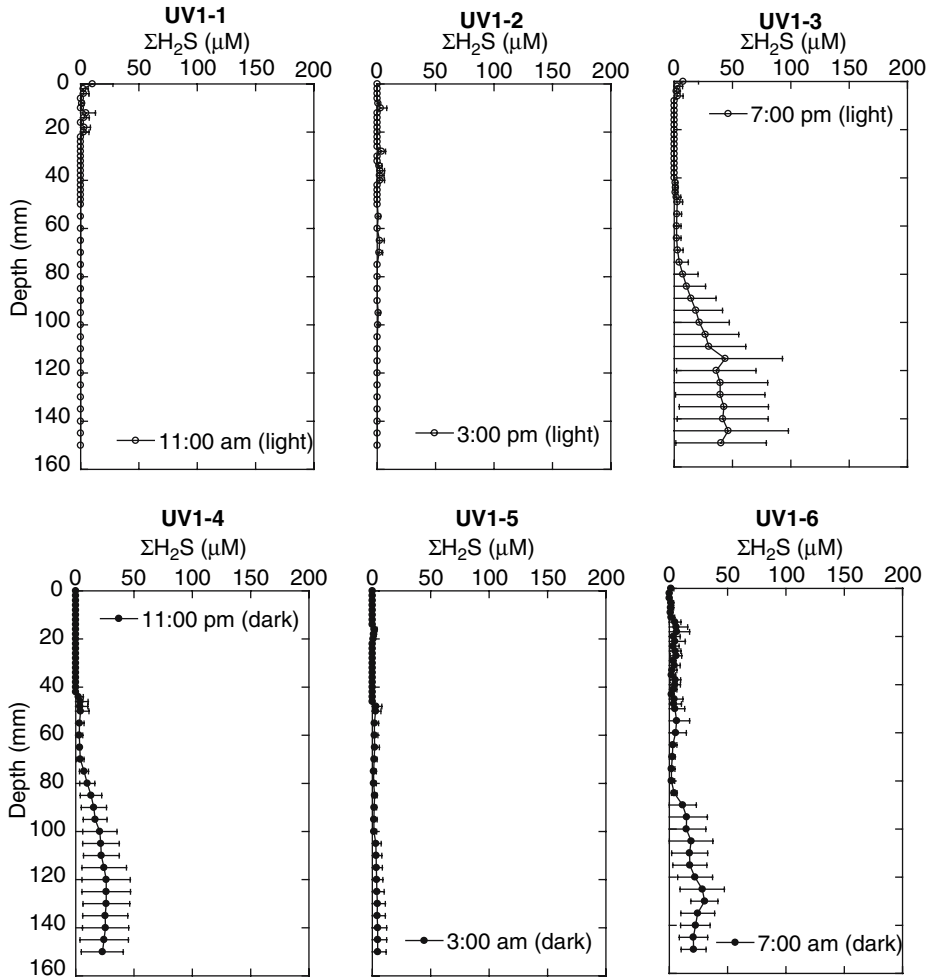


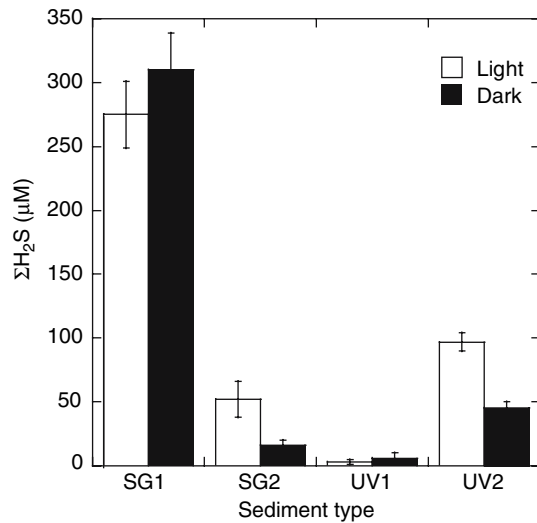
Fig. 3 Average dissolved porewater $\Sigma\text{H}_2\text{S}$ profiles for an unvegetated core (UV1) in a 24 h period (bars represent \pm standard deviation for three profiles)

unvegetated core (UV1) at sediment depths of 10–15 cm (data not shown). In almost all cases where $\Sigma\text{H}_2\text{S}$ and Fe^{2+} were detected simultaneously, an unquantifiable signal for FeS occurred at -1.1 volts (data not shown) indicating the presence of AVS.

3.2 Low depth-resolution sediment geochemistry

NH_4^+ under light conditions of the seagrass sediment had a maximum value of ~ 2.5 mM near the sediment surface with a generally decreasing trend with depth (Fig. 6). In seagrass sediments, NH_4^+ was higher during the light periods than in the dark except at 17 cm depth where a maximum of 2.2 mM occurred for dark conditions. The unvegetated sediments did not exhibit the same diurnal changes that the seagrass sediment porewater exhibited. In fact, porewater NH_4^+ in unvegetated

Fig. 4 Averaged (5–10 cm) $\Sigma\text{H}_2\text{S}$ from microprofiles for various sediment cores



sediments followed the same depth trends with respect to light and dark profiles. Concentrations were similar in magnitude for the both seagrass vegetated and unvegetated sediment types.

NO_3^- concentrations for light and dark seagrass sediments had subsurface maxima of $\sim 40 \mu\text{M}$ and $8 \mu\text{M}$, respectively, just below the water–sediment interface and thereafter fell below detection ($0.2 \mu\text{M}$). The unvegetated sediments showed more variability with depth compared to the seagrass sediments with a nitrate peak occurring at ~ 10 cm depth for both light and dark times.

PO_4^{3-} strongly resembled NH_4^+ profile trends in seagrass sediments. These seagrass sediments, PO_4^{3-} concentrations were higher during light periods with a subsurface maximum of $327 \mu\text{M}$ at ~ 3 cm depth, and dark concentrations were less concentrated than light, but increased slightly with depth. The unvegetated sediments showed the opposite trend where dark concentrations of PO_4^{3-} were higher than the concentrations in the light, as was observed for NH_4^+ concentrations.

DIC showed distinct diurnal variability for the seagrass sediment (Fig. 7). DIC in the light exposed seagrass sediments exhibited the highest concentrations in the top 4 cm and at 13 cm of the sediment at 16 mM and 9 mM, respectively. The concentrations of DIC in the dark seagrass sediments were lower overall (~ 2.2 – 5.4 mM) and less variable with depth. Similar trends were observed in the unvegetated sediments, with higher DIC in the dark than in the light.

DOC exhibited greater depth variability in seagrass sediments than the unvegetated sediments, but DOC in the unvegetated sediments was similar in magnitude than the DOC in seagrass sediments, with a mean value of $1,539 \mu\text{M}$ in unvegetated sediments compared to $2,222 \mu\text{M}$ in seagrass sediments (Fig. 7).

The TOC (Fig. 8) content did not show a large difference between seagrass and unvegetated sediments. The mean dry weight percent of organic carbon content was slightly greater in the seagrass sediments with a mean of $1.3 \pm 0.3\%$ in seagrass sediments and $1.2 \pm 0.3\%$ in unvegetated sediments, however the range was greater in unvegetated sediments.

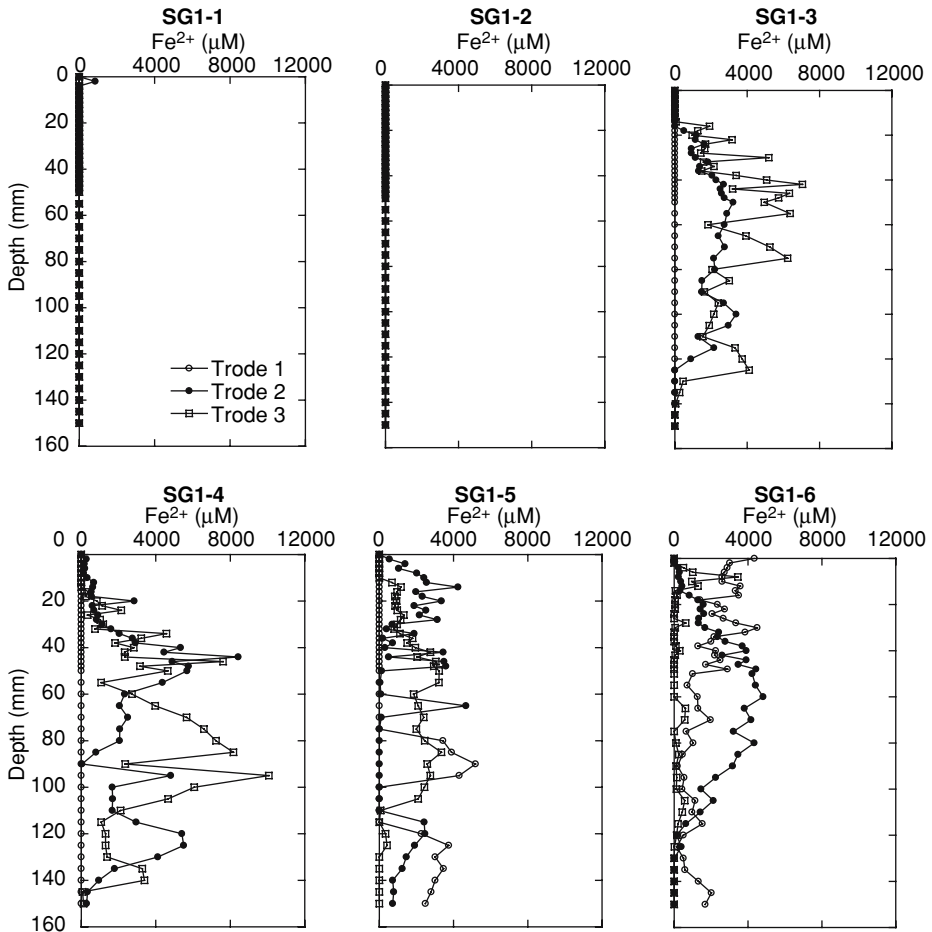


Fig. 5 Dissolved porewater Fe^{2+} for a seagrass core (SG1) in a 24 h period showing all three profiles

A remarkable finding is that there was diurnal variability in TRS for light and dark cycles (Fig. 9), and the standard deviation of TRS in seagrass sediments was much higher than the unvegetated cores. AVS accounted for ~5–25% of TRS, which is typical of many estuarine sedimentary environments, and did not show the same degree of variability (depth or time).

Reactive manganese (HCl-Mn) was less than $1.25 \mu\text{mol gdw}^{-1}$ for all cores. HCl-Fe ranged from $124\text{--}177 \mu\text{mol gdw}^{-1}$ while CDE-Fe was typically half that of the acid-extracted samples (Fig. 10). Table 1 shows selected metal concentrations and significant changes between light and dark cycles. HCl-Fe and Ni indicated diurnal changes in seagrass sediments while TRS showed diurnal changes in both sediments types.

SRR were higher in the light than in the dark (>50% in some cases) for vegetated sediments (Fig. 11). Unvegetated sediments did not show the same diurnal changes in SRR and varied less with depth than seagrass sediments. There were two sub-surface maxima in the seagrass sediments around 3 cm and 11 cm sediment depth.

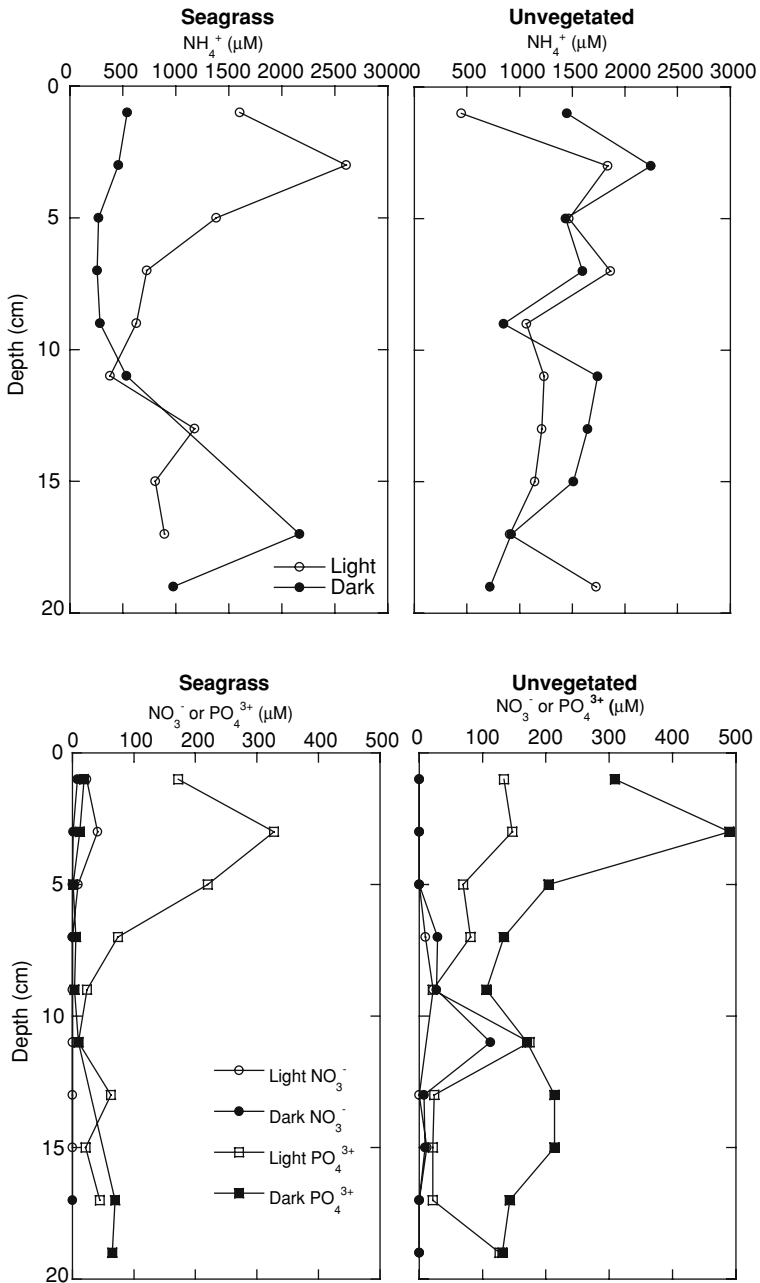


Fig. 6 Nutrient concentrations for seagrass and unvegetated sediments

3.3 Seagrass biomass

Aboveground seagrass biomass was substantially the largest portion of overall biomass in the seagrass sediments (Table 2). Typical rhizome depths were ~4–5 cm

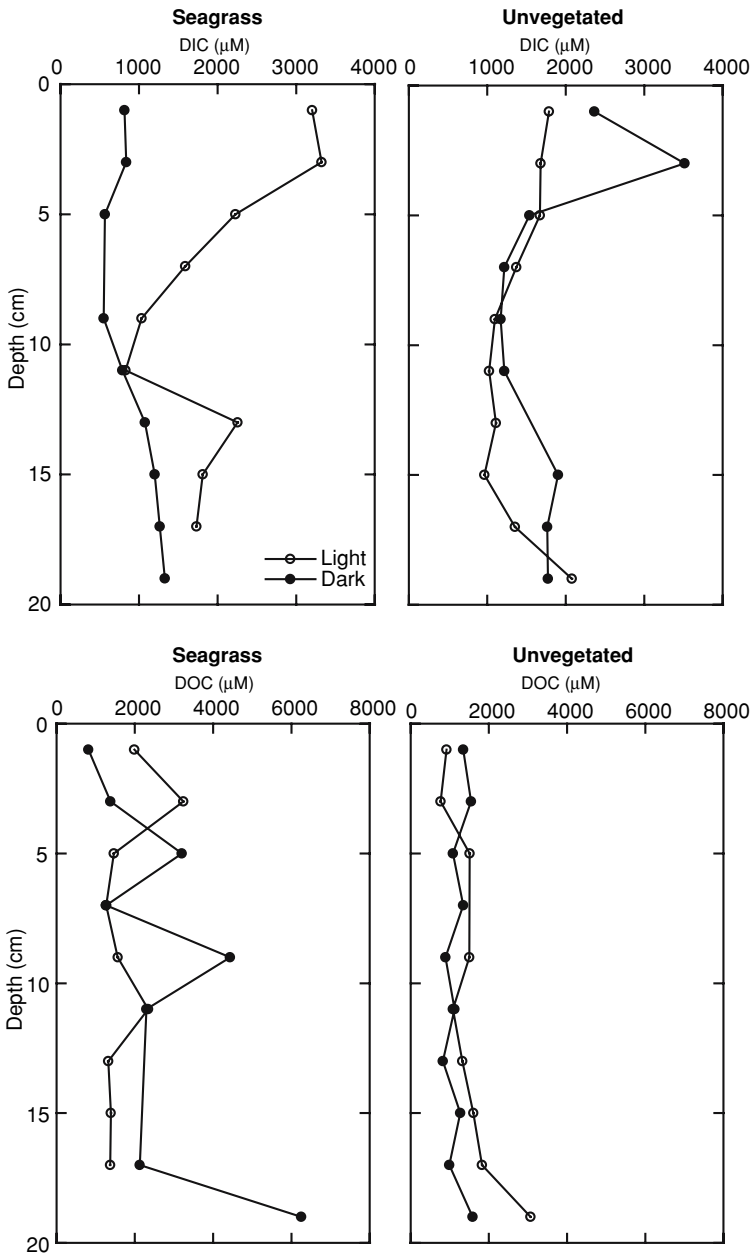


Fig. 7 Dissolved inorganic carbon (DIC) and dissolved organic carbon (DOC) concentrations for seagrass and unvegetated sediments

deep with roots extending down to ~10 cm. Leaves were ~1 m in length, and observationally ranged in epiphytic density (not determined). The total biomass of SG2 was approximately three times the total biomass of SG1, and belowground

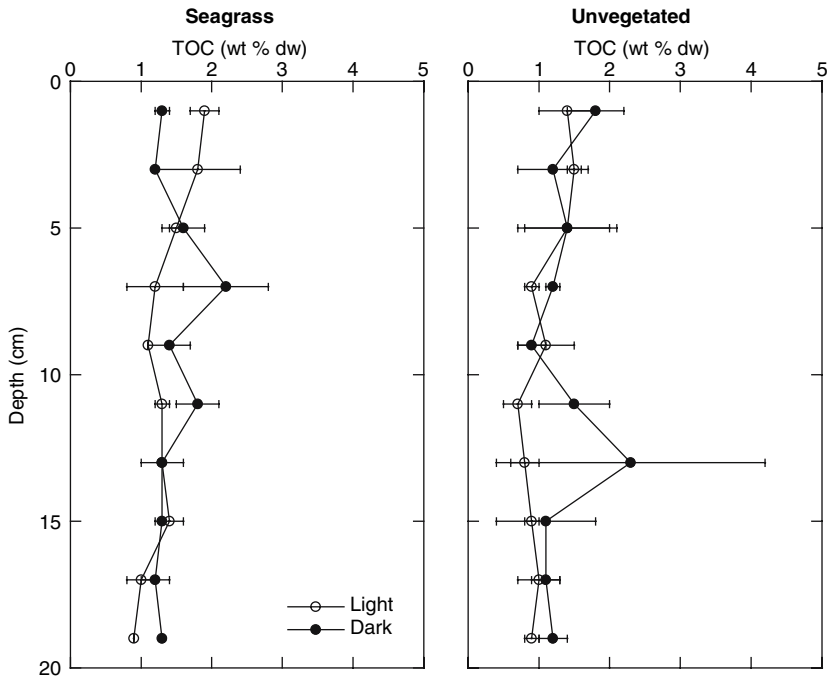


Fig. 8 Total organic carbon (TOC) content for seagrass and unvegetated sediments

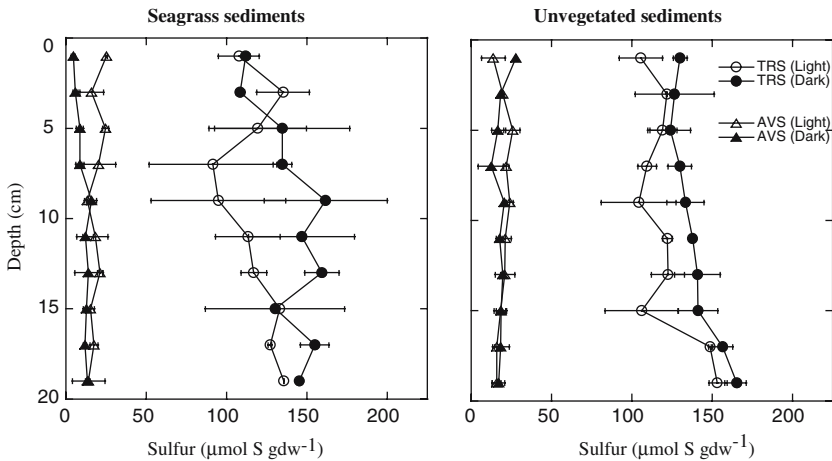


Fig. 9 Reduced sulfur pool for seagrass and unvegetated sediments

biomass only comprised 10–25% of the total plant biomass for each core. %TS of seagrass root biomass was higher in the seagrass cores with the larger dissolved sulfide concentration and lower root biomass.

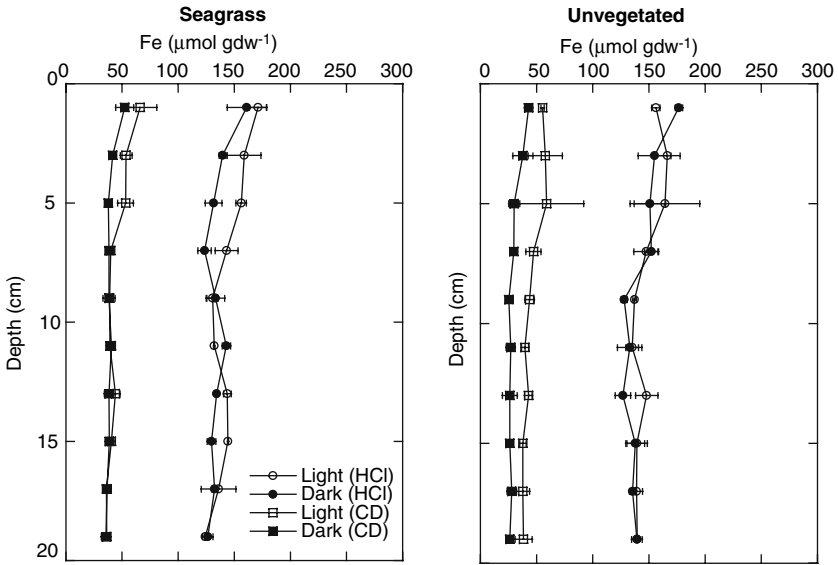


Fig. 10 Reactive iron for seagrass and unvegetated sediments

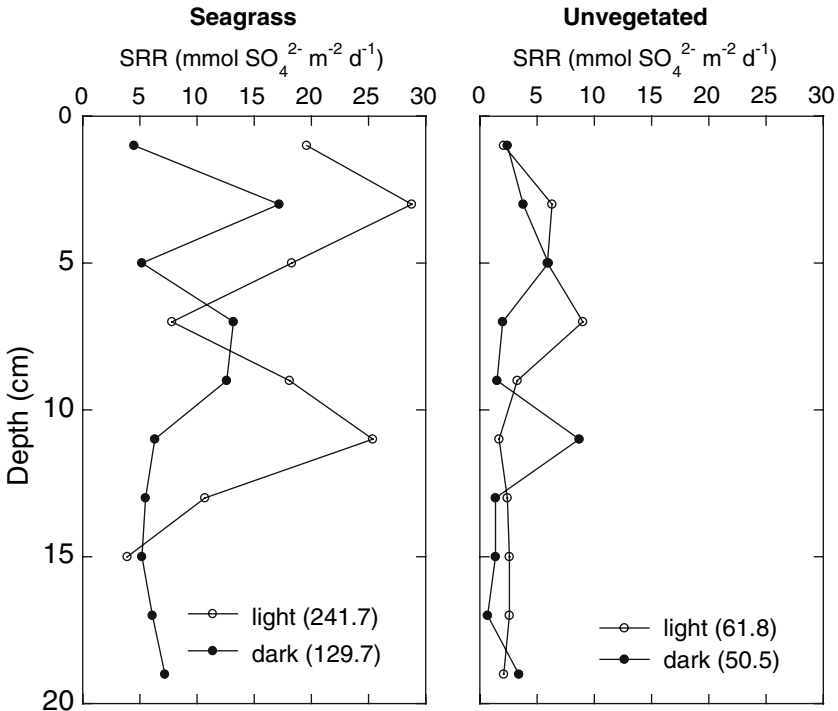


Fig. 11 Sulfate reduction rate (SRR) for seagrass and unvegetated sediments (Integrated rates are shown in legend)

Table 2 Biomass data from microelectrode cores (gdw = grams dry weight; RR:tot = root and rhizome biomass to total biomass; %TS = %total sulfur of plant parts)

	SG1		SG2	
	gdw m ⁻²	%TS	gdw m ⁻²	%TS
Aboveground biomass	246.2	0.04	738.0	No data
Rhizome biomass	39.6	0.12	77.4	No data
Root biomass	19.9	1.83	28.5	1.27
Total Biomass	305.7		843.9	
RR:tot (%)	19.5		12.6	

4 Discussion

4.1 $\Sigma\text{H}_2\text{S}$ and spatial versus temporal heterogeneity

Previous studies have observed diurnal changes in seagrass sediment $\Sigma\text{H}_2\text{S}$ (Goodman et al. 1995; Erskine and Koch 2000; Holmer and Bondgaard 2001; Koch and Erskine 2001). However, the sediment core incubations of SG1 did not exhibit any diurnal changes in $\Sigma\text{H}_2\text{S}$, or that any temporal variability was obscured by the spatial variability. SG2 appeared to exhibit a diurnal change in $\Sigma\text{H}_2\text{S}$, however, opposite of what was expected with higher $\Sigma\text{H}_2\text{S}$ in the light than in the dark. SG2 primary production was probably considerably greater than SG1 given the differences in biomass (Table 2). Given both the greater leaf area for photosynthesis and the greater root rhizome biomass to distribute lacunal O_2 , very little $\Sigma\text{H}_2\text{S}$ developed in SG2 during either the day or night periods. Hence $\Sigma\text{H}_2\text{S}$ concentrations during the diel cycle were so low that they were not geochemically of consequence despite their apparent diurnal difference.

Other investigators have noted that at high densities of seagrass biomass, little difference occurs in sediment $\Sigma\text{H}_2\text{S}$ during diel cycles. Lee and Dunton (2000) showed that in sediments of *Thalassia testudinum*, when shaded, did not exhibit changes in porewater sulfide. In addition, *T. testudinum* usually has much more belowground biomass than *Z. marina* and perhaps varying microbial assemblages that may impact the sediments more (>50% compared to <30%, respectively). The lack of diel differences in the low biomass treatment (SG1) is not surprising. The small amount of biomass and presumably primary productivity during the day resulted in only minor non-significant diel changes in $\Sigma\text{H}_2\text{S}$ that could be masked by other sediment biogeochemical processes. Low light availability from the combination of lower incident sun angles, overcast Pacific Northwest, and substantial self-shading/epiphytic biomass in *Z. marina* may decrease productivity and the subsequent translocation of oxygen to the sediments.

The 7-cm cores obtained adjacent to the cores for microprofiling revealed less ambiguous changes between light and dark cycles. The higher NH_4^+ concentrations during the day in seagrass sediments agreed with increased DIC, and sulfate reduction rate increase during photic periods of seagrass sediments, most likely attributed to enhanced sediment microbial activity from the input of labile DOC from seagrass, similar to what was reported in Blaabjerg et al. (1998) and Blaabjerg and Finster (1998). The unvegetated sediments showed the opposite effect where DIC, NH_4^+ , and PO_4^{3-} were more concentrated during the dark than at night most

likely attributed to nocturnal respiration near the sediment–water interface. Diurnal differences in TRS may have been present, but these differences may be attributed to the lateral variability as well. Sulfate reduction rates for seagrass and unvegetated sediments agreed with SG1 and UV1 microprofiles of $\Sigma\text{H}_2\text{S}$ (note SG2 cores for sulfate reduction rate determination were unusable due to inappropriate experimental handling). Integrated rates of sulfate reduction in the SG1 were much higher than those of unvegetated sediments. This corresponded to the higher measured $\Sigma\text{H}_2\text{S}$ concentrations in the seagrass microprofile core versus those in the unvegetated sediments, which may be because of the low incorporation of seagrass biomass into the smaller core liners for sulfate reduction rate determination as discussed previously.

4.2 Enhanced sediment complexity

Infaunal organisms have been shown to have considerable affect on both concentration and surficial fluxes of $\Sigma\text{H}_2\text{S}$ (Eldridge et al. 2004; Morse and Eldridge 2006). Infaunal tube forming polychaete and mollusca with siphones can increase the entrainment of oxidants to the sediment by a factor of 3 or more times the Fickian fluxes (Morse and Eldridge 2006). In the Pacific North West, the abundance of infauna is significantly greater in seagrass habitats than in any other mudflat estuarine habitats (Ferraro and Cole 2004) often with concentrations of irrigative infauna that strongly alter the BOD of the sediment (D’Andrea, per comm.). Two large burrows (~2 cm diameter) were observed in SG2 upon core dissection. Unfortunately, infaunal biomass was not determined, however a preliminary side investigation utilizing voltammetric profiling of a core at the unvegetated site revealed significant sedimentary oxidation around a shrimp burrow (Fig. 12).

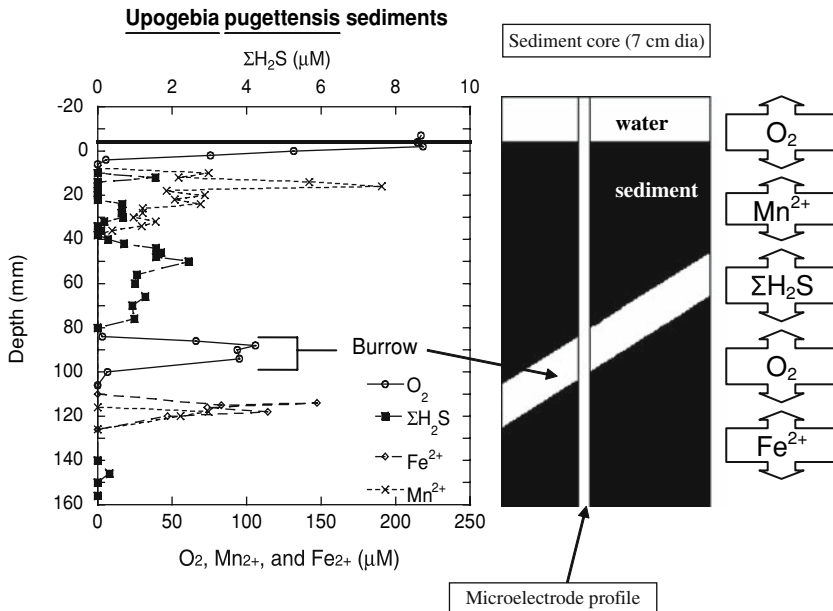


Fig. 12 Geochemical gradients associated with a shrimp burrow in sediments

Despite having tried to avoid obvious burrows, this was difficult especially at night given their ubiquitous distribution in this environment. Variations in infaunal organism diel activity could easily be responsible for the large difference in $\Sigma\text{H}_2\text{S}$ concentrations in our results at SG1 and SG2 (Wenzhofer and Glud 2004).

Cohabitation of benthic infauna and seagrass may be mutualistic, where organic carbon sources and habitat are provided for infauna and sediment ventilation is offered for seagrass to lower sedimentary sulfide concentrations. The benefit of seagrass as a source of nutrition and refuge to infaunal communities has been demonstrated in some studies (Webster et al. 1998; Mattila et al. 1999; Bostrom et al. 2002 etc.). Fewer studies, however, have demonstrated the benefits that seagrasses derive from the presence and activity of infaunal organisms. Peterson and Heck (2001) found a positive relationship between infaunal nutrient cycling and seagrass productivity. Eldridge et al. (2004) suggest that seagrass derive additional benefits from irrigating infauna through the introduction of oxidants from the water column into the root zone. The additional complement of oxidants in the rhizosphere helps maintain low levels of sulfides and other reduced seagrass toxicants.

The large standard deviations associated with $\Sigma\text{H}_2\text{S}$ and TRS make it difficult to discern temporal variations from spatial variations, whether the variability is attributed to dynamic root/rhizome system or infaunal burrow systems. While Figs. 2, 3, and 5 all demonstrate the lateral variability, Fig. 13 shows at higher horizontal resolutions the degree of lateral variability associated with seagrass sediments, where a single electrode measured $\Sigma\text{H}_2\text{S}$ at 0, 50, 100, and 150 mm sediment depth every 5 mm laterally (to avoid interference of the previous profile), and that the same degree of lateral variability is not observed in the unvegetated sediments. However, the surface of the unvegetated sediments does indicate small variability most likely attributed to localized pockets of organic matter degradation from

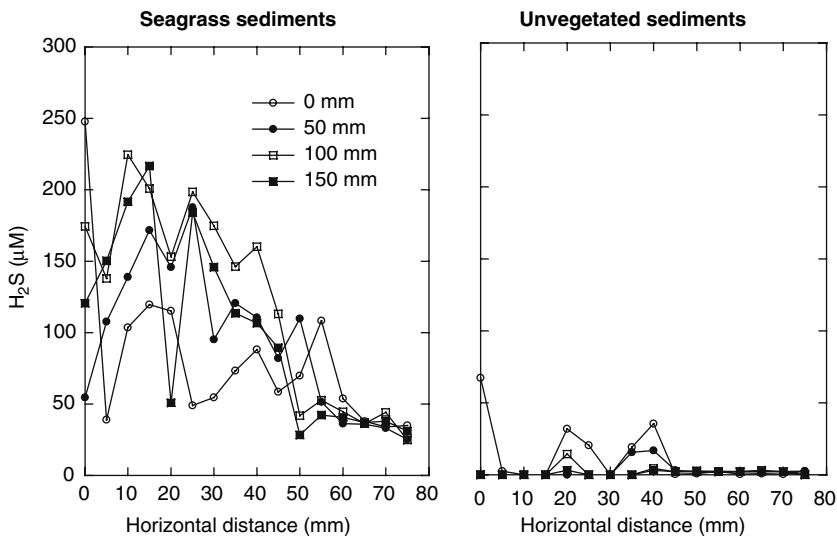


Fig. 13 Lateral scale observations of $\Sigma\text{H}_2\text{S}$ at four different sediment depths for seagrass (SG1) and unvegetated (UV1) sediments (Note $N = 1$ because in replicate experiments analytes were below detection)

Table 3 Scale length results determined by use of the autocovariance function

Site	Sampling time	Scale length H ₂ S (mm)	Scale length Fe ²⁺ (mm)
<i>Yaquina Bay Oct., 2000</i>			
Seagrass	Morse et al. (2003)	9.9	
Unvegetated	Morse et al. (2003)	11.7	
<i>Yaquina Bay Aug., 2003</i>			
Seagrass 1	10:00 am	15.7	BD
	2:00 pm	15.5	BD
	6:00 pm	9.1	10.7
	10:00 pm	13.6	14.0
	2:00 am	14.4	9.6
	6:00 am	15.7	8.0
Average scale		14.0 ± 2.5	10.5 ± 2.5
Unvegetated 1	11:00 am	4.0	
	3:00 am	BD	
	7:00 am	19.5	
	11:00 am	21.9	
	3:00 am	14.7	
	7:00 pm	12.9	
Average scale		15.1 ± 6.9	
Seagrass 2	2:00 pm	14.3	
	6:00 pm	19.2	
	10:00 pm	BD	
	2:00 am	9.1	
	6:00 am	17.2	
	10:00 am	17.5	
		15.5 ± 4.0	
Unvegetated 2	3:00 pm	9.4	
	7:00 pm	14.2	
	11:00 pm	8.9	
	3:00 am	10.0	
	7:00 am	14.0	
	11:00 am	6.7	
Average scale		10.5 ± 3.0	
Total average		13.8 ± 2.3	

BD = ΣH₂S was below detection hence the method could not be performed

patches of SRB. Scale lengths for determining the dominant source of variability using the autocovariance function (see Morse et al. 2003 for details) demonstrated that appropriate lengths of scale in the vertical profile were similar to those measured previously at the site (Morse et al. 2003) and did not vary significantly on a diurnal time scale (Table 3).

5 Summary

Seagrass habitats are now being used as bioindicators for estuarine health. However, managers of these environments must be able to understand the dynamic nature of the sedimentary system and the appropriate scales for facilitating seagrass growth/propagation. These analyses provide better insight into a complicated system where sulfur and carbon cycling vary on short space and time scales. Finally, temporal variability was obscured by spatial variability in some cases making difficult

observations of seagrass–sediment interactions. While direct causality of geochemical parameters on seagrass health cannot be determined from this study, the nature of the observed heterogeneity may be an important factor for seagrass health by establishing different geochemical gradients over small distances that are favorable to seagrass propagation. Biotic processes that foster the development of spatial heterogeneity (e.g., bioirrigation, bioturbation, burrowing, etc.) may facilitate the survival and growth of seagrasses.

Because of seagrass importance in food web ecology and as habitat source, understanding the relationship between sedimentary geochemical processes and seagrass processes is crucial in determining health and distribution. This multi-analyte approach to examining geochemical interactions on various time and space scales is highly recommended when investigating seagrass productivity and vitality. However, we also recommend that while a multi-analyte approach for determining sediment geochemical processes may be advantageous for describing chemical interactions, suitable replication must be obtained given the high degree of heterogeneity. We would recommend additional cores from the site for a more comprehensive study.

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