The Effects of *Uca pugnax* on Pore Water Biogeochemistry in a *Spartina alterniflora* Salt Marsh

Rachel Elizabeth Michaels
Cincinnati, OH

B.S., University of Wisconsin-Madison, 1998

A Thesis presented to the Graduate Faculty
of the University of Virginia in Candidacy for the Degree of
Master of Science

Department of Environmental Sciences

University of Virginia
May 2004

_____

_____

_____

Abstract

Fiddler crabs (*Uca* spp.) are abundant on the mid-Atlantic coast of the U.S., yet few studies have focused on their role in the ecology of salt marshes. As a result of their burrowing activity, fiddler crabs alter sediment structure and pore water movement. The objectives of this study were to determine (1) the effects that changes in fiddler crab burrow density have on pore water chemistry (m^2 scale), and (2) the disc of influence of individual fiddler crab burrows on surrounding pore water chemistry (cm^2 scale), a subject not yet investigated. The site for this study was located on a barrier island within the Virginia Coastal Reserve Long Term Ecological Research site.

To determine changes in pore water chemistry at the m^2 scale, eight locations along a tidal inundation gradient within a salt marsh were examined, each of which contained four treatments arranged parallel to tidal inundation in a randomized block design of 1x1 meter plots. The treatments consisted of: (1) caged crab removal plot (Exclusion), (2) caged burrow addition plot (Artificial Burrow), (3) caged control plot, and (4) un-caged control plot. Pore water samples were analyzed for ammonium, phosphate, and sulfide concentrations, redox potential and salinity. In addition, the effect of the treatments on *Spartina alterniflora* production was determined. Sulfide concentrations increased significantly with increased burrow density ($p = 0.0183$). There was no treatment effect for the other pore water variables or *S. alterniflora* production. The area of the study site that drove the increase in sulfide concentration was poorly drained; the extent of drainage and sediment characteristics seem to determine the effects that fiddler crab burrows have on pore water chemistry and the growth of *S. alterniflora*.

To determine changes in pore water chemistry with distance from individual burrows at the cm^2 scale, four burrows were randomly chosen within a 16 m^2 area of a salt marsh. Four transects were established radially from each burrow in the four compass directions. Pore water was collected at a depth of 10 cm along each transect at distances of 3, 6, and 9 cm from the edge of each burrow, and samples were analyzed for ammonium, phosphate, and sulfide concentrations, redox potential and salinity. Pore water ammonium and phosphate concentrations decreased with distance from the burrow; the difference among sample points was significant for ammonium concentration ($p = 0.0039$), but there was no significant difference for phosphate concentration ($p = 0.0940$). Sulfide concentration had the opposite trend, increasing with distance from the burrow, and showed a statistically significant difference among sample points ($p = 0.0197$). Salinity and redox potential did not vary with distance from the burrow. These results show that crab burrows affect the surrounding sediment pore water to a distance of at least 9 cm from the burrow edge. Therefore the burrowing activity of fiddler crabs substantially increases the heterogeneity of the marsh sediments. This study addresses questions that have not yet been broached in salt marsh research.

Acknowledgements

I would not have been able to complete this work without the encouragement and support of many people. First I would like to thank Jay Zieman, my thesis advisor, for his support and understanding over the years. I would like to thank my committee members, Karen McGlathery for her helpful and constructive feedback on the written document, and Bruce Hayden for his kindness and understanding. I would not have been able to do all my stats work without statistical assistance from Dave Carr, who was always willing to make time to discuss SAS with me.

My first summer in a salt marsh I was mentored by John Walsh. Our instant and continued friendship has meant a great deal to me. He was a continual source of information on salt marsh ecology and Hog Island, and made three and a half hour car rides more fun that imaginable.

My field assistants Drew Gower (summer 2001) and Laurel Woodworth (summer 2002) kept me sane and made me laugh when I was overwhelmed by the amount of work I was trying to accomplish. I thank them for their continued friendship and support, and for making the most mundane tasks much more fun.

Much thanks goes to Jason Restein and Phil Smith for taking me to my field site on south Hog Island no matter how unlikely the possibility, and making me feel safe knowing that they were always looking out for me when I was left on the island alone. Spending time on the water with them was always a pleasure. Mads Thomsen was my research sounding board and one of my housemates during my field campaign he made living on the Eastern Shore for months at a time much more enjoyable. I want to thank

my office mates, Bret Wolfe, Art Schwarzschild, and Eric Bricker for their support and comradery over the years. Thanks go to Nicola McGoff, Tom Mozdzer, Lynette Winters, and Diane Barnes for some field and/or lab help.

I would like to thank Larissa Read and Dave Richardson for their friendship and for tirelessly editing many drafts of this document. Thanks to my friends and family who gave me encouragement and support from near and far. Thank you all.

This research was funded by the Virginia Coast Reserve Long Term Ecological Research Project.

Table of Contents

Abstract i
Acknowledgements iii
Table of Contents v
List of Figures vii
List of Tables viii
Chapter 1. The Role of Fiddler Crabs in Salt Marsh Ecosystems: An Introduction 1
Chapter 2. The Effects of Fiddler Crab Burrow Density on Pore Water Chemistry and Primary Production in a Salt Marsh 10
Introduction 11
Objective 13
Methods 15
Site Description 15
Sampling Scheme 15
Treatments 19
Pore Water Sampling 23
Pore Water Chemistry 23
Spartina alterniflora Production and Stem Density 24
Sediment Analyses 25
Hydrologic and Surface Elevation Parameters 26
Crab Burrow Density, Diameter, and Coverage 27
Burrow Form 27
Data Analysis 27
Results 28
Treatment Effect 28
Overall Trends with Elevation 31
Elevation 31
Pore Water Chemistry 31
Spartina alterniflora 31
Physical Parameters 33
Elevation and Seasonal Effects 33
Pore Water Chemistry 33
Spartina alterniflora 42
Physical Parameters 44
Sediment Organic Content 44
Sediment Texture 48
Sediment Bulk Density 48
Sediment Porosity 49
Infiltration Rate 49
Burrow Density, Diameter, and Coverage 50
Burrow Form 52
Discussion 52

Pore Water Chemistry 52
Spartina alterniflora Production and Stem Density 58
Physical Parameters 60
Chapter 3. The Spatial Scale and Disc of Influence of Individual Fiddler Crab Burrows on Surrounding Pore Water Chemistry 62
Introduction 63
Objectives 66
Methods 68
Results 75
Discussion 76
Chapter 4. The Ability of Fiddler Crabs to Modify Salt Marsh Environments: Broader Implications 83
References 88

List of Figures

Chapter 1

Figure 1.1 Conceptual diagram of fiddler crab burrow interactions with sediment ……. 7

Chapter 2

Figure 2.1 Hypotheses for burrow density experiment ……..……..…..…….. 14
Figure 2.2 Map of Delmarva Peninsula ……. 16
Figure 2.3 Map of Hog Island and study site …...…… 17
Figure 2.4 Diagram of sampling scheme ……. 18
Figure 2.5 Diagram of sampling quadrat ……. 20
Figure 2.6 Elevation by block..……..……. 32
Figure 2.7 Pore water ammonium concentration by block, date, & interaction ..… 35
Figure 2.8 Pore water phosphate concentration by block, date, & interaction …….. 36
Figure 2.9 Pore water sulfide concentration by block, date, & interaction..…….. 38
Figure 2.10 Pore water redox potential by block, date, & interaction …… 40
Figure 2.11 Pore water salinity by block, date, & interaction ……..….. 41
Figure 2.12 *Spartina alterniflora* production by block, date, & interaction ……...… 43
Figure 2.13 *Spartina alterniflora* stem density by block, date, & interaction …...… 45
Figure 2.14 Physical parameters by block …… 46

Chapter 3

Figure 3.1 Hypotheses for individual burrow experiment …….. 67
Figure 3.2 Diagram of individual burrow transects with sample points ……. 69
Figure 3.3 Diagram of pore water sampling probe ……. 70
Figure 3.4 Diagram of apparatus used to collect pore water samples …… 72
Figure 3.5 Pore water variables with distance from burrows ……. 77

List of Tables

Chapter 2

Table 2.1 Analyses conducted within treatment plots or blocks …….. 21
Table 2.2 Pore water and *Spartina alterniflora* treatment effects means ….…… 29
Table 2.3 LS Means Differences in sulfide concentration for artificial burrow treatment paired with all other treatments ……..……...…… 30
Table 2.4 Physical parameter MANOVA correlation matrix …….. 51

Chapter 3

Table 3.1 Bulk density and porosity by burrow and among all burrows …… 75

Chapter 1. The Role of Fiddler Crabs in Salt Marsh Ecosystems: An Introduction

Salt marshes are features associated with non-tropical coastlines around the world. They are found in low-energy environments protected from high-energy wave and tidal forces, such as along the fringing margins of bays and coves, along coastlines protected by barrier islands, and on the lee side of the barrier islands themselves. Salt marshes are highly productive ecosystems; primary production is as much as 8000 $g/m^2/yr$ in some marshes (Mitsch and Gosselink 1993). These ecosystems are globally significant as they provide protection and habitat for fish and shellfish, including nursery habitat for a majority of commercially important species. Wading birds utilize salt marshes as feeding grounds and prey upon the juvenile fish as well as the large invertebrate populations. In addition to supplying habitat and food sources, salt marshes provide geomorphological functions including sediment stabilization and creation of buffer zones that protect adjacent mainland areas from coastal storms. Both of these functions aid to limit coastal erosion (Day et al. 1989, Mitsch and Gosselink 1993).

Spartina alterniflora is the dominant macrophyte in salt marshes on the East Coast of the United States. There are two growth forms of *S. alterniflora* that create distinct zonation patterns within the marsh. The tall-form of *S. alterniflora* is located in well-drained areas along creek banks and the edges of bays (low marsh), where as the short-form is located in the more inland areas (high marsh). Low marsh as defined by Mitsch and Gosselink (1993) is intertidal and usually floods daily; high marsh or upper marsh does not flood regularly and is continuously exposed to the atmosphere for at least one-third of each month.

Although *S. alterniflora* is dominant in these marshes and often has very high production rates, it must overcome multiple stressors. Valiela and Teal (1974) determined that *S. alterniflora* was nitrogen limited in a salt marsh in Massachusetts. Although *S. alterniflora* has aerenchyma to aid in oxygen diffusion to the roots, it cannot conduct enough oxygen when growing in totally water-logged sediments and must overcome increased stress caused by anoxia, decreased redox potential, and increased sulfide concentrations. Under these conditions, *S. alterniflora*'s respiratory metabolism shifts from aerobic to anaerobic. During anaerobic respiration, these plants respond with decreased stem density, stem height, and aboveground standing crop (Mendelssohn et al. 1981, Mendelssohn and McKee 1988). Sulfide concentrations as low as 250 µM have been shown to decrease nitrogen uptake (Bradley and Morris 1990). Koch and Mendelssohn (1989) found that sulfide concentrations of 1000 µM decreased root biomass and altered the belowground structure of *S. alterniflora*, causing multi-branched roots to develop near the sediment surface and rhizomes to lose their roots and begin to deteriorate. Sulfide concentrations of 2000 µM were seen to result in reduced leaf elongation (Koch et al. 1990).

These environmental conditions are all edaphic bottom-up controls on the growth and production of *S. alterniflora*. Recently, top-down controls of this dominant salt marsh macrophyte have been studied. Silliman and Zieman (2001) found that increased densities of snails that graze on *S. alterniflora* were able to significantly decrease stem density and aboveground production of *S. alterniflora* even with the addition of nitrogen fertilizer. Other fauna within the salt marsh can affect *S. alterniflora* by herbivory (ex.

grasshoppers (Daehler and Strong 1995)), grazer-induced defoliation (ex. periwinkles (Silliman and Zieman 2001)), surface fertilization (ex. ribbed mussels (Bertness 1984)), or altering physio-chemical parameters of surface and/or subsurface sediment (ex. fiddler crabs, see refs below).

Fiddler crabs are a prevalent species found in salt marshes that may have a more dominant role than other fauna due to their interactions with sediment chemistry above and belowground. The physiology and biology of fiddler crabs (*Uca* spp.) have been thoroughly studied, but their ecological role has received much less focus (Montague 1980). Fiddler crabs are common detritivorous macrofauna of salt marshes on the eastern coast of North America (Bertness 1985), and populations range in density from 7 /m^2 (Cammen et al. 1980) – 150 /m^2 (Nomann and Pennings 1998). They generally inhabit areas where *Spartina alterniflora* is the dominant primary producer (Bertness 1985, Bertness and Miller 1984, Genoni 1985, Nomann and Pennings, 1998). The detritus that fiddler crabs consume is derived from decayed *Spartina alterniflora*, although their main food source is actually the microorganisms and bacteria that grow on the decomposing *S. alterniflora* (Genoni 1991). Currin et al. (1995) utilized isotopic analyses to determine the food sources of *Uca* spp. Both standing dead *S. alterniflora* and microalgae appeared to be important nitrogen sources for fiddler crabs. The $\delta^{13}C$ vs. $\delta^{34}S$ and $\delta^{13}C$ vs. $\delta^{15}N$ plots with values for *U. pugnax*, *U. pugilator*, and primary producers showed that microalgae could be the main food source for fiddler crabs; standing dead *S. alterniflor*a and sediment detrital *S. alterniflora* are possible secondary sources (Currin et al. 1995).

Genoni (1985) states that fiddler crabs are food-limited. Reasons for this view include the lag time for *S. alterniflora* to degrade into detritus, the limited time available for feeding due to tidal cycles, and the quality of their food source (Genoni 1985). Burrowing by fiddler crabs brings buried organic matter to the sediment surface, where it can be used as an additional food source (Genoni 1991) and aid in *S. alterniflora* growth by providing more available nutrients (Genoni 1991, Nomann and Pennings 1998). Katz (1980) determined the sediment turnover rates and percent increase in sediment surface area for a site in the Little Sippewissett marsh, MA. The yearly sediment turnover was 20% per year for the top 15 cm of sediment, and the average surface area increase for this site was 60%. These results from Little Sippewissett marsh were for relatively small populations (42 crabs/ m^2) of fiddler crabs, indicating that higher densities of fiddler crabs would more significantly alter the sediment structure.

The presence of crab burrows also modifies the hydraulic parameters of the sediment. Hydraulic conductivity can be increased by 1 or 2 orders of magnitude resulting in a value of 0.1 – 1.0 m/day (Hughes et al. 1998). Overall surface infiltration is increased also, and the crab burrows themselves cause extremely large infiltration rates having an average of 11m/day (Hughes et al. 1998).

S. alterniflora in turn has positive impacts on fiddler crab burrows. The presence of *S. alterniflora* roots and rhizomes gives support to fiddler crab burrows (Nomann and Pennings 1998, Bertness 1985). When their burrow openings are adjacent to *S. alterniflora* stems fiddler crabs also have added protection from predation (Nomann and Pennings 1998). Fiddler crabs have a preference for sediment that is associated with tall-

form *Spartina alterniflora*. The root mat of this form is not too dense for burrowing as in the short-form *Spartina alterniflora*, and the sediment is not too soft as in areas beyond the marsh edge (Bertness and Miller 1984). The physiology, habitat, and living strategies of *Spartina alterniflora* and *Uca* spp. allow for beneficial interactions between this flora and fauna (Nomann and Pennings 1998, Bertness and Miller 1984, Walsh 1998).

Fiddler crab burrows are believed to have important effects on sediment chemistry and other sediment characteristics (Figure 1.1) (Katz 1980, Montague 1980, Bertness and Miller 1984, Bertness 1985, Genoni 1991, Nomann and Pennings 1998, Walsh 1998). Some of the interactions between fiddler crab burrows and sediment chemistry and other characteristics have been studies directly, but most interactions have only been speculated. Fiddler crab burrows are thought to facilitate general aeration of the sediment (Genoni 1991, Nomann and Pennings 1998). The burrows may act as oxygen inlet tubes, increasing sediment oxygen levels (Katz 1980, Bertness 1985). Burrows are also speculated to act as toxin outlet tubes, reducing the accumulation of metabolic products, such as sulfide, in the sediment (Katz 1980, Bertness and Miller 1984). Bertness (1985) in his studies of fiddler crab burrow interactions with sediment, found that they can increase soil drainage, sediment redox potential, and belowground decomposition, each of these effects had be previously speculated by others. All of these changes increase *S. alterniflora* growth and its ability to prosper in its location (Bertness 1985, Walsh 1998).

Fiddler crabs potentially assume an important role in both the structure and function of salt marshes. Their eating and burrowing behavior may have significant

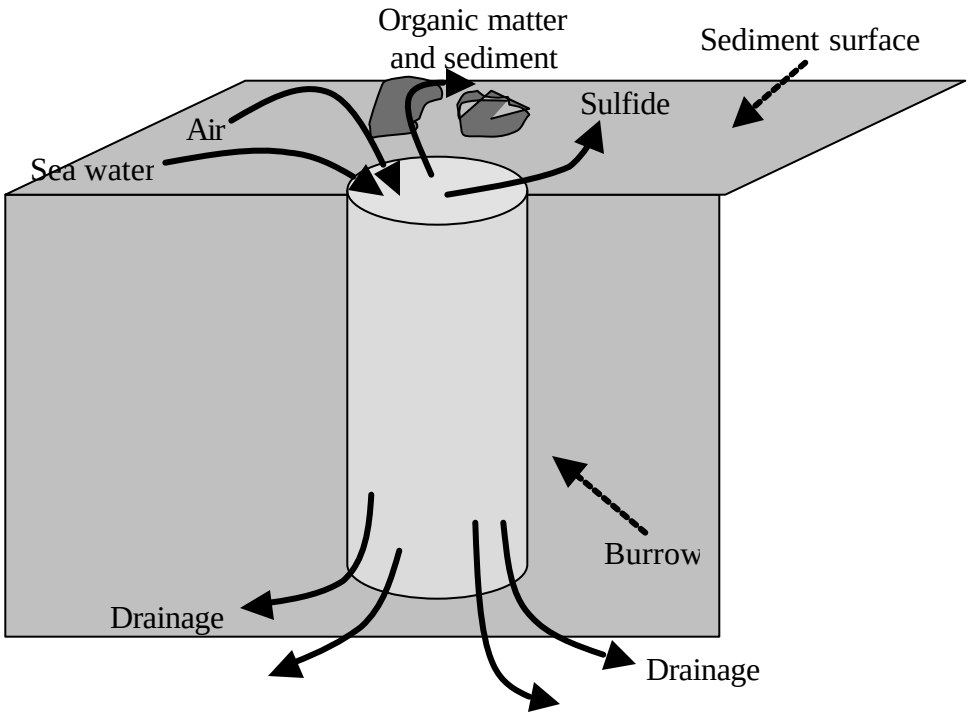

Figure 1.1. Conceptual diagram of fiddler crab burrow interactions with sediment.

impacts on energy and nutrient transfer within salt marshes. Although their burrows primarily provide shelter from hot and cold temperatures and protection from predation, they may also initiate a positive feedback loop within the marsh. The burrows that fiddler crabs make in the salt marsh potentially alter sediment chemistry, which may result in an increase in *S. alterniflora* production. This increased *S. alterniflora* production would increase detritus formation, the food source of fiddler crabs, and could potentially support larger fiddler crab populations (Montague 1980).

Although the general effects of fiddler crab burrows on pore water chemistry have been speculated (Katz 1980, Bertness and Miller 1984, Bertness 1985, Genoni 1991, Hughes et al. 1998, Nomann and Pennings 1998, Walsh 1998), the specific changes in pore water chemistry caused by the presence of fiddler crab burrows have been studied on a limited basis by Bertness (1985). Bertness (1985) studied the effects of the presence and absence of burrows on redox potentials of marsh sediment. Redox potential at 2 – 10 cm depth in the sediment increased significantly with increased burrow density in the short-form zone, but there was no difference in redox with crab removal in the tall-form marsh flat zone. Walsh (1998) examined changes in pore water chemistry relating to marsh age. In his study, fiddler crab density and pore water redox potential showed significant positive correlation. As marshes age the sediments become more anoxic decreasing redox potential and allowing the buildup of organic matter. It was determined that the presence of fiddler crabs, from their ability to increase redox potential, was able to slow signs of marsh aging by increasing aeration of the sediments.

Little quantitative data have been collected to support the speculated effects of fiddler crab burrows on pore water chemistry in salt marshes. The main focus has been on sediment aeration and sulfide concentration, but the effects on nutrient concentrations have not been considered. Also, the research involving fiddler crab burrows has been conducted in relatively well-drained sediments. There is a lack of focus on the effects of fiddler crabs in poorly drained sediments, which they also inhabit. This study addresses the effects that fiddler crab burrows have depending on the degree of drainage within the marsh. Additionally, changes in pore water chemistry directly surrounding crab burrows have not been quantified in salt marshes as of yet.

In this study, the degree to which fiddler crabs are capable of influencing sediment chemistry and salt marsh primary production were investigated using field experiments conducted during the 2002 growing season in a salt marsh on Hog Island, a barrier island off of the Eastern Shore, Virginia. In order to quantitatively determine the effects of fiddler crab burrow density on pore water chemistry as well as *Spartina alterniflora* production and stem density, a crab density manipulation experiment utilizing exclosures was conducted (Chapter 2). To assess the spatial scale at which individual crab burrows affect pore water biogeochemistry, pore water from sediments surrounding fiddler crab burrows was collected (Chapter 3). In both experiments, pore water was analyzed for ammonium, phosphate, and sulfide concentrations, oxidation-reduction potential (redox), and salinity. The combined findings from the two experiments as well as their broader implications are subsequently discussed (Chapter 4).

Chapter 2. The Effects of Fiddler Crab Burrow Density on Pore Water Chemistry and Primary Production in a Salt Marsh

Introduction

Previous studies have suggested that fiddler crab burrows can affect the biomass of *Spartina alterniflora* and the sediment chemistry in salt marshes (Howarth and Teal 1979, Katz 1980, Montague 1980, Howes et al. 1981, Bertness and Miller 1984, Genoni 1991, Walsh 1998). However, few studies have directly examined these effects (Montague 1982, Bertness 1985, Nomann and Pennings 1998). Bertness (1985) found that increased burrow densities significantly increased the aboveground biomass and stem density of *S. alterniflora* within the short-form *S. alterniflora* zone. Also, decreased burrow density (by crab removal) significantly decreased the aboveground biomass and stem density of *S. alterniflora* within the tall-form *S. alterniflora* marsh flat zone. Redox potential at 2-10 cm depth in the sediment increased significantly with increased burrow density in the short-form zone, but there was no difference in redox with crab removal in the tall-form marsh flat zone. Montague (1982) found that the addition of artificial burrows to the short-form *S. alterniflora* high marsh produced a significant increase in aboveground production with 16 and 36 burrows per 0.44 m^2. Nomann and Pennings (1998) did not find a difference in aboveground plant cover or biomass in areas where they removed crabs compared to areas that contained natural crab densities. Walsh (1998) found a significant positive correlation between fiddler crab densities and pore water redox potential. No studies have examined other sediment chemistry characteristics in conjunction with changes in fiddler crab burrow densities. The mechanisms affecting pore water sulfide and nutrients with increased burrow density

have been speculated by Katz (1980), Montague (1980), Bertness and Miller (1984), Bertness (1985), and Genoni (1991).

In the above studies, where increased or decreased *S. alterniflora* production was determined with increased or decreased fiddler crab densities, there must have been changes in the nutrients or stressors affecting the plant growth to yield such a change. Therefore, the presence of fiddler crab burrows must have altered the concentration or availability of nutrients (ammonium and/or phosphate), the concentration of toxic sulfide, the level of anoxia, the salinity, or a combination of these. The cost-benefit of increases or decreases in these variables would determine the amount of *S. alterniflora* production that could be possible when affected by these environmental conditions.

The above environmental variables all affect the growth of *S. alterniflora* through different mechanisms. Macronutrients are necessary for plant growth and ammonium and phosphate are especially important in *S. alterniflora* salt marshes. These marshes are nitrogen limited ecosystems. Salinity can also have a major effect on *S. alterniflora* production if salinity becomes too high even salt tolerant plants cannot survive. Anoxia is another main stress that occurs in salt marshes. *S. alterniflora* has adapted to living in frequently flooded environments, but when anoxia becomes too severe it can also be lethal to the plants. As sediments remain in an anoxic state for long periods of time sulfide begins to build up. Sulfide has been shown to decrease ammonium uptake and also decrease aboveground production in *S. alterniflora*. All of these stressors occur in unison and make plant growth in salt marshes a challenge (Mitsch and Gosselink 1993).

Objective

This experiment explored the effects of crab burrow densities on various pore water characteristics and on *Spartina alterniflora* production and stem density. Experimental plots that consisted of four treatments of different crab burrow densities were set up within the marsh. Pore water was analyzed for ammonium, phosphate, and sulfide concentrations, redox potential and salinity. Based on increased aeration and flushing of the sediment with increased burrow densities speculated by previous studies (Katz (1980), Montague (1980), Bertness and Miller (1984), Bertness (1985), and Genoni (1991)) it was hypothesized (Figure 2.1) that increased burrow densities would decrease ammonium, phosphate, and sulfide concentrations, decrease salinity, and increase oxidation-reduction potential (redox). Increased aeration would also increase the rate of organic mater oxidation, which would increase ammonium and phosphate concentrations, the products of this reaction. But, the increased flushing and oxidation in the case of ammonium facilitated by additional fiddler crab burrows would have a dominant effect and negate the increase in ammonium and phosphate concentrations. The opposite trends were expected for a decrease in fiddler crab burrow density. With an increase in fiddler crab burrow density, *Spartina alterniflora* production and stem density were expected to increase. The opposite trends were expected for a decrease in fiddler crab burrow density.

Due to increased flushing and aeration, increased burrow density would cause:

Decreased {
- ammonium concentration
- phosphate concentration
- sulfide concentration
- salinity

Increased {
- redox potential
- *Spartina alterniflora* production
- *Spartina alterniflora* stem density

Decreased burrow density would have the opposite effect.

Null Hypothesis: Changes in burrow density would have no effect.
Alternative Hypotheses: Increased burrow density would have the opposite effect of those stated above.

Figure 2.1 Hypotheses for the effects of artificially increased and decreased fiddler crab burrow density on pore water chemistry and *Spartina alterniflora* growth.

Methods

Site Description

The study site for this research was on a barrier island off the coast of the southern end of the Delmarva Peninsula, Virginia, USA (Figure 2.2). This area is part of the Virginia Coast Reserve – Long Term Ecological Research Site. The research was conducted on the southern end of Hog Island (Figure 2.3) in the back barrier salt marsh adjacent to Hog Island Bay (37.39 N Latitude and 75.71 W Longitude).

Sampling Scheme

Research plots were located in two 18 m x 50 m sites, which were in close proximity (about 100 meters apart). The sampling layout at each site consisted of rows of 1 m^2 quadrats set up perpendicular to tidal inundation to block statistically for tidal influence and elevation. The marsh edge was not wide enough to fit eight rows of quadrats, which made it necessary to divide the rows into two sites each containing four rows. The rows (henceforth referred to as blocks) progressed from low marsh towards high marsh, and were 12.5 meters apart. The lowest elevation block in each site was 15.3 meters horizontal distance from the edge of the marsh. The edge of the marsh for both sites was defined as the location and elevation in Site 1 that dropped off to a mud flat. Each block consisted of four treatments, one exclusion plot (Figure 2.4, in black), one artificial burrow plot (white), one caged control plot (light gray), and one un-caged control plot (dark gray). The order of the plots in each block was randomized, but two consecutive blocks could not have the any plots in the same position. The distance

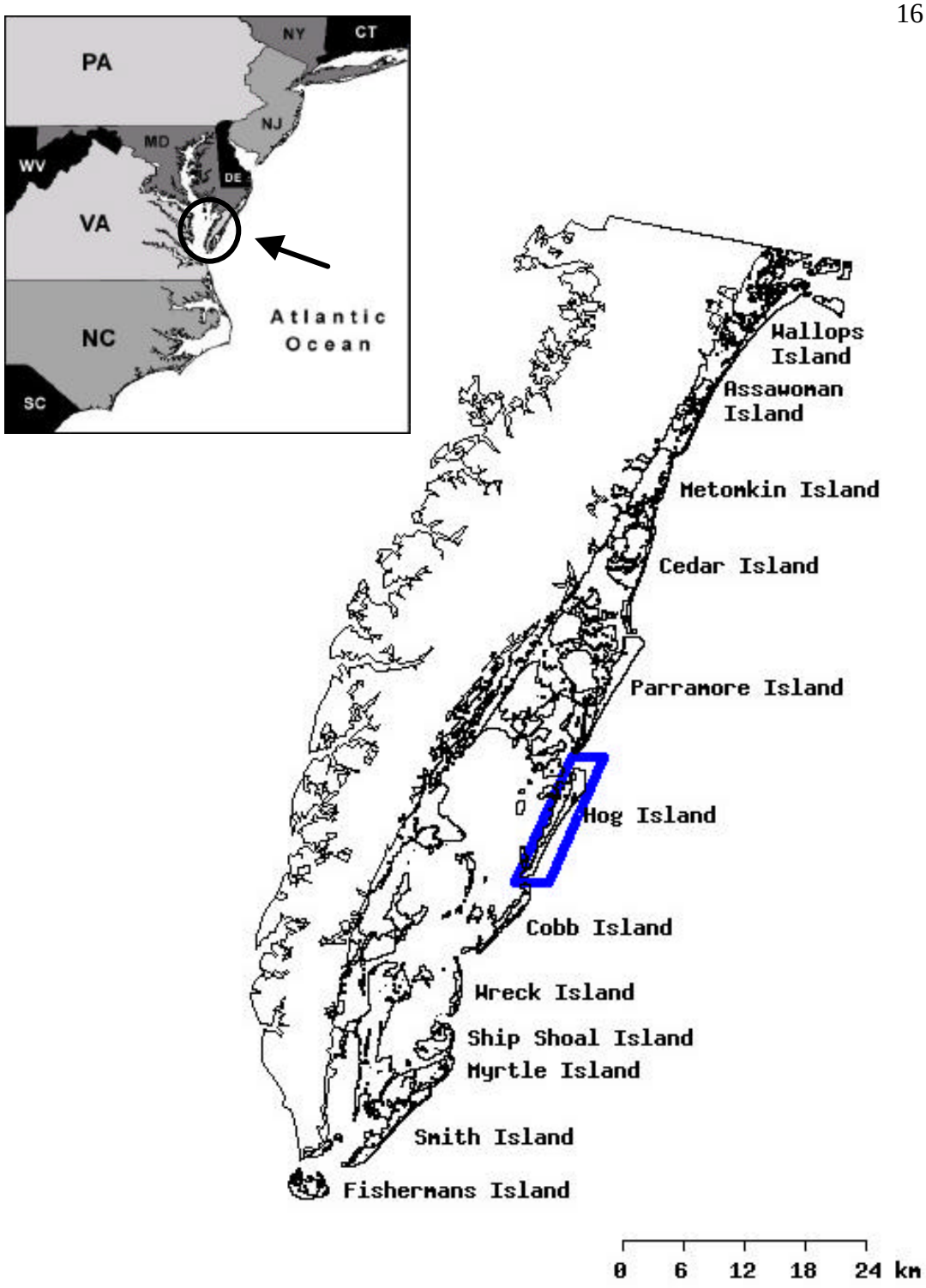

Figure 2.2. Location of the Eastern Shore of Virginia on the Delmarva Peninsula (inset). Map of Eastern Shore, Virginia including barrier islands, Hog Island indicated by box.

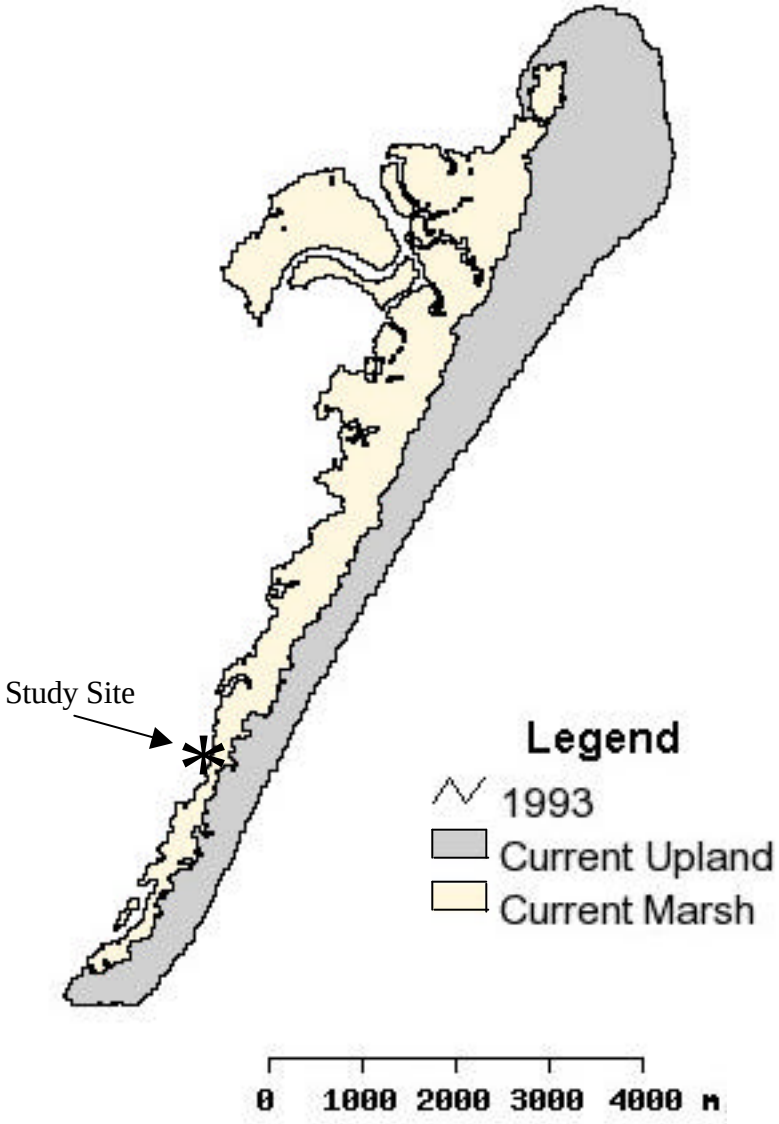

Figure 2.3. Map of Hog Island, study site marked with an asterisk.

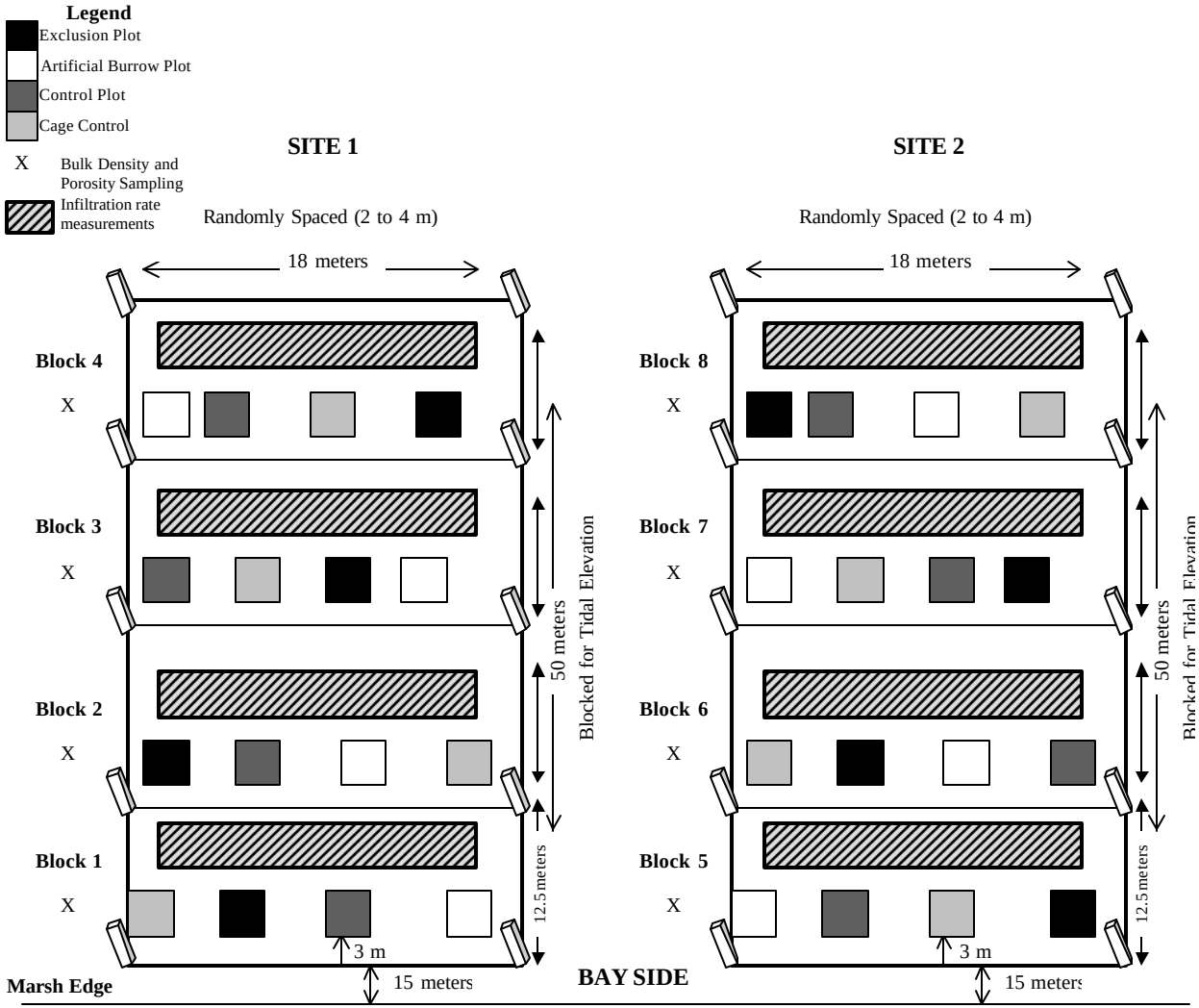

Figure 2.4. Diagram of sampling scheme, containing two sampling sites.

between the plots was also randomized ranging from 2-4 m. Site 1 contained Blocks 1-4 and Site 2 contained Blocks 5-8; the eight blocks total between the two sites were treated as eight blocks within a single site for most analyses as there was a steady increase in elevation from Block 1 to Block 8. In each sampling quadrat (Figure 2.5) or block, the same analyses were conducted (Table 2.1). Because the sampling quadrats were setup in random locations they contained different densities of *Geukensia demissa* (ribbed mussel), as well as *Salicornia* spp. (pickleweed) and *Limonium carolinianum* (sea lavender) plants.

Treatments

The exclusion plots and artificial burrow plots (Figure 2.5) were established by surrounding a 1 meter squared quadrat with plastic coated nylon window screening. The screen was buried vertically to a depth of 30 cm below the sediment surface. The screen emerged from the sediment surface to a height of 30 cm; roof flashing was attached to the top most edge of the screen with silicone calk. The flashing was 6.5 cm wide with a rim that jutted out away from the quadrat interior. The metal rim prevented crabs from entering the exclosure from the sediment surface and the belowground screening prevented crabs from entering the exclosure from the subsurface (Bertness 1985). Shading was minimal and the screening was cleaned as necessary.

Crabs were removed from the exclosure and artificial burrow plots by hand during low tide when they were active. After the first pore water sampling, plastic (8 ounce) crab trap cups with 7.5 cm diameter mouth were added to each quadrat in the southeast

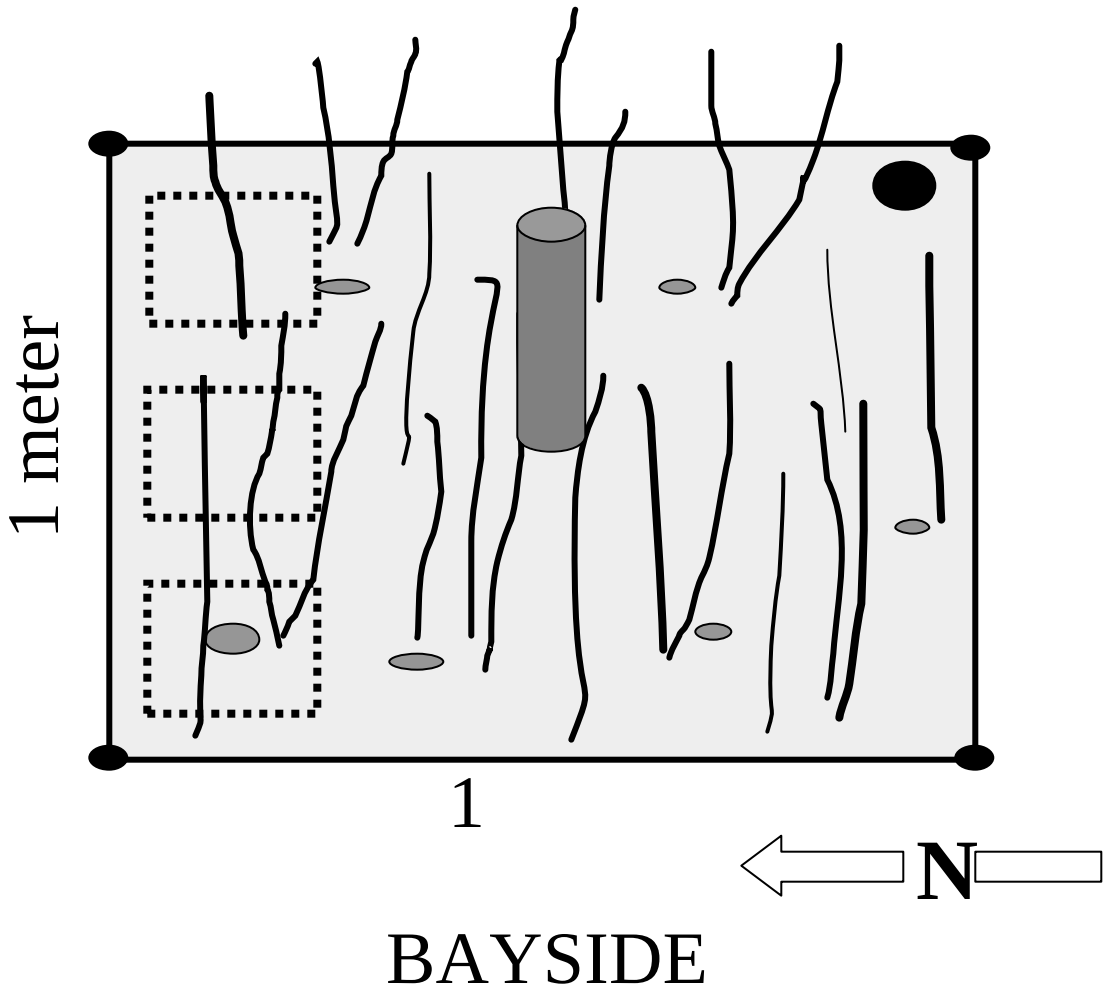

Figure 2.5. Diagram of sampling quadrat representing all four treatments. A sipper is located in the center of the 1 meter x 1 meter quadrat. Dotted squares on north side indicate the three randomized positions of the *Spartina alterniflora* sampling quadrats. The filled circle in the southeast corner represents the crab trap cup. The black perimeter represents screening in all treatments but the un-caged control plot.

Table 2.1. Analyses conducted within treatment plots or blocks.

Categories of Analysis	Physical Parameters	Collection Frequency
Pore Water (in plot)	Ammonium concentration Phosphate concentration Sulfide concentration Salinity Redox potential	Monthly for 4 months
Spartina alterniflora (in plot)	Aboveground production Stem density	Monthly for 5 months
Sediment (in block)	Organic content Bulk density Porosity Texture	Once
Hydrology (in block)	Initial infiltration rate	Once
Topography (in block)	Elevation	Once
Fiddler Crab Burrows (in block)	Density Diameter	Once
Fiddler Crab Burrows (outside study site)	Depth Surface area Volume	Once

corner. Cups were inserted into the sediment so that the lip was at the sediment surface. In the two kinds of control plots the mouth of the cups was covered with screening so they did not function as crab traps.

Artificial burrow plots were created using a 1.27 cm diameter mini auger to excavate additional burrows to a depth of 20 cm without compacting the sediment. The artificial burrows were added after initially having crabs removed and burrows fill in naturally for a few months, so as to begin with zero burrows in the quadrat prior to augering. One hundred burrows were augered by hand in each artificial burrow plot in June, July, August and, September, prior to collection of pore water. The quadrats were divided into quarters and 25 burrows were made per quarter. The artificial burrows were aligned in a grid pattern 5 burrows by 5 burrows in each quarter to distribute them evenly. The burrows remained open for at least 10 days after they were added.

The caged control plot was created using the same method as the exclusion plot and the artificial burrow plot, except there was no metal added to the top of the screening. Also, the screening was cut along the sediment surface and the bottom 10 cm of screening was removed. This allowed free movement of the crabs in and out of the caged control plot. The un-caged control plot was marked with a piece of PVC at each corner and sediment was sawed to a depth of 30 cm along the outline of the quadrat to sever the *S. alterniflora* roots as had been done in the caged treatments. The two types of control treatments contained natural crab densities and did not receive any further manipulations.

Pore Water Sampling

A suction lysimeter (sipper) was installed to a depth of 10 cm in the middle of each quadrat. The sippers had an inner diameter of 4 cm and pore water collected from it represented generalized or average pore water chemistry for each quadrat. Pore water was collected monthly from June to September 2002. The day before pore water samples were collected, N_2 gas was delivered into each sipper to expel any standing water and to create anoxic conditions in the sipper. Pore water samples were collected in syringes and transferred to vacutainers, or analyzed in the field. All pore water samples were collected on a rising tide during spring tide associated with the full moon.

Pore Water Chemistry

Samples were analyzed for ammonium, phosphate, and sulfide concentrations, redox potential, and salinity. Redox potential was determined in the field by collecting pore water samples in a syringe and injecting the sample into an anaerobic chamber and measuring the oxidation-reduction potential with a Beckman (511290-AA) 255 waterproof Eh-pH probe. Once collected in a syringe, ammonium and phosphate samples were filtered in the field into vacutainers through 0.45 micron membrane filters; sulfide samples were not filtered before being transferred into vacutainers. The samples were kept on ice until they were analyzed in the lab directly after returning from the field.

Salinity was measured after returning to the lab using a Vista refractometer model A344ATC. Ammonium, phosphate, and sulfide concentrations were determined in the lab colorimetrically using a Shimadzu UV-1201 spectrophotometer. Ammonium

concentrations were measured using the method of Parsons et al. (1984). Phosphate concentrations were measured using an ammonium molybdate method (Strickland and Parsons, 1972). Sulfide concentrations were measured using the method described in Cline (1969) as modified by Otte and Morris (1994).

***Spartina alterniflora* Production and Stem Density**

Spartina alterniflora stem densities and stem heights were determined for each quadrat monthly during the growing season. A small area of each quadrat (25 cm x 25 cm) was marked with small stakes in the corners. These small quadrats were located randomly in one of three positions along the north edge of the quadrats (Figure 2.5) to eliminate any minor effects from shading. The Morris and Haskin (1990) technique was followed, to estimate aboveground production of *S. alterniflora* within the treatment plots. In April/May, each *S. alterniflora* stem within the small quadrat was measured and marked with a numbered bird band. Each month between June and September, stem heights were re-measured and recorded, and any new stems were measured and banded with a numbered bird band. Dead stems were noted as well. Allometric growth equations were determined from harvesting 48 *S. alterniflora* stems of a variety of heights in areas adjacent to the eight blocks. Stems were collected in May, July and September to produce three different allometric equations for different stages in the growing season. The May allometric equation was used for April/May, the July equation for June and July, and the September equation for August and September. These

equations were developed to predict stem biomass from the heights of the marked stems within the small quadrats.

Sediment Analyses

Approximately 100 cm^3 of sediment from the top 10 cm of the marsh surface was collected from each quadrat in July 2001 during sipper installation. Two sediment characteristics were determined for each quadrat from these sediment samples: sediment organic content and sediment texture. The organic content (%) was determined by drying each sediment sample at 60°C until constant weight. The weight was recorded and the sample was ashed in a muffle furnace for six hours at 600°C, and then reweighed. Organic content is the difference between the dry weight and the ash free dry weight divided by the dry weight. Sediment texture (grain size distribution) was analyzed using a hydrometer to determine the sand: silt: clay proportions following the method in Brower and Zar (1984).

Bulk density and porosity were obtained for each block at a depth equivalent to the depth of the pore water samples collected from the sippers. Three or four cores were taken from the area adjacent to the north side of each block outside the site parallel with the row of treatment plots (marked with X on Figure 2.4). Cores were 30 cm long with an inner diameter of 4.4 cm and were hammered into the sediment to a depth of 20 cm. Cores were removed from the ground when the sediment was saturated. The cores were filled with seawater to the top of the open end and stoppered to create suction so the core could be removed from the ground without losing the sediment. Cores were kept on ice

until returned to the lab. The sediment plugs obtained from the cores were greater than 10 cm long. Two 1 cm thick sediment slices were removed from the middle of each core at depths of 9-10 cm and 10-11 cm. The wet weight of each slice was measured, the slices were dried at 60° C until constant weight, and the slices were reweighed. Bulk density was calculated from the dry weight of the slices and their volume. Porosity (volumetric water content) was calculated from the difference between wet weight and dry weight divided by the volume of the slice.

Hydrologic and Surface Elevation Parameters

Initial infiltration rate was measured within each of the eight blocks. Three 5 cm diameter infiltrometers (open ended PVC pipe) were installed to a depth of 10 cm at random locations in the upper marsh portion of each block (striped rectangles on Figure 2.4). Each infiltrometer was filled with 9 cm of standing water. Water was added periodically (about every 10-30 min.) to keep the water level in the infiltrometer constant. The volume of added water and the time of the water addition were recorded and from this the rate of infiltration was calculated. Surface elevation was surveyed using a Trimble 4000 GPS unit with sub-centimeter accuracy. Elevation was measured in the middle of each quadrat on the east side of the sipper. Elevation was measured in meters above or below Mean Sea Level (MSL). Conversions to MSL were all based on the High Resolution and Accuracy Network (HARN) monument VCR1 in Oyster, VA, which is tied to the North American Vertical Datum 1988 (NAVD88).

Crab Burrow Density, Diameter, and Coverage

Crab burrow densities and diameters were measured within each block of the study site during July 2001. Three 25 cm x 25 cm quadrats were randomly distributed within the upper marsh portion of each block (striped rectangles on Figure 2.4). All of the crab burrows within each of the quadrats were counted and their diameter measured to the nearest tenth of a millimeter. The areas of the burrows were calculated using the diameters and summed for each small quadrat.

Burrow Form

Burrow casts were made to determine various fiddler crab burrow characteristics. The surface area and volume of the burrows was obtained by filling burrows in burrow cast plots (between the two sites) with a polyester resin to create a burrow cast (Shinn 1968). The volume of the burrows was determined by measuring the volume of water displaced when the casts were completely submerged in water. The surface area was measured by wrapping each cast with one layer of aluminum foil and weighing the amount foil used for each cast. The area to mass ratio of the foil was determined to convert mass to area (Katz 1980).

Data Analysis

The treatment effect of the pore water chemistry and *Spartina alterniflora* data were analyzed with a repeated measures analysis of variance using "proc mixed" in the Statistical Analysis System (SAS 1999-2001). Where there was no treatment effect or

interaction, the data from the four treatments within each block were used as replicates for that block. An analysis of variance (ANOVA) was used to determine if there was a significant difference among blocks and among collection dates, and also if there was a block*date interaction. Where there was a significant difference a post hoc test (Ryan's Q or Tukey-Kramer) was used to determine which blocks or dates differed from one another. If the sample sizes were equal, Ryan's Q was used; when the sample sizes were unequal, Tukey-Kramer was used.

Bulk density, burrow characteristics, elevation, sediment texture, infiltration, organic content, and porosity were analyzed by block with an ANOVA. When there was a significant difference among blocks, a post hoc test (Ryan's Q or Tukey-Kramer) was performed on the data. Regressions were performed in Microsoft Excel. The above physical parameters were analyzed with elevation as the dependent variable using a multiple analysis of variance (MANOVA) procedure (SAS 1999-2001). Burrow cast data were not analyzed statistically because they were created in random locations within the marsh.

Results

Treatment Effect

Ammonium and phosphate concentrations, redox potential, and salinity had no significant difference among the four treatments (Table 2.2). Sulfide concentrations did yield a significant difference ($p = 0.0183$) among treatments (Table 2.2). There was also a significant difference among collection dates ($p = 0.0031$) for sulfide concentration.

Table 2.2. Pore water and *Spartina alterniflora* treatment effects: mean (SE) for each treatment over all blocks and months. * indicates significant difference ($p < 0.05$).

Treatment	Artificial Burrow Plot		Un-Caged Control Plot		Exclusion Plot		Caged Control Plot	
Ammonium (uM)	39.7	(13.0)	37.7	(13.0)	26.1	(13.0)	49.2	(13.0)
Phosphate (uM)	26.8	(7.9)	32.6	(7.8)	28.3	(7.9)	45.3	(7.9)
Sulfide (uM)	568.1*	(136.1)	247.2	(135.2)	191.7	(136.1)	314.6	(136.1)
Redox (mv)	-43	(21)	-42	(21)	-44	(21)	-37	(21)
Salinity (ppt)	39	(2)	42	(2)	39	(2)	40	(2)
***S. aterniflora* production (g/m2)**	53	(10)	42	(10)	45	(10)	38	(10)
***S. alternifora* stem density (#/m2)**	500	(65)	387	(65)	422	(65)	339	(65)

For the pairwise differences of least squares means of sulfide concentration, only the Artificial Burrow treatment yielded significant differences when paired with each of the other treatments (Table 2.3).

Table 2.3. Least Squares Mean Differences in Sulfide Concentration for Artificial Burrow treatment paired with all other treatments.

Treatment Pair	LS Mean	Standard Error	Pr > |t|
Artificial – Exclusion	376.38	115.31	0.0037
Artificial – Un-Caged Control	320.87	114.37	0.0106
Artificial – Caged Control	253.55	115.31	0.0392

Because no significant treatment effects were determined for ammonium and phosphate concentrations, redox potential, salinity, and *Spartina alterniflora* production and stem density the data collected for these variables in each of the four quadrats of each block were treated as replicate measurements for that block. Subsequently, the effects of elevation and season on these variables were determined. Because there was a significant treatment effect for sulfide concentration within the artificial burrow plots the data used to determine the effects of elevation and season did not include measurements from artificial burrow plots. The effects of elevation and season were not part of this study initially, so there are no hypotheses on their effects.

Overall Trends with Elevation

Elevation

The mean elevation of Site 1 (Blocks 1-4) and Site 2 (Blocks 5-8) differed significantly ($p < 0.0001$); Site 1 had a mean elevation of – 0.12 meters above Mean Sea Level (MSL), and Site 2 had a mean elevation of 0.22 meters above MSL. There was a significant difference ($p < 0.0001$) in elevation among blocks (Figure 2.6a). A regression of elevation against block number for all eight blocks determined that elevation increased with block number, and block number explained 93% of the variation in elevation (Figure 2.6b). Block number is a proxy for elevation and therefore extent of tidal inundation. Block 1 had the lowest elevation, and elevation increased with block number through Block 8. Some of the data presented here have been analyzed in terms of trends among the eight blocks.

Pore Water Chemistry

The pore water chemistry showed some general trends among the blocks. Ammonium, phosphate, and sulfide were low in Blocks 1 and 8 and peaked in the middle blocks. Redox was lowest in blocks with high sulfide and highest in blocks with low sulfide. Salinity was constant in the lowest blocks and increased in Blocks 5 – 8.

Spartina alterniflora

Spartina alterniflora did not show any definite trends among blocks, although stem density and production followed similar patterns as expected. They increased from

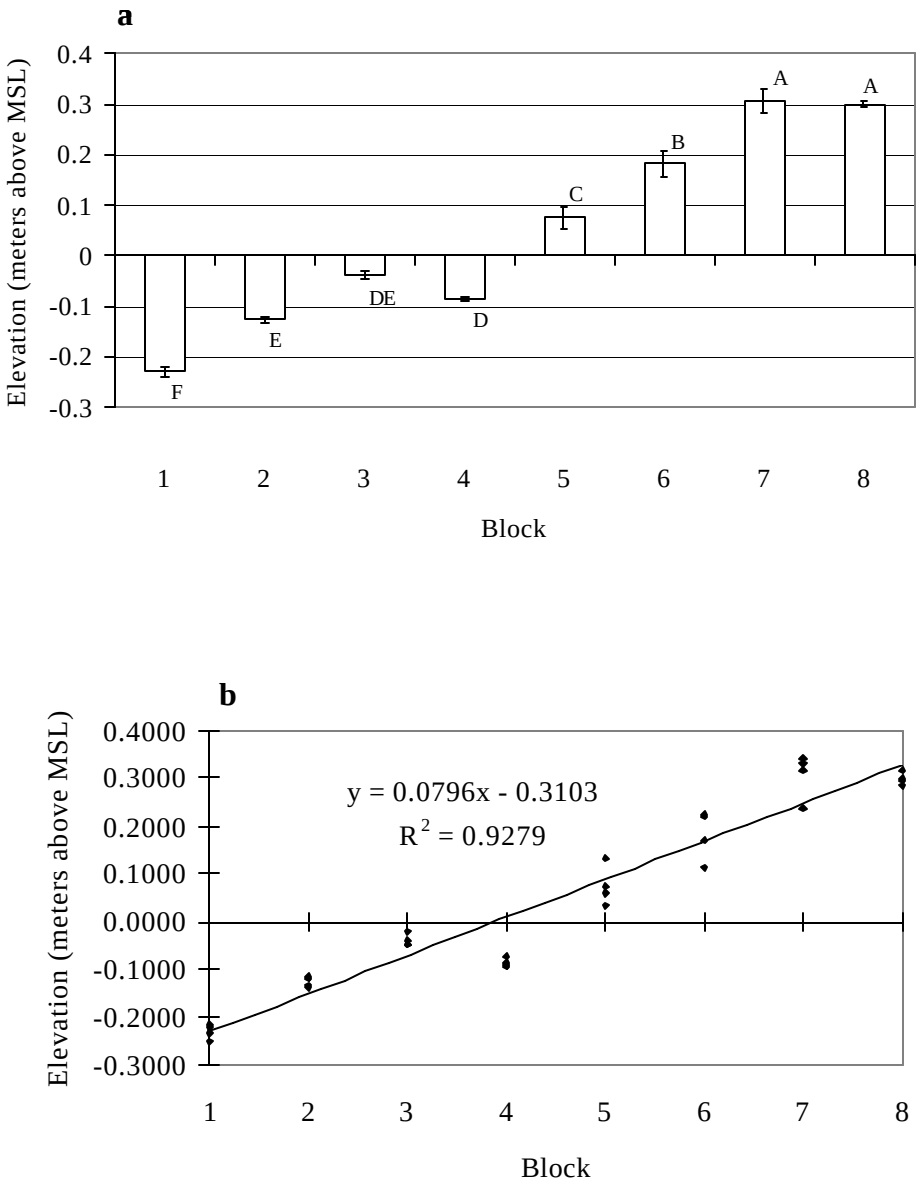

Figure 2.6. (a) Elevation by block, significant differences as determined by ANOVA are indicated by letters above the bars (mean ± 1 SE, n = 4), (b) regression of elevation vs. block ($p < 0.0001$).

Blocks 1 – 3 and were low in Block 4. In the upper four blocks the stem density and production were moderately disparate. Stem density increased in Block 5, decreased in Block 6, and increased from Block 6 – 8. Production was low compared to stem density in Blocks 5 and 8, as the *S. alterniflora* was more stunted. In Block 6, production was low and comparable to stem density. For Block 7, production was high compared to stem density as the block contained taller stems, but fewer individuals.

Physical Parameters

Many of the physical parameters showed trends from the lower elevation blocks to the upper ones. These trends were particularly evident for the physical soil parameters. Infiltration rate, bulk density, and percent sand were all low in the lower four blocks and increased in the upper four blocks. Percent silt, clay, and organic content were higher in the lower four blocks and decreased in the upper four blocks. Porosity was low in the lower blocks, peaked in the middle, and decreased in the upper blocks. Burrow cover and density were moderately variable among blocks, but with no trend; burrow diameter did not vary among blocks.

Elevation and Seasonal Effects

Pore Water Chemistry

Ammonium

Ammonium concentrations in all four treatment types ranged from 0 – 189.7 μM with a mean of 38.2 μM ± 9.4. There was an overall significant difference ($p < 0.0001$) in

ammonium concentration among blocks along the elevation gradient (Figure 2.7a). An ANOVA of the concentrations by block for each date determined that there was no significant difference in ammonium concentration among blocks for June and July; however, there was a significant difference among blocks for August ($p = 0.0210$) and September ($p = 0.0031$). Among the pore water collection dates throughout the growing season there was a significant difference ($p < 0.0001$) in ammonium concentration (Figure 2.7b). June had an intermediate ammonium concentration, followed by a decrease to the lowest value in July, then concentration increased through August and September. Within each block the means for each month followed the same date trend as described above (Figure 2.7c).

Phosphate

Phosphate concentrations in all four treatment types ranged from 0.1 – 312.9 μM with a mean of 32.5 μM ± 4.8. There was no overall significant difference in phosphate concentration among blocks along the elevation gradient (Figure 2.8a). Among the pore water collection dates throughout the growing season there was a significant difference ($p < 0.0001$) in phosphate concentration (Figure 2.8b). Phosphate concentration was lowest in June, increased slightly in July, and was considerably higher in August and September. The middle blocks (2-5) exhibited the date trend described above. The higher blocks (6-8) had low concentrations from June-August and increased dramatically in September. Block 1 remained at low concentrations throughout the sampling season (Figure 2.8c).

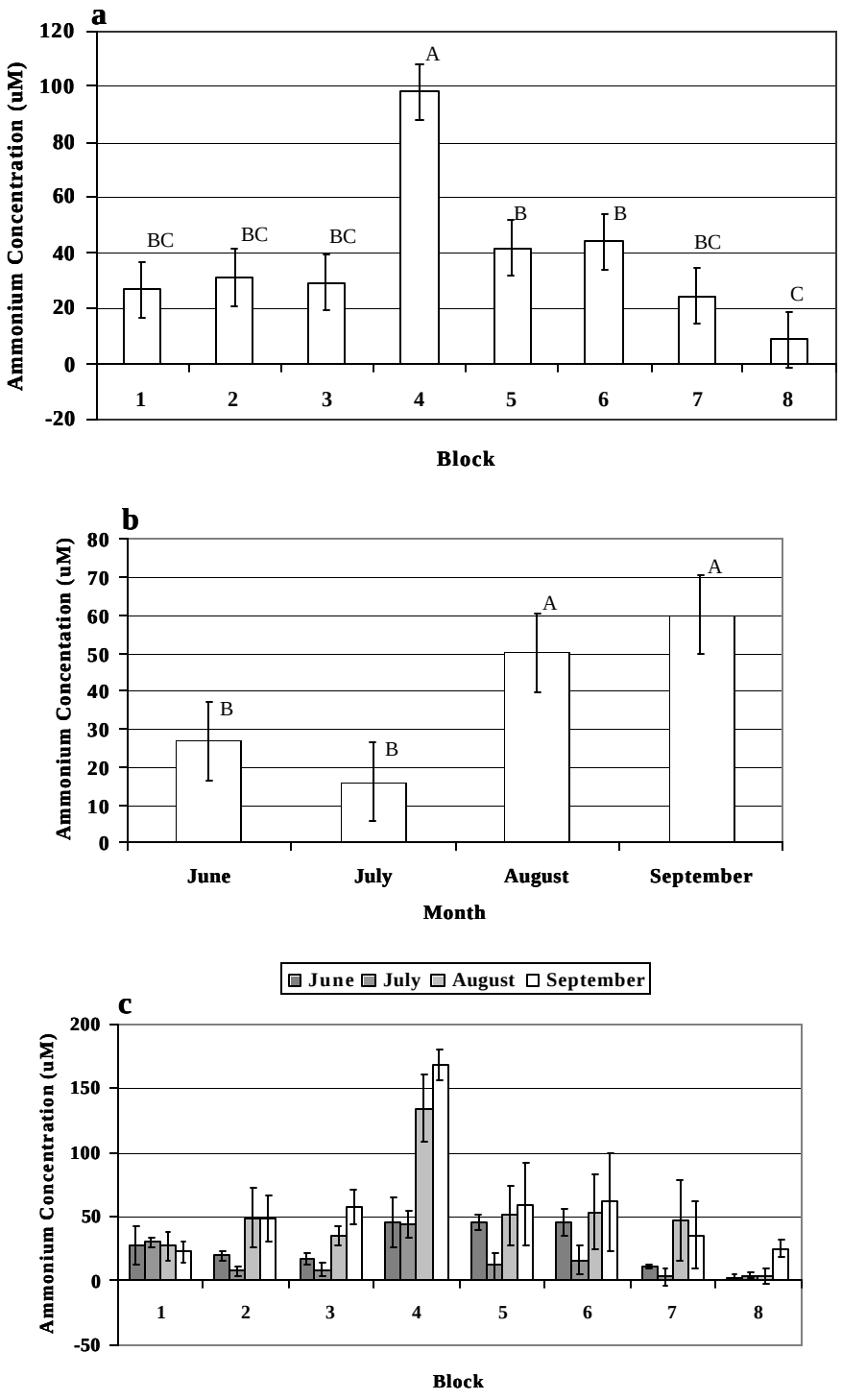

Figure 2.7. Pore water ammonium concentration (a) by block (n = 16), (b) by date (n = 32), (c) by block and date (n = 4). Significant differences in (a) and (b) as determined by LS Mean Differences are indicated by letters above the bars (mean ± 1 SE).

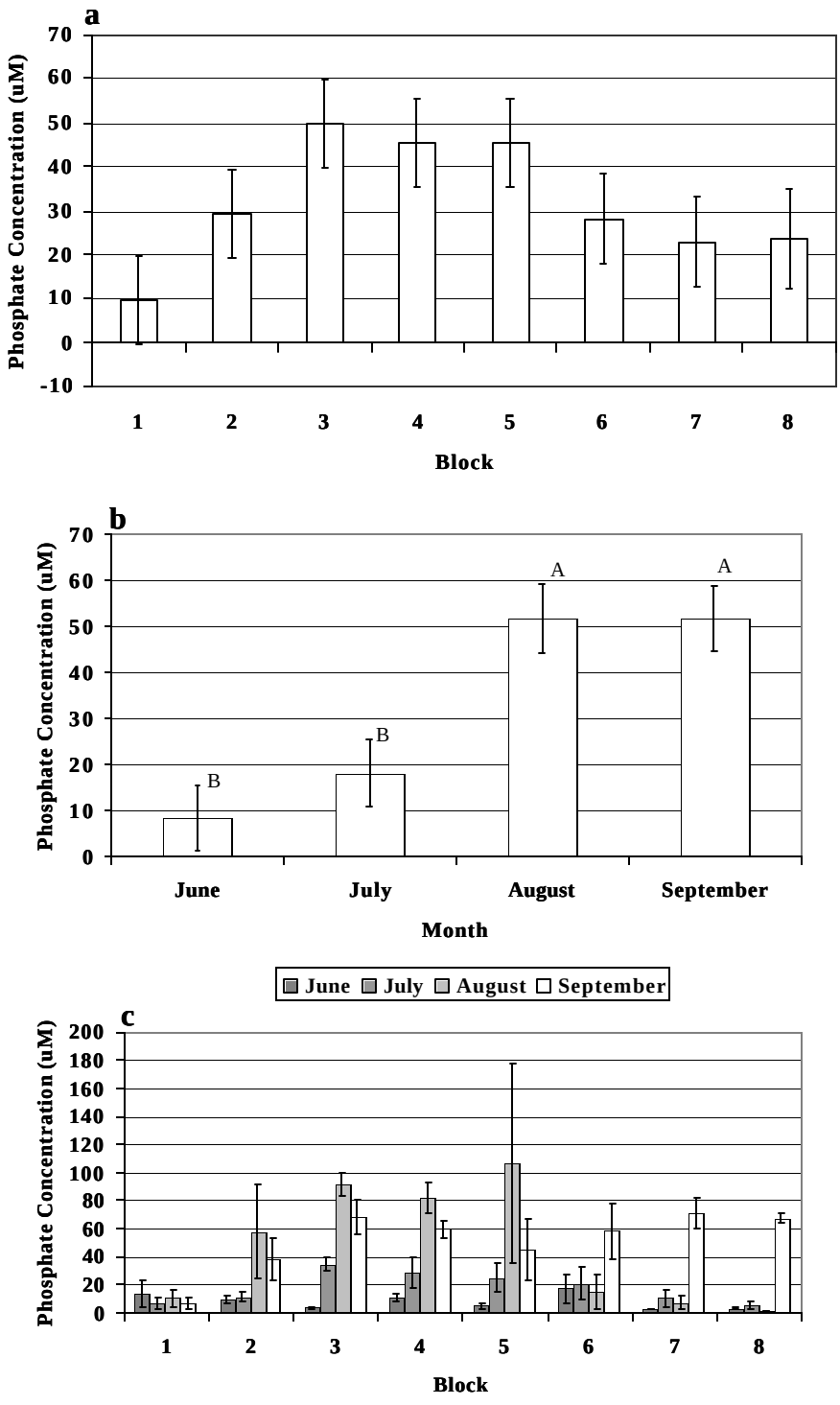

Figure 2.8. Pore water phosphate concentration (a) by block (n = 16), (b) by date (n = 32), (c) by block and date (n = 4). Significant differences in (b) as determined by LS Mean Differences are indicated by letters above the bars (mean ± 1 SE).

Sulfide

Sulfide concentrations in all four treatment types ranged from 0.3 – 2784.4 μM with a mean of 330.4 μM ± 116.2. With the artificial burrow treatments removed from the dataset, the range was decreased to 0.3 – 2086.3 μM, and the mean decreased to 252.9 μM ± 89.0. This new data set was used to determine if there were differences among blocks and among collection dates. There was an overall significant difference in sulfide concentration among blocks along the elevation gradient ($p < 0.0001$) (Figure 2.9a). An ANOVA of the concentrations by block lacked the power to show the significant differences among blocks for each collection date. There was almost a significant difference ($p = 0.0662$) for sulfide concentration among the four collection dates throughout the growing season (Figure 2.9b). Overall, sulfide concentration was lowest in June and July, and increase through August and September. Blocks 1-4 never drained and had continuously high sulfide concentrations throughout the sampling period; blocks 7 and 8 were relatively well drained and had low sulfide concentrations (Figure 2.9c). Blocks 5 and 6 shifted from low to high sulfide concentration in August and September respectively, this is most likely the cause of the overall increase in concentration for the latter part of the sampling period. This shift was most likely caused by increased periods of tidal inundation and lack of drainage as the summer progressed.

Redox

Redox potential in all four treatment types ranged from –181 mv to 120 mv with a mean of –42 mv ± 20. There was an overall significant difference in redox potential among

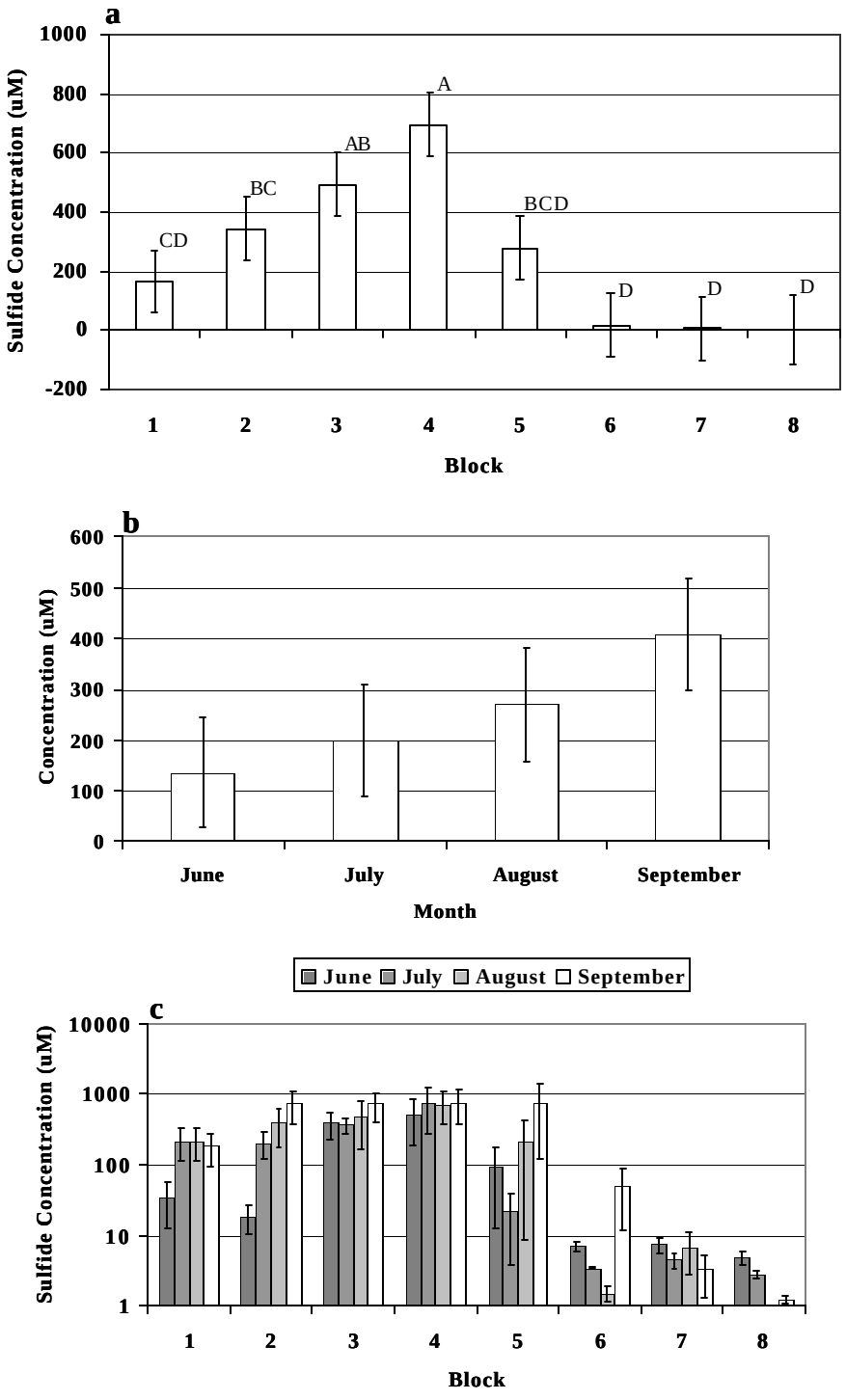

Figure 2.9. Pore water sulfide concentration with artificial burrow treatments removed (a) by block (n = 12), (b) by date (n = 24), (c) by block and date (n = 3). Significant differences in (a) as determined by LS Mean Differences are indicated by letters above the bars, (b) showed no difference (mean ± 1 SE).

blocks along the elevation gradient ($p < 0.0001$) (Figure 2.10a). An ANOVA of the redox potentials by block for each date (June, July, August, September) determined that there was a significant difference ($p < 0.0001$) among blocks for each date. Among the pore water collection dates throughout the growing season there was a significant difference ($p < 0.0001$) in redox potential (Figure 2.10b). Overall, redox was intermediate in June and moderately negative, but it increased to just over zero in July, then decreased to the most negative value in August, finally increasing to a moderately negative value in September. Blocks 1-4 never drained and had continuously low redox potential throughout the sampling period, but followed the date pattern described above; Blocks 7 and 8 were relatively well drained and had high redox potential, but followed the same date pattern (Figure 2.10c). Blocks 5 and 6 shifted from high to low redox potential in August and September. This shift was most likely caused by increased periods of tidal inundation and lack of drainage as the summer progressed.

Salinity

Salinity concentration in all four treatment types ranged from 34 – 62 ppt with a mean of 40 ppt ± 2. There was an overall significant difference ($p < 0.0001$) in salinity among blocks along the elevation gradient (Figure 2.11a). Salinity increased with elevation; a regression of elevation vs. salinity determined that elevation accounted for 79% of the variance in salinity. An ANOVA of the salinity by block for each date determined that there was a significant difference ($p < 0.05$) among blocks for each date. Among the pore water collection dates throughout the growing season there was a

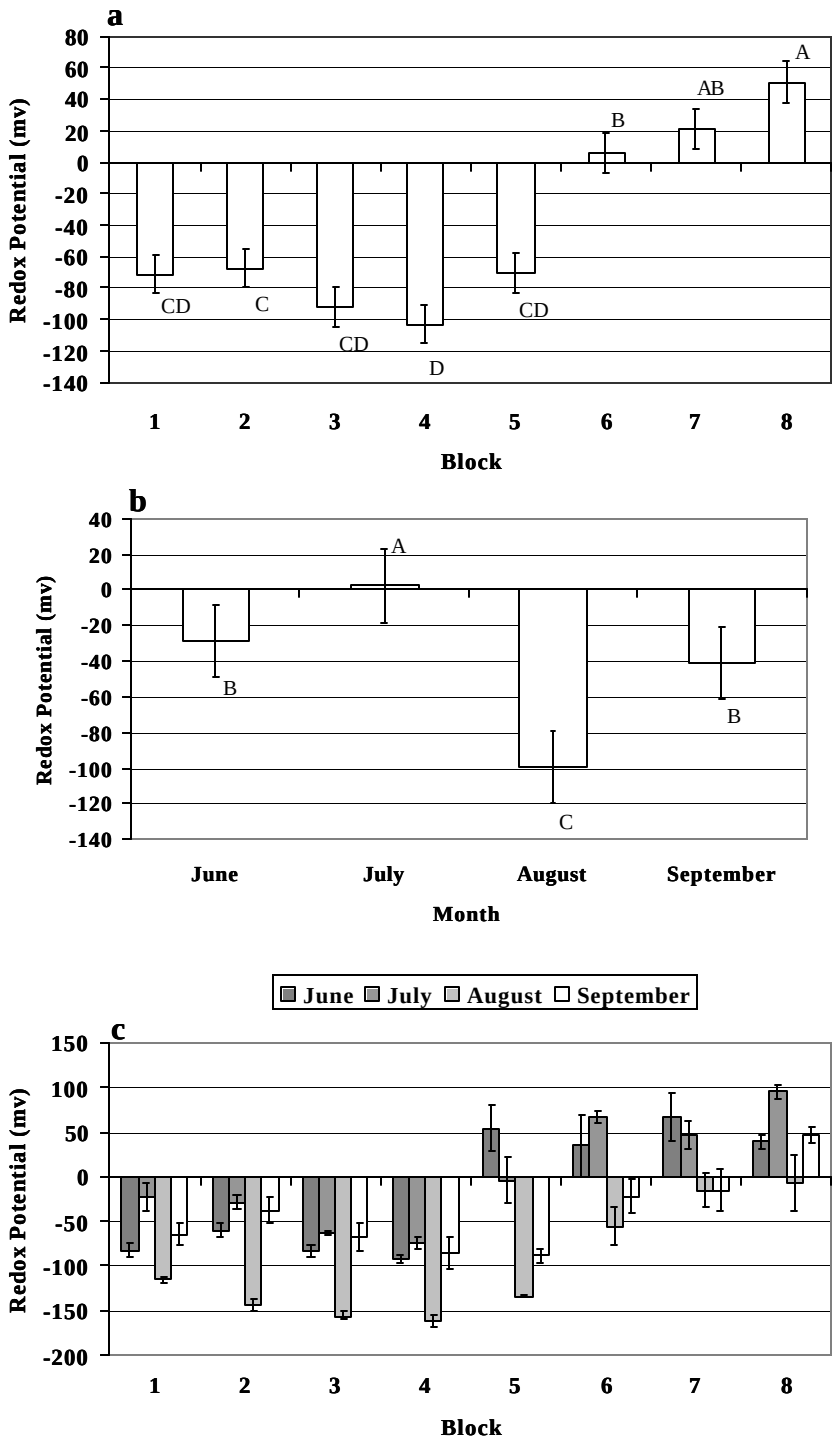

Figure 2.10. Pore water redox potential (a) by block (n = 16), (b) by date (n = 32), (c) by block and date (n = 4). Significant differences in (a) and (b) as determined by LS Mean Differences are indicated by letters by the bars (mean ± 1 SE).

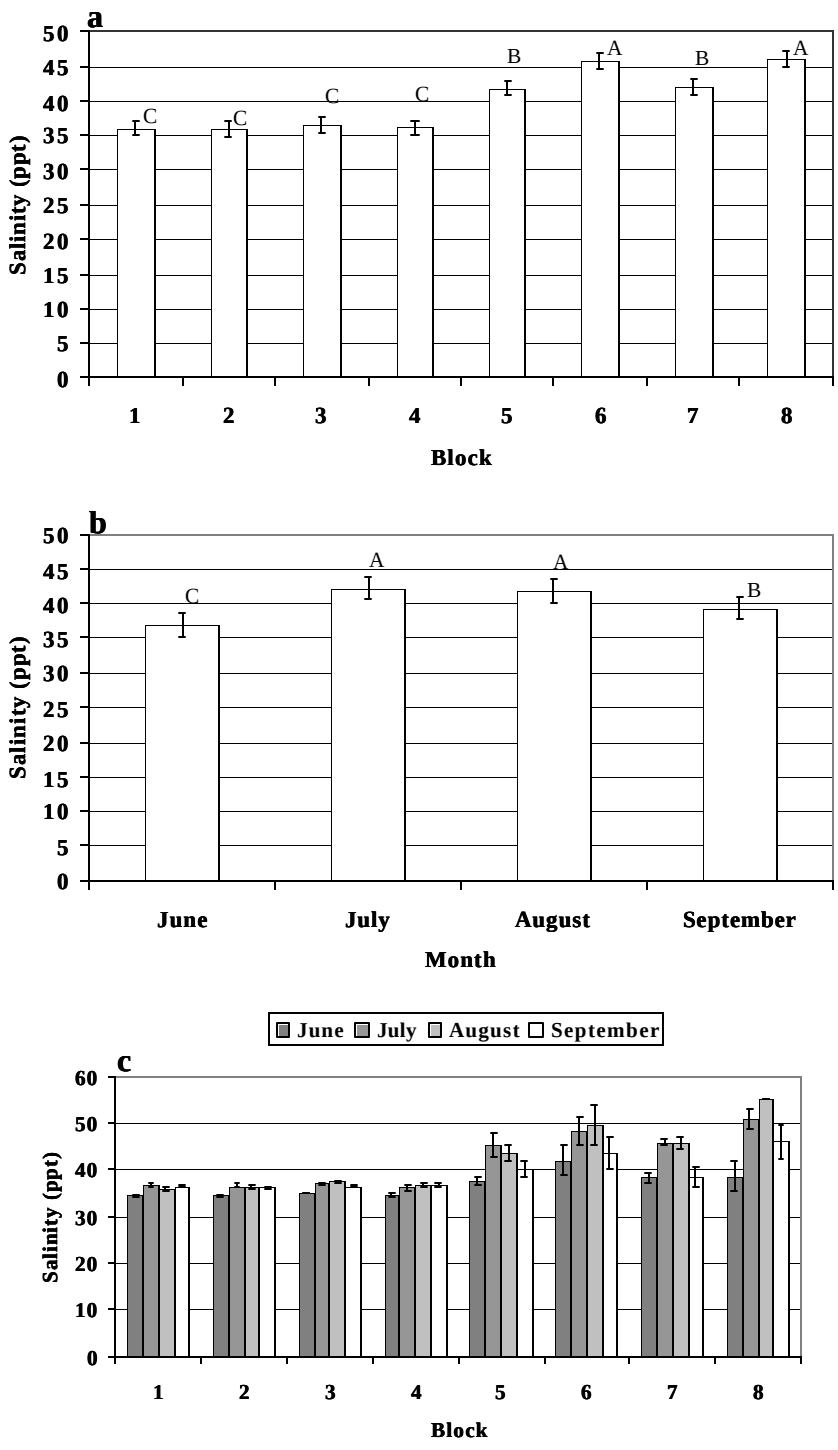

Figure 2.11. Pore water salinity (a) by block (n = 16), (b) by date (n = 32), (c) by block and date (n = 4). Significant differences in (a) and (b) as determined by LS Mean Differences are indicated by letters above the bars (mean ± 1 SE).

significant difference ($p < 0.0001$) in salinity (Figure 2.11b). June had the lowest salinity, followed by an increase to higher salinities for July and August; in September the salinity decreased to an intermediate value. Overall, within each block the salinity followed the date trend described above, however the trend was more pronounced in the upper four blocks (5-8) (Figure 2.11c).

Spartina alterniflora

Production

Monthly *Spartina alterniflora* production in all four treatment types ranged from a maximum of 325 g/m^2 to a minimum of -110 g/m^2 with a mean of 44 g/m^2 ± 8. There was no overall significant difference in production among blocks along the elevation gradient (Figure 2.12a). Among the sampling dates throughout the growing season there was a significant difference ($p < 0.0001$) in *S. alterniflora* production (Figure 2.12b). May had high production, followed by June with the highest production of the season; there was a dramatic decrease for July and then August, which had a negative production; in September production increased to a positive value again. The production within each block followed a similar trend throughout the growing season as described above (Figure 2.12c).

Stem Density

Spartina alterniflora stem density in all four treatment types ranged from 48 stems/m^2 to 1136 stems/m^2 with a mean of 412 stems/m^2 ± 52. There was an overall significant difference ($p < 0.0001$) in stem density among blocks along the elevation

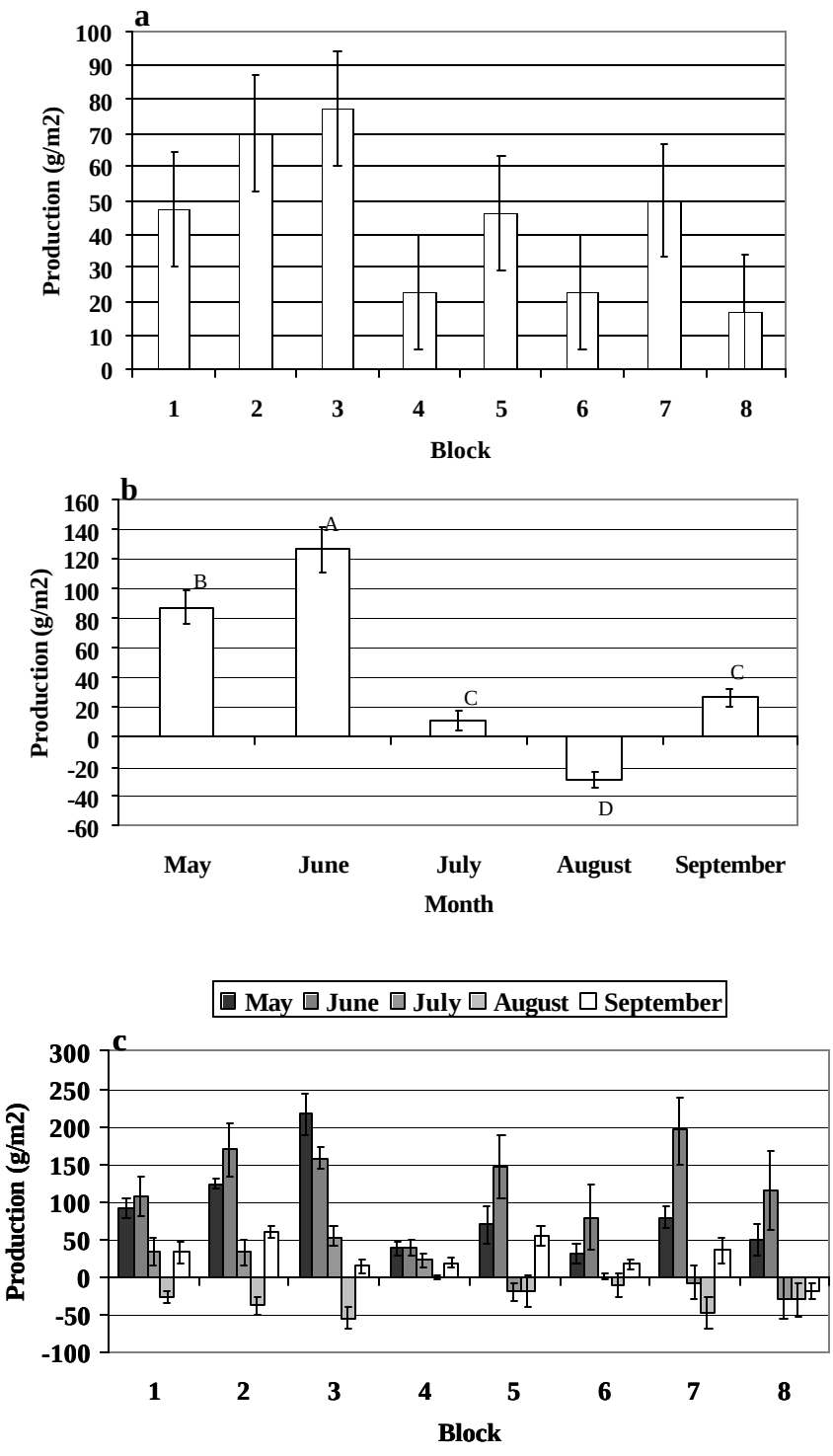

Figure 2.12. *Spartina alterniflora* production (a) by block (n = 16), (b) by date (n = 32), (c) by block and date (n = 4). Significant differences in (b) as determined by LS Mean Differences are indicated by letters by the bars, (a) showed no difference (mean ± 1 SE).

gradient (Figure 2.13a). An ANOVA of the stem density by block for each date determined that there was a significant difference ($p < 0.05$) in stem density among the eight blocks for all months May-September. Among the sampling dates throughout the growing season there was an overall significant difference ($p < 0.0001$) in stem density (Figure 2.13b). May had the highest stem densities followed by a steady decrease through August; September showed an increase in stem density with a mean reaching that of between June and July. Overall, each block showed a similar trend in production throughout the growing season; Blocks 4, 6, 7, and 8 had the lowest stem densities for all five months (Figure 2.13c).

Physical Parameters

Sediment Organic Content

The percent organic content for surface sediment collected from each quadrat ranged from 1.2% - 10.8% with a mean of 3.8%. An ANOVA by block yielded a significance difference ($p < 0.0001$) in sediment organic content among blocks (Figure 2.14a). Blocks 1, 3, and 4 had the highest organic content, blocks 2 and 5 were intermediate, and blocks 6, 7, and 8 had the lowest organic content. There was a significant difference ($p < 0.0001$) in organic content between the two sites. A regression of percent organic content against block determined that organic content decreased as block number (elevation) increased. Block number accounted for 59% of the variation in organic content.

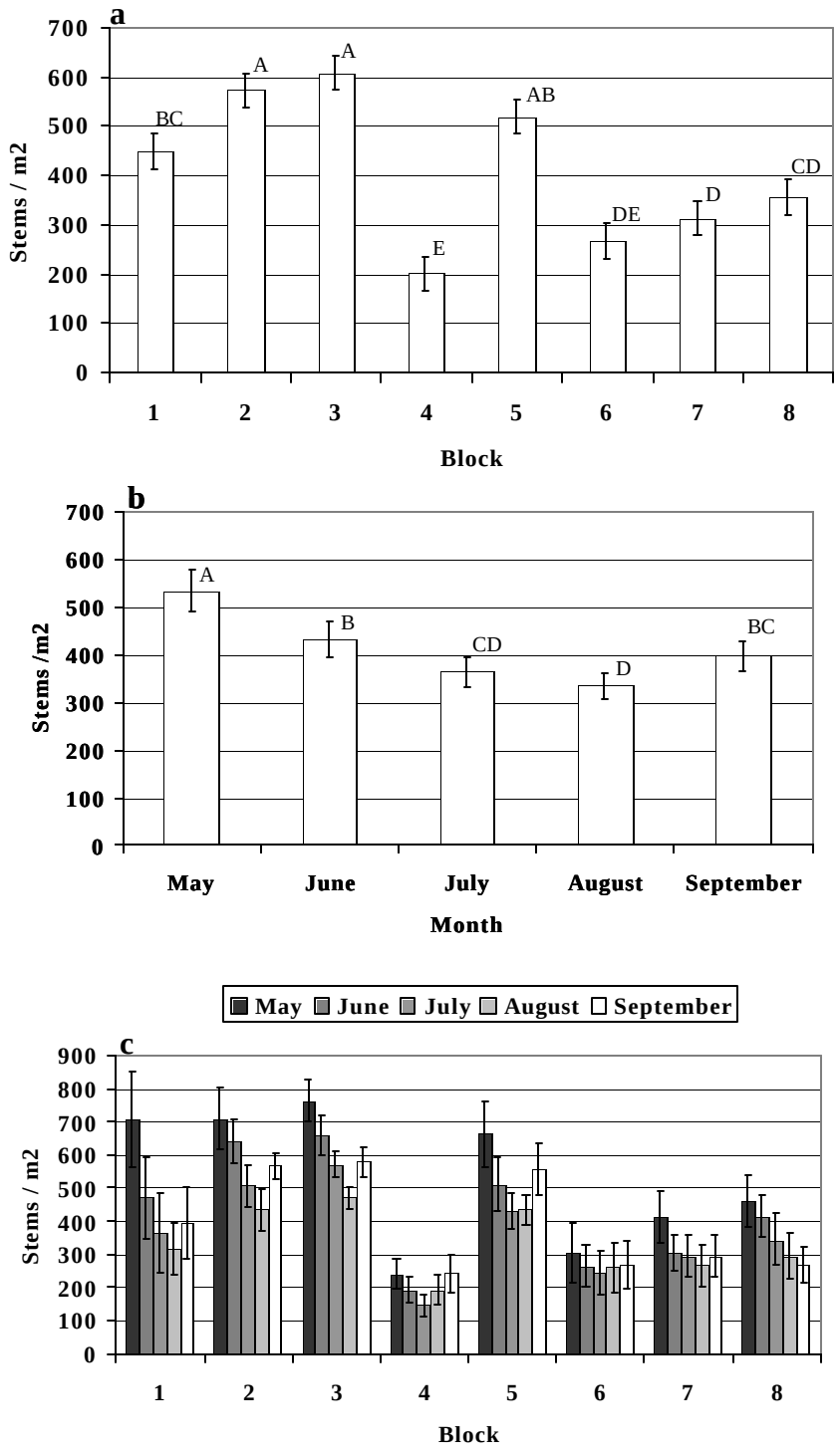

Figure 2.13. *Spartina alterniflora* stem density (a) by block (n = 16), (b) by date (n = 32), (c) by block and date (n = 4). Significant differences in (a) and (b) as determined by LS Mean Differences are indicated by letters above the bars (mean ± 1 SE).

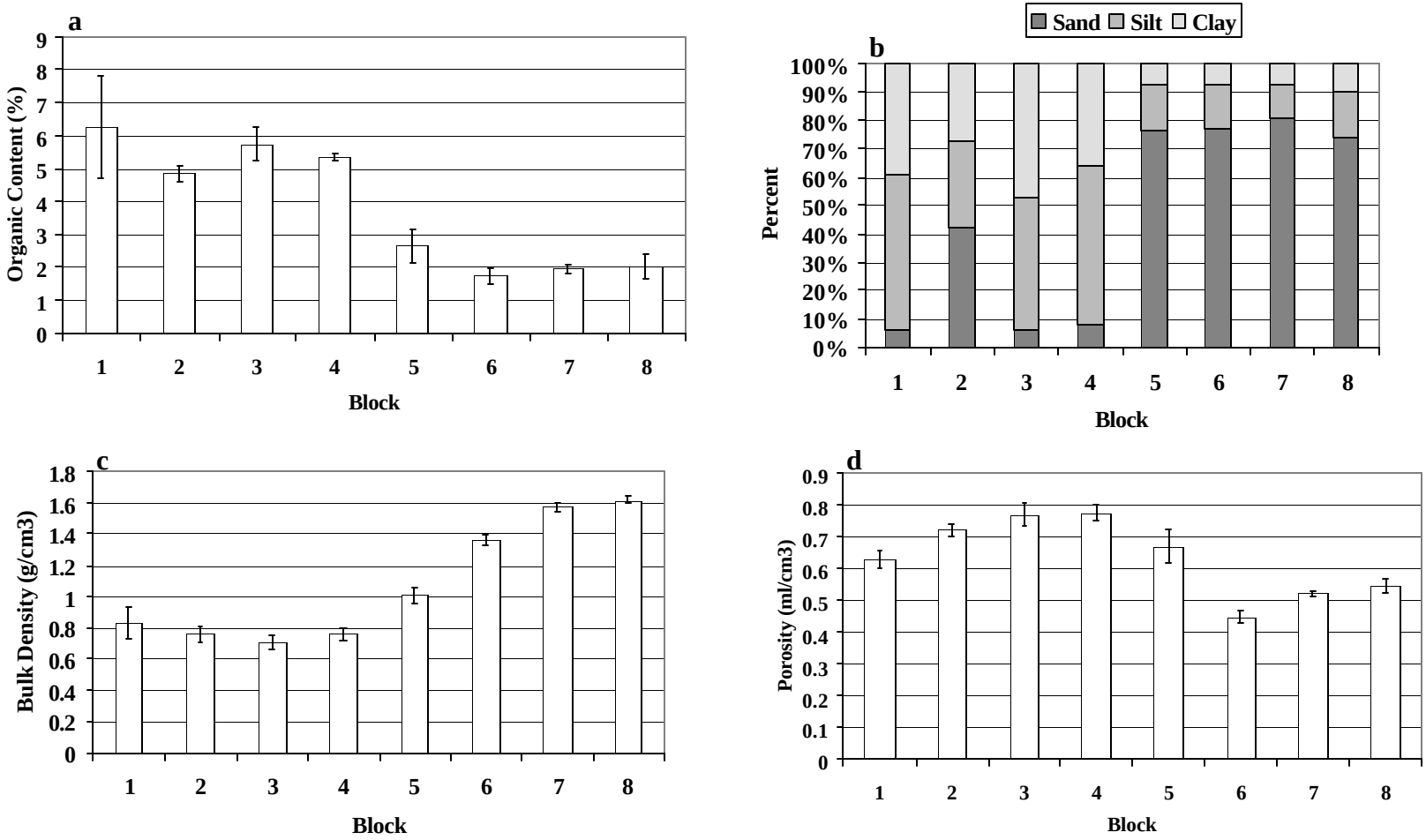

Figure 2.14. (a) Organic content (n = 4), (b) sediment texture (n = 4), (c) bulk density (n = 6), (d) porosity (n = 6), (e) infiltration rate (n = 4), (f) burrow density (n = 3), (g) burrow diameter (n = 3), (h) burrow coverage (n = 3) by block (mean ± 1 SE).

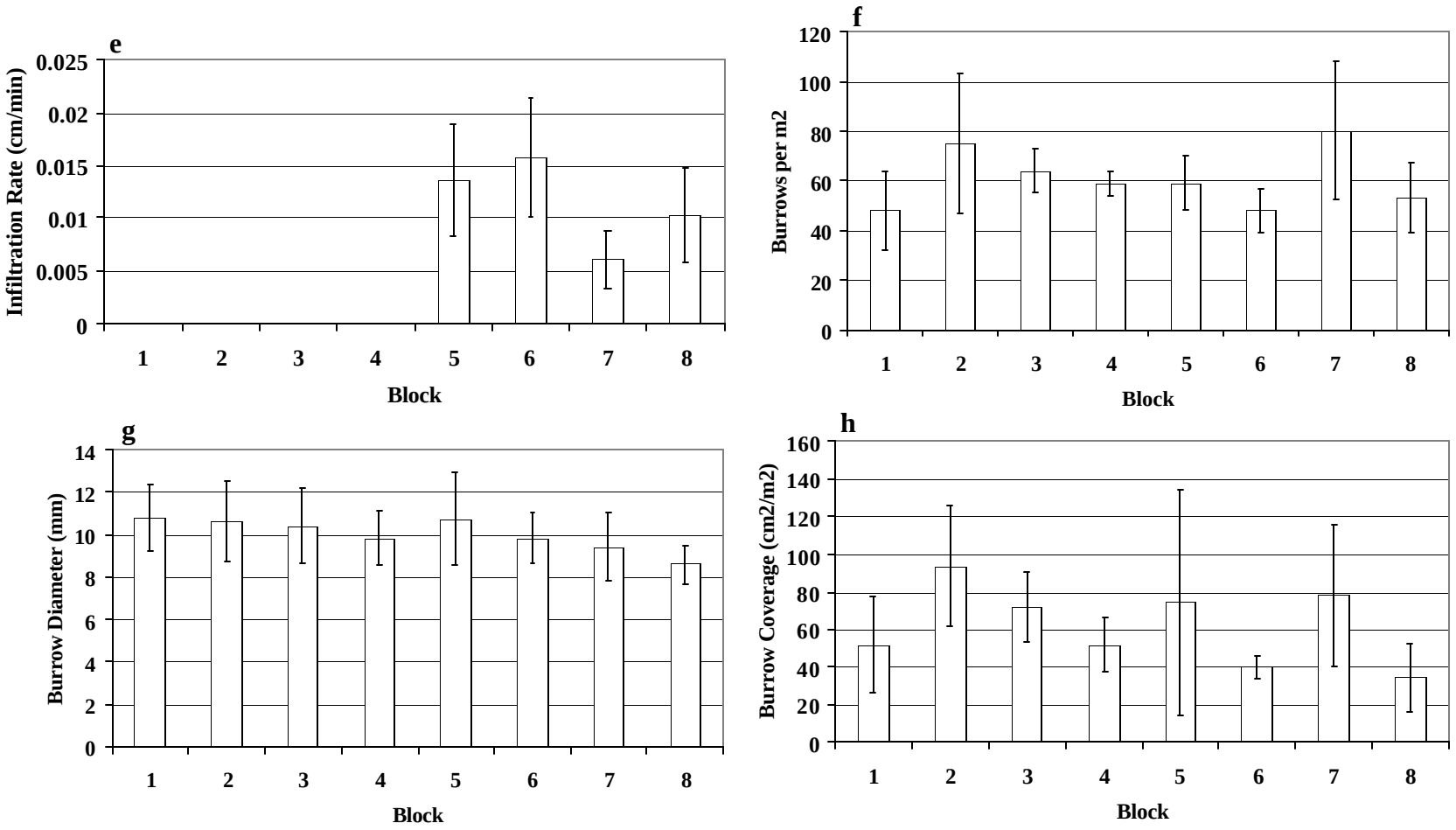

Figure 2.14 con'd. (a) Organic content (n = 4), (b) sediment texture (n = 4), (c) bulk density (n = 6), (d) porosity (n = 6), (e) infiltration rate (n = 4), (f) burrow density (n = 3), (g) burrow diameter (n = 3), (h) burrow coverage (n = 3) by block (mean ± 1 SE).

Sediment Texture

Sediment percent size class (sand, silt, and clay) was significantly different ($p < 0.0001$) between Site 1 and Site 2. Site 1 had means of 20%, 45%, and 35% sand, silt, and clay particles respectively; a texture of silty clay loam. The textural ranges for Site 1 were from clay loam to silty clay loam to silty clay. Site 2 had means of 77%, 15%, and 8% sand, silt, and clay respectively; a texture on the border of loamy sand and sandy loam, which was the textural range of Site 2. There were significant differences ($p < 0.0001$) in percent size classes among blocks. The main differences were that Blocks 5-8 had significantly higher percentage of sand and significantly lower percentage of silt and clay. Blocks 1-4 had the lowest and intermediate percentages of sand, and the highest and intermediate percentages of silt and clay (Figure 2.14b). A regression of percent size class against block number determined an increase in percent sand ($r^2 = 0.57$), decrease in percent silt ($r^2 = 0.52$), and decrease in percent clay ($r^2 = 0.57$) with increasing block number.

Sediment Bulk Density

Sediment bulk density was significantly different ($p < 0.0001$) between Site 1 and Site 2. The bulk density for Site 1 ranged from 0.52 - 1.11 g/cm^3 and had a mean of 0.77 g/cm^3. In Site 2 the bulk density ranged from 0.76 - 1.67 g/cm^3 and had a mean of 1.37 g/cm^3. There was a significant difference ($p < 0.0001$) in bulk density among blocks (Figure 2.14c). Blocks 1-4 had the lowest bulk density, but did not significantly differ between one another ($p = 0.7275$). There was a significant difference ($p < 0.0001$) in

bulk density among Blocks 5-8. A regression of the data for these blocks revealed an increase in bulk density with an increase in block number. Block number accounted for 80% of the variation in bulk density for these four blocks.

Sediment Porosity

Sediment porosity differed significantly ($p < 0.0001$) between Sites 1 and 2. Sediment porosity of Site 1 ranged from 0.53 – 0.86 ml/cm^3 with a mean of 0.72 ml/cm^3. Site 2 had a range of 0.41 - 0.87 ml/cm^3 with a mean of 0.55 ml/cm^3. There was a significant difference ($p < 0.0001$) in porosity among blocks (Figure 2.14d), but there was no distinct pattern. A regression of porosity against block for Blocks 1-4 determined an increase in porosity with and increase in block number; block number accounted for 48% of the variation in porosity. For Blocks 5-8 porosity decreased with block number, and block number accounted for only 12% of the variation in porosity.

Infiltration Rate

The infiltrations rates between Site 1 and Site 2 were significantly different ($p < 0.0001$). There was no infiltration in blocks 1-4; standing water was continuously present, and the area did not drain. Infiltration rates in blocks 5-8 ranged from 0.0 – 0.027 cm/min with a mean of 0.011 cm/min. There was no significant difference among the infiltration rates in blocks 5-8 (Figure 2.14e). The values within each block were highly variable and ranged an order of magnitude.

Burrow Density, Diameter, and Coverage

Burrow density ranged from 16 – 128 /m^2 with a mean of 61 /m^2. There was no significant difference in burrow density between sites or among blocks (Figure 2.14f). Burrow densities over a larger area of south Hog Island ranged from 22 – 127 /m^2 (Walsh 1998). Burrow diameters ranged from 2.9 – 29.4 mm with a mean of 10.0 mm. There was no significant difference in burrow diameter between sites or among blocks, but there was a trend in mean burrow diameter among blocks (Figure 2.14g). Mean burrow diameter decreased with increasing block number. Burrow coverage ranged from 8.2 – 194.8 cm^2/m^2 (0.08 – 1.95 percent coverage) with a mean of 62.0 cm^2/m^2 (0.62 percent coverage). There was no significant difference in burrow coverage between sites or among blocks (Figure 2.14h).

A multiple analysis of variance (MANOVA) was performed on the above site characteristic data; elevation was used as the independent variable. Many of the characteristics were highly correlated (Table 2.4); within a pair of correlated characteristics only one of the pair was retained for the final MANOVA analysis. Organic content, sediment porosity, and mean burrow diameter were the dependent variables used in the final MANOVA. There was a significant elevation effect for the final three dependent variables used in the analysis (Wilks' Lambda = 0.0628; 3 numerator and 4 denominator degrees of freedom; $p = 0.0072$). The three variables all decreased with increasing elevation.

Table 2.4. Multiple analysis of variance (MANOVA) correlation matrix of physical parameters, shaded cells are significant ($p < 0.05$).

DF = 6	burrow diameter	organic content	porosity	bulk density	infiltration	% sand	% silt	% clay
burrow diameter	1							
organic content	-0.50533	1						
	0.2473							
porosity	-0.119794	0.494171	1					
	0.7981	0.2596						
bulk density	-0.267946	-0.226821	-0.809283	1				
	0.5613	0.6248	0.0275					
infiltration	0.509334	-0.830797	-0.44304	0.085708	1			
	0.243	0.0206	0.3195	0.855				
% sand	0.608432	-0.928842	-0.40525	0.228308	0.666511	1		
	0.1471	0.0025	0.3671	0.6224	0.102			
% silt	-0.695699	0.817936	0.309485	-0.091774	-0.575225	-0.954879	1	
	0.0826	0.0246	0.4994	0.8449	0.1767	0.0008		
% clay	-0.474394	0.954797	0.448936	-0.329986	-0.705918	-0.952091	0.818739	1
	0.2821	0.0008	0.3123	0.4698	0.0763	0.0009	0.0243	

Burrow Form

The depth of burrow casts ranged from 2.1 – 13.0 cm with a mean of 6.9 cm. Burrow opening diameters ranged from 8.6 – 48.3 mm with a mean of 27.7 mm. Burrow volume ranged from 0.6 – 85 cm^3 with a mean of 24.7 cm^3. Burrow surface area ranged from 5.5 – 166.6 cm^2 with a mean of 68.2 cm^2. The surface area: volume ratio ranged from 1.4 – 9.7. The burrow casts were taken from random areas of the marsh so no statistical analyses were performed.

Discussion

In this study, the sediment characteristics of the marsh were an important contributing factor in determining the effect of fiddler crab burrows on pore water chemistry. There were a few unanticipated results in this experiment; an increase in sulfide concentration within plots to which artificial burrows were added and the lack of difference in redox potential, nutrient concentrations, and aboveground *Spartina alterniflora* production within these plots. Although these results were unexpected they bring to light effects of fiddler crab burrowing that have not been previously considered.

Pore Water Chemistry

Typically, it is thought that the presence of fiddler crab burrows aerates sediments, increasing redox potential and releasing hydrogen sulfide (Howarth and Teal 1979, Katz 1980, Montague 1980, Bertness and Miller 1984, Bertness 1985, Walsh 1998). Studies that have considered the interactions between fiddler crabs and pore water

chemistry have been focused on marsh areas that drain and are not water-logged for long periods of time (Montague 1982, Bertness 1985). The chemical reactions that occur in water-logged marsh sediments are quite different from the reactions that occur in well-drained sediments (Howarth 1993).

In this study site, the sediment did not drain very well or at all, and as burrows were added in many of the plots, they immediately filled with anoxic pore water. The higher sulfide concentrations in the artificial burrow treatments was mainly influenced by the concentrations in experimental blocks that did not drain at all (Blocks 1-4), and had standing water at the sediment surface. When the sulfide concentration data were analyzed by site, Site 1 (Blocks 1-4) almost had a significant treatment effect ($p = 0.0917$), where as Site 2 (Blocks 5-8) did not have a significant treatment effect ($p = 0.4473$). This indicates that Blocks 1-4 were assuredly the cause of the significant treatment effect when the data from all blocks were used. Using only four blocks (Site 1) for the analysis the power was not great enough to show a significant treatment effect at $\alpha = 0.05$ due to the resulting small sample size.

Among the unexpected findings of this study, it was surprising that redox potential did not have a significant treatment effect, because sulfide concentration has a close inverse relationship to redox potential (Koch et al. 1990). Howarth (1993) states that other studies have found sulfate reduction occurring at high redox potentials within salt marsh sediments. Also, it is possible that the method used for measuring redox potential may not have been sensitive enough to show changes in redox among treatments.

High sulfide concentration is likely a result of either increased sulfate reduction, or decreased sulfide oxidation. There are a few possible explanations for the unexpected increase in sulfide concentration with the addition of artificial burrows. In these salt marsh sediments, organic matter decomposition can occur by five different reactions. These five reactions each utilize a different inorganic ion (oxygen (O_2), nitrate (NO_3^-), manganese (Mn^{4+}), iron (Fe^{3+}), sulfate (SO_4^{2-})) as a terminal electron acceptor; the reactions can occur at the same time, but in different proportions (adding up to the total amount of decomposition) (Howarth 1993). If the proportions in which these reactions occurred were altered by the presence of the artificial burrows, then the percent of organic matter oxidation that occurred through sulfate reduction could have increased. In turn, one or more of the other pathways of organic matter oxidation would have decreased. Hines and Jones (1985) found that sulfate reduction was 4.5 times faster in their bioturbated (polychaetes, bivalves, and mollusks) site compared to non-bioturbated site. An increase in sulfate reduction would have increased the amount of sulfide produced, but not affected the amount of ammonium and phosphate produced, as ammonium and phosphate are produced in the same stoichiometric ratios no matter which pathway of organic matter oxidation is utilized.

As these marshes flood from the bottom up, is possible that sulfate-reducing bacteria were less inhibited in the burrow addition plots because they were not receiving oxygen inputs from incoming seawater during tidal inundation; therefore, more sulfate reduction would be able to occur (Boulegue et al. 1982, Howarth 1993, Marschall et al. 1993, Krekeler et al. 1998, Sigalevich el al. 2000). Oxygen penetration into the standing

water in micro and macro pore spaces occurs primarily by diffusion, rather than by mixing during tidal inundation (Harvey and Nuttle 1995). The other treatments had sediment pores that were smaller and evapotranspiration or subsurface drainage may have allowed these micro pores to fill with air each low tide. If so, this would allow oxygen into the sediment, thus inhibiting the activity of the sulfate-reducing bacteria (Howarth 1993, Marschall et al. 1993, Krekeler et al. 1998, Sigalevich el al. 2000).

Because anoxic water dominated the artificial burrow plots, little sulfide would be oxidized (Howarth 1993). A decrease in sulfide oxidation would produce a buildup of sulfide in the sediment.

There are different processes that could have increased the rate of organic matter oxidation within the sediment. Increased availability of organic matter can stimulate sulfate reducing bacteria and shift the type of oxidation reaction to sulfate reduction, decreasing the rates of the other pathways of reduction (Westrich and Berner 1984, Howarth 1993). Material from the sediment surface with higher organic content could have fallen into the newly formed artificial burrows (Berner and Westrich 1985, Hines and Jones 1985). This would have increased the amount of organic material available for oxidation. The rates of the reduction reactions involved, especially sulfate reduction would have increased (Westrich and Berner 1984, Howarth 1993), and in turn the amount of sulfide produced would have increased. Howarth (1993) concluded that the major control on sulfate reduction in water-logged salt marsh sediments is the rate of supply of organic matter. Agitation of sediment can also increase sulfate reduction reaction rates because more sulfate can be transported through the sediment by physical processes than

diffusion; therefore, addition of artificial burrows could have increased the rate of sulfate reduction.

Increased reduction rates could have likewise increased the amount of the other products of the oxidation reactions. Therefore, ammonium and phosphate concentrations could have similarly increased, or they may have been preferentially lost within the bioturbated area (Berner 1977). Additionally, Hines and Jones (1985) found that bioturbation caused an increase in the removal of ammonium and phosphate from the pore water. There are a few chemical reactions that consume ammonium and phosphate removing them from the pore water. These reactions might have occurred in conjunction with either of the above increases in organic matter oxidation. Ammonium can be oxidized to form nitrate (nitrification) and phosphate can react with iron oxide and ferric iron to form iron phosphate compounds (Berner 1977, Fenchel et al. 1998). Also, ammonium and phosphate can be adsorbed onto sediment particles, removing then from solution (Berner 1977).

These explanations for increased sulfide concentrations are speculations as the data are not currently available to fully understand these chemical processes. Further research could be conducted to determine which of these processes occur in conditions similar to those seen in this experiment. There are a number of ion concentrations and chemical parameters that were not collected that would help to elucidate the chemical reactions within the sediment. Because the amounts of ammonium and phosphate produced depend on the initial C:N:P ratios within the reacting organic matter (Berner 1977, Lord and Church 1983), knowing the C:N:P ratio of the organic matter as well as

the following parameters would aid in balancing the stoichiometric equations of the organic matter oxidation reactions. Reduction rates (most importantly sulfate, but also oxygen, nitrate, and iron; manganese is a minor electron acceptor in these systems, and is deemed unimportant (Howarth 1993) would greatly aid in determining the proportions of the different reduction pathways utilized in organic matter oxidation. Also, the sulfate reduction rate would allow calculation of the amount of sulfide produced, and make the cause of the increased sulfide concentration more clear. The concentrations of certain oxidized ions would indicate the amount of a compound that is available for each pathway of reduction. Sulfate, nitrate, and iron (III) oxide concentrations would indicate the amount of each ion available for reduction. The concentrations of reduced ions (end products) would show the proportions of organic matter oxidation that occurred through each reduction pathway. Iron sulfide (FeS) and pyrite (FeS_2) concentrations in the sediment would indicate the proportion of iron and sulfur that was unavailable, because they are end products of sulfate reduction, and are only reactive with O_2 oxidation (Lord and Church 1983, Giblin and Howarth 1984, Howarth 1993, Fenchel et al. 1998). Dissolved iron (II) concentration would indicate the amount of reduced iron formed from iron reduction that is not bound in the solid phase. Elemental sulfur concentration would aid in writing a mass balance for sulfate reduction, as it is one of the end products (Howarth 1993). Iron phosphate concentration would also indicate the amount of phosphate bound in the sediment. Measuring the pH would enable the positioning of the sediment on an Eh-pH diagram, indicating the field of stability of the ions and compounds involved.

***Spartina alterniflora* Production and Stem Density**

Monthly aboveground *Spartina alterniflora* production did not yield the significant treatment effect that was expected, but there may have been differences in belowground production, for which data were not collected. Growth of *S. alterniflora* is affected by sulfide in the sediment pore water; sulfide concentrations of 0.2 mM or more affect the ability of *S. alterniflora* to uptake ammonium (Bradley and Morris 1990). Koch and Mendelssohn (1989) found that sulfide concentrations of 1.0 mM significantly reduced the root biomass in *S. alterniflora*. The sulfide concentrations in this study were as high as 2.8 mM. The aboveground biomass low within the study area because the plants were already exposed to high stress growing conditions; there were high sulfide concentrations in Blocks 1-4 and high salinity in Blocks 5-8. The increase in sulfide concentration within the artificial burrow plots may not have been enough to decrease aboveground production more than it already was.

The lack of difference in aboveground *Spartina alterniflora* production and stem density was possibly due to a shift in belowground production. Because the aboveground production did not change with increased sulfide concentrations, and because increased sulfide concentration interferes with nutrient uptake by the roots, the plants would need to tap into belowground stored energy reserves to be able to continue to support the existing aboveground tissue. The rhizomes of *S. alterniflora* contain stored starch that could be utilized under the high stress conditions of elevated sulfide concentrations to temporarily subsidize the aboveground portions of the plant, or to grow more advantageous roots as a means to 'find' and utilize 'un-tapped pockets' of oxygen, or both. Such an increase in

root production might increase the overall belowground production and balance out the loss of mass in the rhizomes for the short term depending on how successful and efficiently the new roots could find and exploit 'new' soil resources. However, as continued elevated sulfide concentrations would eventually deplete the carbohydrate reserves, the energy needed to produce new 'searching' roots might be too costly, and the plants may not be able to support the aboveground portions first and then the belowground portions, eventually leading to a dieoff.

As ecosystem engineers sensu Jones et al. (1994), fiddler crabs affect their abiotic surroundings. Because additional burrows did affect pore water sulfide concentrations, crab burrowing activity and growth of *S. alterniflora* likely form an indirect animal-plant interaction (Peterson and Heck 1999, Bertness 1985). It can be inferred that fiddler crabs have an indirect bottom-up control on *S. alterniflora* within the salt marshes that they inhabit. This raises further questions regarding the dichotomy of the top-down vs. bottom-up control of structure within the salt marsh. Rather than the typical top-down interaction of herbivores consuming plants (Heck and Valentine 1995, Silliman and Zieman 2001), fiddler crabs may affect *S. alterniflora* by altering the sediment pore water chemistry. The specific chemical and plant effects of fiddler crab burrowing likely vary depending on the initial conditions of the sediment physical parameters. From this study there are potential negative effects from increased crab burrow densities rather than positive effects (found by Bertness (1985) and Montague (1982)) on *S. alterniflora* production, because of the increased sulfide concentrations when burrows were added in the artificial burrow plots.

Physical Parameters

Many of the physical parameters analyzed had a strong relationship with elevation and with each other; many of them also affect each other. Higher organic content in the sediment clogs the pore space making it more difficult for water to infiltrate through the sediment, and slowing the infiltration rate. Higher bulk density decreases the capacity for the sediment to hold water in the pore spaces; therefore lowering the porosity. Higher fractions of silt and clay in sediment (fine material) decrease the fraction of sand (course material) that the sediment can contain. As silt and clay build up in sediment, so does organic matter, since they are all products of breaking down of parent materials. Organic matter can hold water within the sediment; therefore as it increases so can porosity.

All of these physical factors of the sediment have a strong influence on the way in which crab burrows affect the sediment pore water. As the content of organic matter and fine material in the sediment increased the marsh would drain less and become water-logged. When sediment is in a water-logged state this property dictates the chemical reactions and pathways of organic matter oxidation that occur with the presence of fiddler crab burrows. The shift from well-drained marsh to poorly drained marsh is associated with marsh age and change in tidal elevation. As sea level rises there is a potential for marshes to become more water-logged and instead of the presence of fiddler crabs keeping marshes from aging by increasing redox potential and organic matter decomposition, the presence of crabs may accelerate marsh aging by increasing sulfide concentrations.

Bertness (1985) reports common fiddler crab burrow depths of 5 – 25 cm. The burrows from areas between the two study sites in this study were not nearly as deep as those reported in the literature. Because burrow depth differs in different marshes or areas of a marsh the surface areas and volumes would be different also, which would affect the interactions between fiddler crab burrows and the pore water chemistry in the marsh. Greater surface area of burrows would allow more interaction of the burrow wall with either air if the marsh drains at low tide, or interstitial water if the marsh does not drain. Also if the marsh floods from the surface down then more flushing of oxic seawater would occur with greater burrow volumes.

Unlike previous studies conducted in well-drained salt marshes that found increases in *S. alterniflora* production and redox potential associated with increased fiddler crab activity, this study found that in poorly drained marshes increased crab burrow densities lead to increased sulfide concentrations and no change in aboveground *S. alterniflora* production. Existing sediment characteristics and extent of drainage seem to determine the effects that crab burrows have on pore water chemistry and the growth of *S. alterniflora*.

Chapter 3. The Spatial Scale and Disc of Influence of Individual Fiddler Crab Burrows on Surrounding Pore Water Chemistry

Introduction

The chemical processes that fiddler crab burrows facilitate within marsh sediments have been speculated by Katz (1980), Montague (1980), Howes et al. (1981), Bertness and Miller (1984), Genoni (1991), and Harvey et al. (1995). However, few studies have explicitly examined the alterations in sediment chemistry caused by the presence of crab burrows within the sediment. Bertness (1985) determined the effects of increased and decreased fiddler crab burrow density on redox potential within the top 10 cm of the sediment. In the marsh flat zone, redox potential did not change when fiddler crabs were removed from plots. However, in the high marsh short-form *Spartina alterniflora* zone, with no existing burrows, the addition of fiddler crab burrows caused a significant increase in redox potential. Montague (1982) determined differences in ammonium and phosphate concentrations and salinity between pore water within natural fiddler crab burrows and interstitial pore water in spring and fall. However, in his study, Montague (1982) did not collect interstitial pore water near to the natural burrows from which he collected pore water. Thus far, no studies have determined the extent of the effect of individual crab burrows on the surrounding sediment chemistry.

Most often sediment pore water chemistry data are collected in one dimension, as a depth profile (Berner 1977, Howarth and Teal 1979, Lord and Church 1983, Giblin and Howarth 1984, Berner and Westrich 1985, Hines and Jones 1985, Koretsky et al. 2003). Only a few studies have determined sediment pore water chemistry in two dimensions, usually along a vertical plane (Huettel et al. 1998, Shuttleworth et al. 1999, Bull and Williamson 2001, Nielsen et al. 2003) or in three dimensions (Luther et al. 1998, Bull

and Taillefert 2001). Huettel et al. (1998) examined the effects of pore water flow on downstream sediment iron, manganese, and nutrient chemistry using a flume with sandy substrate. The 2-D nature of the pore water data was obtained by analyzing the vertical profiles of 10 cm long sediment cores spaced 50 - 100 mm apart along a transect and creating contours from linear interpolation. This experiment was conducted on a fine-scale with millimeter resolution of the vertical profiles along the 500 mm transect. Shuttleworth et al. (1999) studied spatial heterogeneity of iron and manganese within sediment pore water, employing the diffusive equilibration in thin-films (DET) technique to form a 2-D vertical profile with 3 mm spatial resolution. Both Huettel et al. (1998) and Shuttleworth et al. (1999) found that the concentrations of these metal ions were highly heterogeneous on this fine-scale. Bull and Williamson (2001) used color image analysis to determine concentrations of hydrous iron oxide and acid-volatile sulfides. They were able to obtain spatial resolution of 0.2 mm for the 2-D flat cross-section of sediment cores. Bull and Taillefert (2001) utilized voltammetric profiling to determine 3-D iron (II) and total sulfide concentrations on a millimeter scale. Their findings show the highly heterogeneous nature of marsh sediments, and indicate the importance of obtaining data in three dimensions. The need for pore water data to be collected in more than one dimension is becoming more apparent, because these studies have found such a high level of heterogeneity within sediments when studied in more than one dimension.

A few studies have applied multi-dimensional millimeter-scale profiles to determine the effects of burrow structures on sediment pore water. Luther et al. (1998) created three-dimensional maps of oxygen and manganese (II) concentrations

surrounding a worm burrow. They used voltammetric microelectrode vertical profiles (7 cm long) to obtain data on a millimeter scale. The profiles surrounded the burrow in a 10 cm^2 area, and extended to a maximum distance of 2.7 cm from the burrow. The effects of the worm burrow were an increase in oxygen penetration and increased depth of manganese (II) detection. Nielsen et al. (2003) created radial micro-profiles of sediment chemistry surrounding fiddler crab burrows within mangrove sediments. At three depths, they determined sulfate reduction rates, particulate iron, and reduced sulfur surrounding the burrows to a distance of 3 cm from the burrow edge. The authors found that sulfate reduction rates increased with distance from the burrow, while iron (III) concentrations decreased steeply with distance from the burrow at all depths. Total reduced sulfur and total iron were variable with distance from the burrow. These results demonstrate that some chemical changes can occur within a distance as small as a few millimeters from the edge of a burrow.

Even though a few studies have examined pore water surrounding various animal burrows, these studies have all been on a micro-scale and did not extend more than 30 mm from the burrow edge. Also, they have focused on metal ions and did not question the effects of the burrows on pore water nutrients. There is still much to be examined to determine the extent to which burrows and other bioturbation structures affect the chemistry of surrounding pore water.

Objectives

In well drained tidal marshes, the presence of fiddler crab burrows has been widely hypothesized to act to increase aeration and flushing of the surrounding sediments and increase exchange with tidal waters and the atmosphere. The objective of this study was to determine the sphere of influence of individual fiddler crab burrows on surrounding pore water chemistry (cm^2 scale) in a salt marsh. To accomplish this, pore water was collected at distances up to 9 cm from the edge of the multiple crab burrows, and analyzed for ammonium, phosphate, and sulfide concentrations, redox potential, and salinity.

It was hypothesized that individual burrows would have an effect on the pore water variables analyzed, causing them to either increase or decrease with distance from the burrow (Figure 3.1). Increased flushing was hypothesized to decrease the concentration of ammonium, phosphate, and salinity close to the burrow; therefore, concentrations would increase with distance from the burrow. The effect of increased oxygen reduction and decreased sulfate reduction due to increased aeration was hypothesized to decrease the concentration of sulfide close to the burrow; therefore, concentrations would increase with distance from the burrow. The effect of increased aeration was also hypothesized to increase redox potential close to the burrow; therefore redox would decrease with distance from the burrow.

Near individual burrows, increased flushing and aeration within a burrow would cause:

Decreased	ammonium concentration phosphate concentration sulfide concentration salinity
Increased	redox potential

Increased distance from burrows would have the opposite effect.

Null Hypothesis: Individual burrows would have no effect.

Alternative Hypotheses: Individual burrows would have the opposite effect of those stated above.

Figure 3.1 Hypotheses for the effects of individual fiddler crab burrows on surrounding pore water chemistry.

Methods

The location for this study was a back barrier marsh on south Hog Island, Virginia (See Chapter 2 Methods and Figures 2.2 and 2.3). The study area was six meters south of Site 2 in the previous experiment (Figure 2.4). This area of the marsh was well drained and contained sparse numbers of *Spartina alterniflora* and *Salicornia* spp. stems. The elevation for this area was 0.18 meters above Mean Sea Level, which is approximately the same elevation as Block 6 in the previous experiment.

In early October 2002, four crab burrows (2 – 3 cm diameter) were randomly chosen within a 16 m^2 area of the salt marsh. Each burrow was the only one present in the vicinity; other burrows were at least 20 cm away. Four transects were established radially from each burrow in the four compass directions (Figure 3.2). Pore water was collected along each transect at distances of 3, 6, and 9 cm from the edge of each burrow. The pore water was collected at a depth of 10 cm using a sampling probe.

The pore water sampling probe design of Berg and McGlathery (2001) was modified in order to obtain pore water from silty sediments, which are finer than the sandy sediments for which the probe was designed. The original design consisted of a stainless steel tube (outside diameter 2.4 mm, inside diameter 1.8 mm) that was closed with silver solder at one end at which pore water could be sucked into the tube through four small inlet holes (d = 0.38 mm), which were evenly spaced in a ring around the circumference of the tube. This sampling probe was modified with the addition of 16 more inlet holes for a total of 20 holes arrayed in five aligned rings of 4 holes each (Figure 3.3). The 20 holes in the modified probe were much smaller than in the original

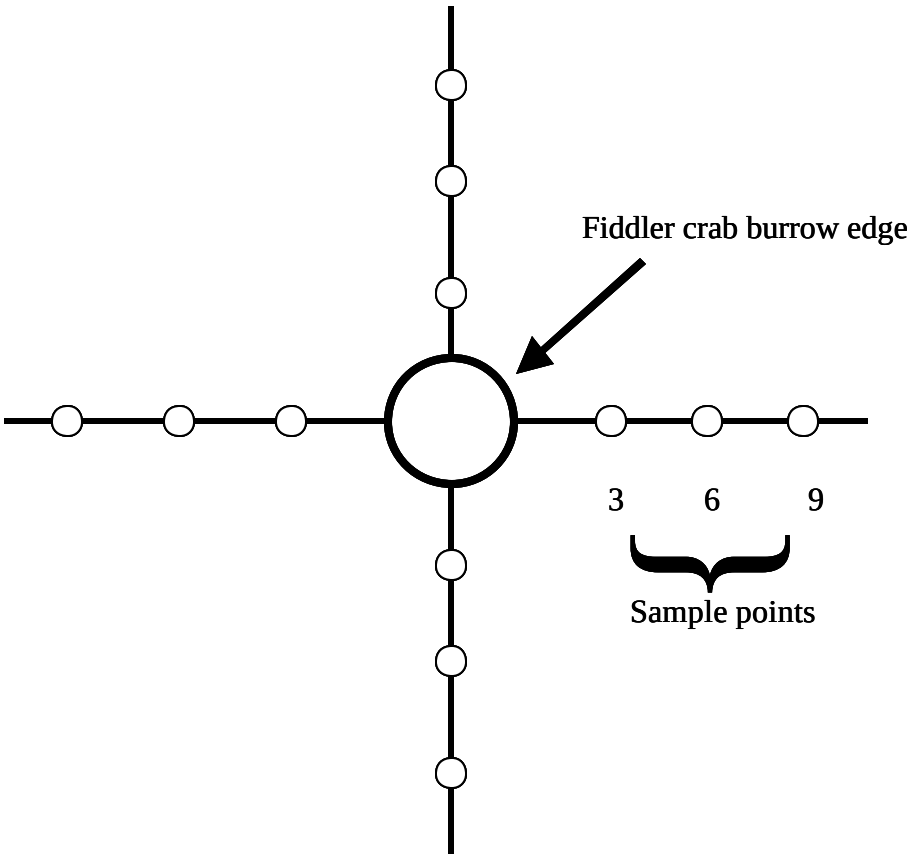

Figure 3.2. Transects and sample points surrounding a fiddler crab burrow, sample points are at distances of 3, 6, and 9 cm from the edge of the burrow.

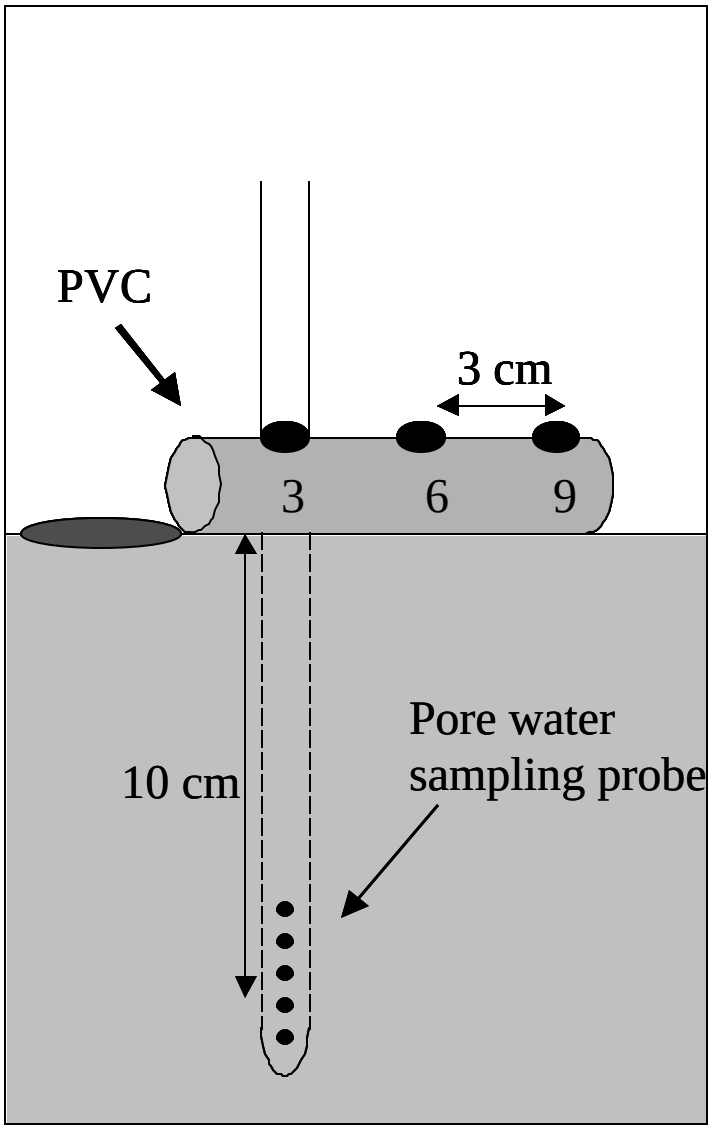

Figure 3.3. Diagram of pore water sampling probe positioned to collect water at 10 cm depth, detailing modifications made to original probe.

probe, so that the probe would not become clogged. The terminal ring of holes was 3 mm from the end of the probe. The end rings of holes were 8 mm apart resulting in a zone of intake of the same. This probe enables the collection of pore water samples that represent both a specific time and space (centimeter scale), allowing for a snapshot view of the pore water profile.

To collect pore water centered at a depth of 10 cm from the sediment surface, the sampling probe was inserted vertically into the sediment through the width of a piece of PVC pipe that lay on the sediment surface (Figure 3.3). Three guide holes (through which the probe could slide) had been drilled through the width of the PVC at 3, 6, and 9 cm from the end of the pipe. The end of the pipe was placed at the edge of the burrow to correctly measure the distance from the burrow edge and to guide the sampling probe vertically into the sediment. A small piece of Tygon tubing that fit tightly on the probe was used to mark the depth to which to insert the probe (Berg and McGlathery 2001).

To collect a pore water sample using the probe, the open end of the sampling probe was connected to a length of Tygon tubing that was connected to a stainless steel 3-way stopcock (Figure 3.4). The second stopcock valve was connected to tubing that led into a vacuum flask. A hand pump was also connected to the vacuum flask with tubing. A 1.0 micron syringe filter and a needle were attached to the third valve of the stopcock. To collect a pore water sample once the probe was in place, the stopcock was turned to connect the probe and the flask. The hand pump was used to obtain a vacuum in the flask. Once pore water began to flow into the flask, the position of the stopcock was switched, and the probe was connected to the needle. At this moment, the needle was

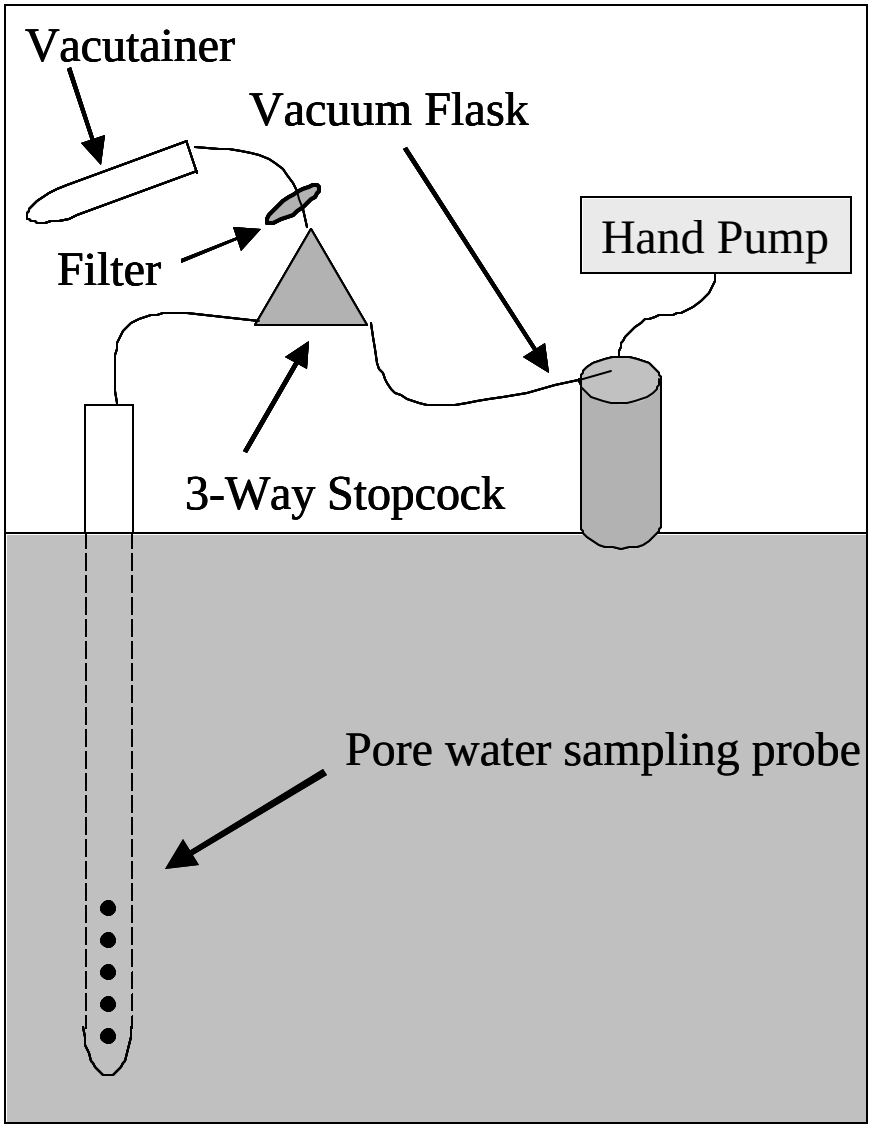

Figure 3.4. Diagram of vacuum apparatus attached to pore water sampling probe to used to collect samples.

used to puncture the stopper of a vacutainer used to store the sample, and pore water would flow into the vacutainer until the vacutainer was removed or the vacuum had been extinguished (Thomas 2003). All pore water samples were collected on a rising tide.

The samples collected were kept on ice until they were analyzed in the lab directly after returning from the field. The pore water was analyzed for ammonium, phosphate, and sulfide concentrations, redox potential, and salinity. Ammonium, phosphate, and sulfide concentrations were determined in the lab colorimetrically using a Shimadzu UV-1201 spectrophotometer. Ammonium concentrations were measured using the method of Parsons et al. (1984). Phosphate concentrations were measured using an ammonium molybdate method (Strickland and Parsons 1972). Sulfide concentrations were measured using the method described in Cline (1969) as modified by Otte and Morris (1994). Redox potential was determined by injecting the sample into an anaerobic chamber and measuring the oxidation-reduction potential with a Beckman (511290-AA) 255 waterproof Eh-pH probe. Salinity was measured using a Vista refractometer model A344ATC.

Bulk density and porosity were measured to determine if the pore space and porosity were the same near each of the burrows at a depth equivalent to the depth of the porewater samples collected with the probe. Three cores were taken near each burrow. Cores were 30 cm long with an inner diameter of 4.4 cm and were hammered into the sediment to a depth of 20 cm. Cores were removed from the ground when the sediment was saturated. The cores were filled with seawater to the top of the open end and stoppered to create suction so the core could be removed from the ground without losing

the sediment. Cores were kept on ice until returned to the lab. The sediment plugs obtained from the cores were greater than 10 cm long. Two 1 cm thick sediment slices were removed from the middle of each core at depths of 9-10 cm and 10-11 cm. The wet weight of each slice was measured, the slices were dried at 60° C until constant weight, and the slices were reweighed. Bulk density was calculated from the dry weight of the slices and their volume. Porosity (volumetric water content) was calculated from the difference between wet weight and dry weight divided by the volume of the slice. Sediment porosity was analyzed to determine the volume of sediment from which the pore water samples were extracted.

Data were analyzed using the Statistical Analysis System (SAS 1999-2001). Pore water was analyzed using a nested analysis in a General Linear Model (GLM). Burrow and transect were treated as random effects, and sample point was treated as a fixed effect; transect was nested within burrow, and sample point was a continuous variable. When significant differences were determined among sample points for a dependent variable, a TUKEY test was used to determine which sample points differed from each other. For the sample point means, least squares means and standard error were calculated by making sample point a class variable; these are the means and standard errors presented. The bulk density and porosity data were analyzed for differences among the four burrows using an analysis of variance (ANOVA) on the means from each burrow (n = 4). The six sediment samples obtained for each burrow area were used as replicates to represent each burrow.

Results

Sediments surrounding the four sampled fiddler crab burrows were similar to each other and similar to those of Block 6 in the previous experiment. Bulk density (mean of 1.785 g/cm^3 ± 0.010 (n = 4)) showed no significant difference among the four burrows. Likewise, porosity (mean of 0.454 ml/cm^3 ± 0.006 (n = 4)) showed no significant difference among the four burrows. The sediment was relatively uniform, as the spatial variance of bulk density and porosity among burrows was similar to the variation among cores surrounding individual burrows (Table 3.1).

Table 3.1 Bulk Density and Porosity (Means ± SE) by Burrow, and Among All Burrows.

Burrow Number	n	Bulk Density (g/cm^3) Mean ± SE	Porosity (ml/cm^3) Mean ± SE
1	6	1.816 ± 0.039	0.445 ± 0.027
2	6	1.794 ± 0.032	0.467 ± 0.012
3	6	1.723 ± 0.056	0.465 ± 0.016
4	6	1.806 ± 0.018	0.441 ± 0.014
All Burrows	24	1.784 ± 0.020	0.454 ± 0.008
Among Burrows	4	1.784 ± 0.010	0.454 ± 0.007

The volume of sediment from which the volume of pore water was obtained was 66.1 cm^3.

Pore water nutrients and sulfide concentrations and salinity did not show the coordinated decreases near the burrow that was expected; nor did redox potential show a concurrent inverse pattern. Instead, while sulfide concentration did decrease near the

burrow ammonium and phosphate concentrations increased and redox potential and salinity were unchanged.

Ammonium concentration significantly decreased with distance from burrows ($p = 0.0039$). The 3 cm and 9cm sample points were significantly different from each other and the 6 cm sample point was not significantly different from the other two (Figure 3.5a). Phosphate concentration did not yield a significant difference among sample points ($p = 0.0940$). There was a trend of decreasing concentration with distance from burrow (Figure 3.5b). Sulfide concentration significantly increased with distance from burrows ($p = 0.0197$). The 3 cm and 9cm sample points were significantly different from each other and the 6 cm sample point was not significantly different from the other two (Figure 3.5c). Redox potential did not yield a significant difference among sample points, and there was no evident trend with distance from burrows (Figure 3.5d). Salinity did not yield a significant difference among sample points, and there was almost no difference with distance from burrows (Figure 3.5e).

Discussion

This experiment has demonstrated that in salt marshes individual fiddler crab burrows can have a direct effect on the chemistry of the surrounding pore water. Ammonium, phosphate, and sulfide concentrations were affected more dramatically than redox potential and salinity. While the predicted increase of sulfide concentration with distance from the burrows did occur, the concurrent decreases in ammonium and phosphate were unexpected. The nutrient concentrations may have been higher near the

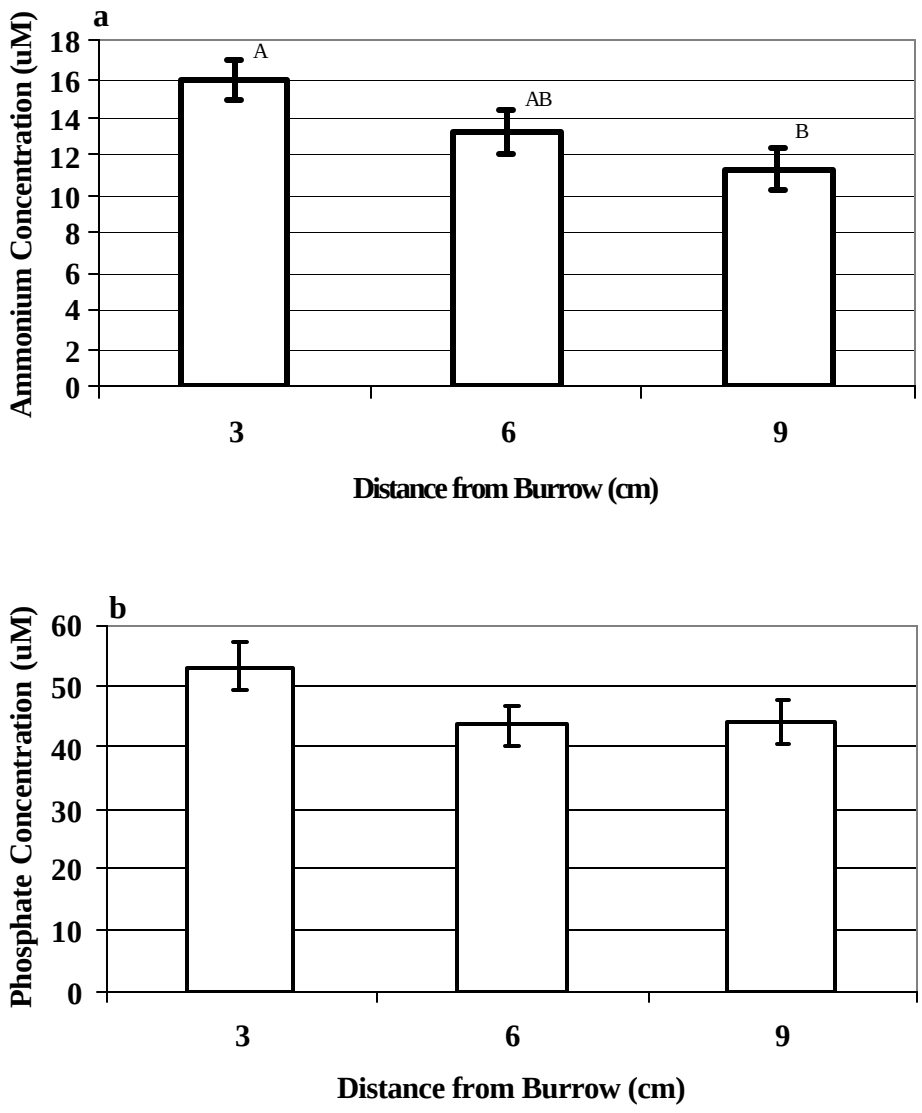

Figure 3.5. Pore water variables with distance from the edge of burrows (a) ammonium concentration, (b) phosphate concentration, (c) sulfide concentration, (d) redox potential, and (e) salinity. For (a) and (c), significant differences as determined by GLM are indicated by letters above the bars (mean ± 1 SE, n = 14).

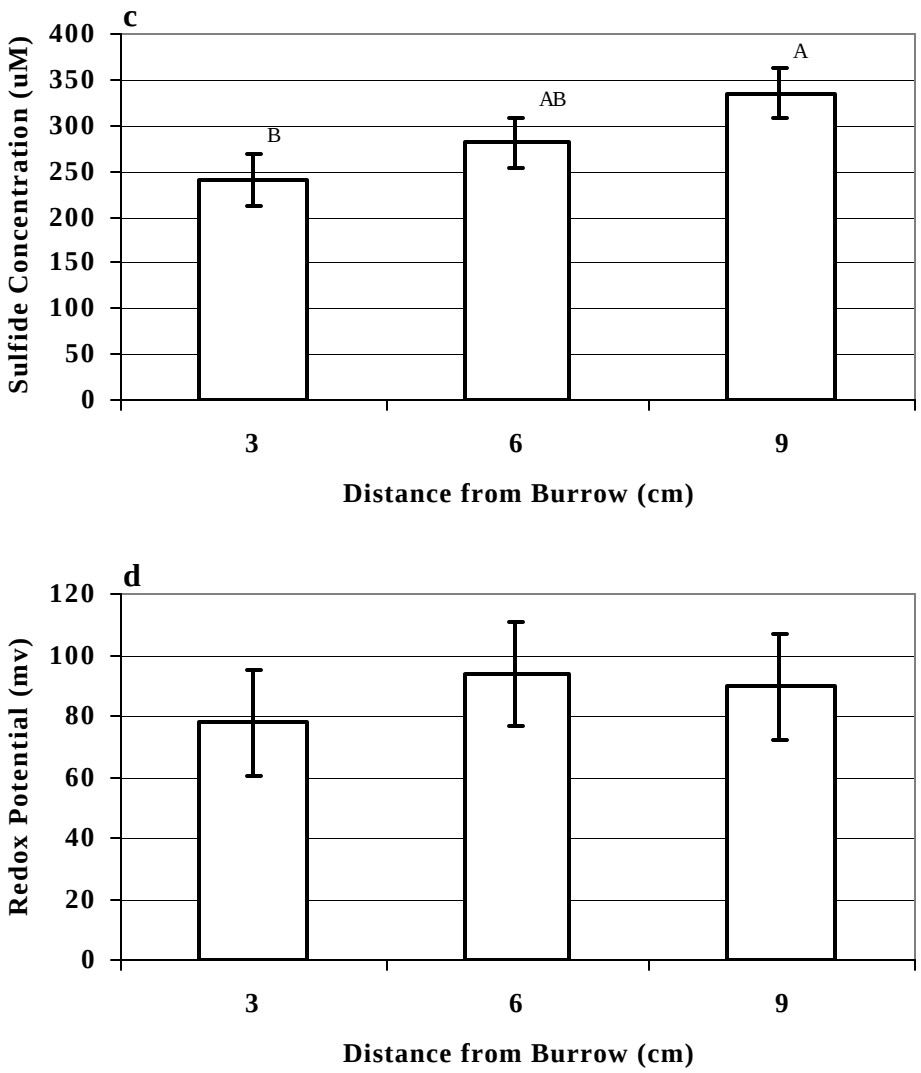

Figure 3.5 con'd. Pore water variables with distance from the edge of burrows (a) ammonium concentration, (b) phosphate concentration, (c) sulfide concentration, (d) redox potential, and (e) salinity. For (a) and (b), significant differences as determined by GLM are indicated by letters above the bars (mean ± 1 SE, n = 14).

Figure 3.5 con'd. Pore water variables with distance from the edge of burrows (a) ammonium concentration, (b) phosphate concentration, (c) sulfide concentration, (d) redox potential, and (e) salinity. For (a) and (b), significant differences as determined by GLM are indicated by letters above the bars (mean ± 1 SE, n = 14).

burrow and lower with distance away because organic matter from the sediment surface could have fallen into the burrows increasing mineralization within the burrows (Berner and Westrich 1985, Hines and Jones 1985). As the organic matter content of the sediments was relatively low (less than 2 % in nearby Block 6 (Ch. 2)) the addition of this new organic matter could have fueled an increase in reduction rates. These burrows were drained and exposed to the air during low tide, which would allow aerobic organic matter oxidation to occur at higher rates. Fiddler crab excretion could also account for the higher ammonium concentrations near the burrow; fecal matter could also be falling into the burrows from the sediment surface.

These marshes flood from the bottom up, therefore seawater with low ammonium concentration was not entering the sediment from above. Interstitial water from the water table and below would have flooded the marsh from underneath. Therefore, the water surrounding the bottom of the burrows where more mineralization would have occurred would have moved upward around the burrows as the tide rose. Flushing of ions away from the burrows was not a major mechanism as these marshes flood from underneath. The absence of any pronounced flushing, plus the low sulfide concentration near the burrow, indicates that the proportion of sulfate reduction relative to other pathways was lower and/or sulfide oxidation occurred simultaneously. Sulfate reduction did not appear to be dominant in this area; therefore, other pathways of reduction (oxygen, nitrate, and iron) may have been utilized. Ammonium is an end product of nitrate reduction; increased nitrate reduction could be the cause of the significantly higher ammonium concentration near the burrow. Phosphate had a higher concentration near the burrow,

but the difference with distance from the burrow was not significant. The higher phosphate near the burrow may have been solely due to increased organic matter oxidation; this effect may not have been great enough to yield a significant difference for phosphate concentration along the distance gradient. It was surprising that redox potential did not have a significant difference with distance from burrows because redox potential usually has a close inverse relationship to sulfide concentration (Koch et al. 1990). Redox potential was highly variable; it is possible that the method used for measuring redox potential may not have been sensitive enough to show changes in redox with distance from burrows.

As these measurements were collected *in situ*, it was not known for how long the crab burrows had been present, if they were still active, or their shape. Knowing the length of time the burrows had been present and whether they were currently inhabited might have helped explain why redox potential did not show a trend or significant difference with distance from the burrow. Future studies could be performed in mesocosms containing active fiddler crabs, which could be monitored more easily, and the length of time a burrow had been maintained could be observed. A time dimension could be incorporated to see how the pore water chemistry changed as a burrow was present for longer periods. Creation of three-dimensional pore water profiles composed of nutrient, metal, and other ion concentrations within the top 20 cm of the sediment throughout a 0.25 m^2 area surrounding each burrow would likely further illustrate the effects of individual burrows at different spatial scales (mm – cm). Conducting this study over a certain timescale would give another dimension to the data. The shapes of the

burrows could be determined after the pore water was collected and a spatial and temporal model of chemical changes in the sediment could be made. Examining the effects of fiddler crab burrows on difference spatial scales and through time would increase the understanding of how bioturbators affect the system that they inhabit.

Chapter 4. The Ability of Fiddler Crabs to Modify Salt Marsh Environments: Broader Implications

From these experiments, it is evident that fiddler crab burrows can have an important effect on pore water biogeochemistry within salt marsh sediments. Although pore water ammonium and phosphate concentrations did not show a significant difference with increased burrow density, both ions showed a trend with distance from individual fiddler crab burrows, and the trend for ammonium was significant. Pore water sulfide concentrations showed a significant increase with increased burrow density in the poorly drained marsh site, as well as a significant decrease close to individual burrows near the relatively well-drained marsh site. These results indicate that individual crab burrows can affect pore water ion concentrations within a 10 cm radius circle from the burrow center. Therefore, the influence of a single crab burrow can cover an area of 314 cm^2. For a 1 m^2 area of marsh to be influenced by the presence of similar crab burrows, only 32 evenly spaced burrows are necessary. As 32 burrows /m^2 is a low density for most marshes, it is quite possible that pore water within the burrow zone of the sediment (sediment surface to 10-30 cm depth) throughout the marsh is affected by the presence of fiddler crab burrows.

The effects of fiddler crab burrows in salt marshes are different depending on whether the marsh tends to remain in a drained or undrained state. Marshes in a poorly drained state, where the soil remains saturated throughout most of the month, have a water table at or near the sediment surface. Well-drained marshes include not only the low marsh where tall-form *Spartina alterniflora* grows, but also can include higher elevations of the high marsh where the water table remains well below the sediment surface during much of the month. In this study, sulfide concentration was higher and

less variable in the undrained marsh area (Blocks 1-4) compared to the well-drained marsh area (Blocks 5-8). The effect of increased burrow densities in the undrained marsh increased sulfide concentrations; similarly, decreased burrow densities resulted in decreased sulfide concentrations. While the same trend, or the opposite trend, may have been present in the well-drained marsh, the sulfide concentrations were so low that any difference was masked by the variability.

In addition, Blocks 5 and 6 seemed to be intermediate and switch from being well drained early in the season to poorly drained later in the season, which has confounding effects. It is reasonable that this change from a well-drained state to poorly drained state is due to a gradual seasonal increase in mean water level, leading to increased tidal inundation or simply a higher water table within the marsh resulting in more saturated sediments. Block 5 had a slightly lower elevation and seemed to switch earlier in the season than Block 6. Tidal data from NOAA collected in nearby Wachapreague, Virginia, support this as a possible mechanism; monthly mean water level (MWL, the average of the monthly mean high water level and mean low water level) is typically lower in the late spring/early summer and gradually rises through summer and into autumn.

The lack of difference in aboveground *Spartina alterniflora* production and stem density could be due to a change in belowground production. Because the aboveground production did not change with increased sulfide concentrations, and because increased sulfide concentration interferes with nutrient uptake by the roots, the plants would need to use their belowground stored energy reserves to be able to continue to support the

existing aboveground portion of the plant. The rhizomes of *S. alterniflora* contain stored starch that could be utilized under the high stress conditions of elevated sulfide concentrations to temporarily subsidize the aboveground plant tissue. Also, the plant could grow more near-surface roots as a means to acquire the necessary oxygen. Such an increase in root production might increase the overall belowground production and temporarily balance out the loss of mass in the rhizomes depending on how successful and efficiently the new roots could find and exploit the necessary soil resources. However, as continued elevated sulfide concentrations would eventually deplete the carbohydrate reserves, the energy needed to produce new roots might be too costly, and the plants may not be able to support their above or belowground portions, leading to a dieoff.

Within poorly drained interior areas of short-form *S. alterniflora* marshes, fiddler crabs may accelerate aging of the marsh as their burrowing increases sulfide concentrations. Instead of having a positive feedback where the presence of burrows increases *S. alterniflora* production, causing an increase in detritus formation, as is likely in well-drained marshes, it would appear that in poorly drained marshes, crab burrows have a negative feedback that can lead to less food for the crabs, but also to a dieoff of *S. alterniflora*. A dieoff of *S. alterniflora* in this poorly drained area would cause it to become an unvegetated mud flat, which would increase evaporation and possibly cause eventual colonization by other high marsh species.

The impact of fiddler crab burrows on marsh sediment chemistry and primary production differs greatly within poorly drained marshes compared to the well-drained

marshes that have received more attention. The changes in chemical pathways caused by the interactions of fiddler crab burrows with sediment in poorly drained salt marshes need further attention.

References

Berg, P. and K. J. McGlathery. 2001. A high-resolution pore water sampler for sandy sediments. Limnology and Oceanography 46 (1): 203-210.

Berner, R. A. 1977. Stoichiometric models for nutrient regeneration in anoxic sediments. Limnology and Oceanography 22 (5): 781-786.

Berner, R. A. and J. T. Westrich. 1985. Bioturbation and the early diagenesis of carbon and sulfur. American Journal of Science 285: 193-206.

Bertness, M. D. 1984. Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh. Ecology 65 (6): 1794-1807.

Bertness, M. D. 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. Ecology 66 (3): 1042-1055.

Bertness, M. D. and T. Miller. 1984. The distribution and dynamics of *Uca pugnax* (Smith) burrows in a New England salt marsh. Journal of Experimental Marine Biology and Ecology 83: 211-237.

Boulegue, J., C. J. Lord III, and T. M. Church. 1982. Sulfur speciation and associated trace metals (Fe, Cu) in the pore waters of Great Marsh, Delaware. Geochimica et Cosmochimica Acta 46 (3): 453-464.

Bradley, P. M. and J. T. Morris. 1990. Influence of oxygen and sulfide concentration on nitrogen uptake kinetics in *Spartina alterniflora*. Ecology 71 (1): 282-287.

Brower, J. E. and J. H. Zar. 1984. Field and Laboratory Methods for General Ecology, 2nd edition. Brown: Dubuque, Iowa.

Bull, D. C. and M. Taillefert. 2001. Seasonal and topographic variations in porewaters of a Southeastern USA salt marsh as revealed by voltammetric profiling. Geochemical Transactions 2001: 13.1-13.8.

Bull, D. C. and R. B. Williamson. 2001. Prediction of Principal Metal-Binding Solid Phases in Estuarine Sediments from Color Image Analysis. Environmental Science & Technology 35 (8): 1658-1662.

Cammen, L.M., E.D. Seneca, and L.M. Stroud. 1980. Energy flow through the fiddler crabs *Uca pugnax* and *U. minax* and the marsh periwinkle, Littorina irrorata in a North Carolina salt marsh. The American Midland Naturalist 103(2): 238-250.

Cline, J. D. 1969. Spectrophotometric determination of hydrogen sulfide in natural waters. Limnology and Oceanography 14: 454-456.

Currin, C. A., S. Y. Newell, and H. W. Paerl. 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. Marine Ecology Progress Series 121: 99-116.

Daehler, C. C. and D. R. Strong. 1995. Impact of high herbivore densities on introduced smooth cordgrass, Spartina alterniflora, invading San Francisco Bay, California. Estuaries 18 (2): 409-417.

Day, J. W., Jr., C. A. S. Hall, W. M. Kemp, and A. Yanez-Arancibia. 1989. Estuarine Ecology. Wiley: New York.

Fenchel, T., G. M. King, and T. H. Blackburn. 1998. Bacterial Biogeochemistry: The Ecophysiology of Mineral Cycling. Academic Press: San Diego.

Genoni, G. P. 1985. Food limitation in salt marsh fiddler crabs *Uca rapax* (Smith) (Decapoda: Ocypodidae). Journal of Experimental Marine Biology and Ecology 87: 97-110.

Genoni, G. P. 1991. Increased burrowing by fiddler crabs *Uca rapax* (Smith) (Decapoda: Ocypodidae) in response to low food supply. Journal of Experimental Marine Biology and Ecology 147: 267-285.

Giblin, A. E. and R. W. Howarth. 1984. Porewater evidence for a dynamic sedimentary iron cycle in salt marshes. Limnology and Oceanography 29 (1): 47-63.

Harvey, J. W. and W. K. Nuttle. 1995. Fluxes of water and solute in a coastal wetland sediment. 2. Effect of macropores on solute exchange with surface water. Journal of Hydrology 164 (1-4): 109-125.

Harvey, J.W., R. M. Chambers, and J. R. Hoelscher. 1995. Preferential flow and segregation of porewater solutes in wetland sediment. Estuaries 18 (4): 568-578.

Heck, K. L. and J. F. Valentine. 1995. Sea urchin herb ivory: Evidence for long-lasting effects in subtropical seagrass meadows. Journal of Experimental Marine Biology and Ecology 189: 205-217.

Hines, M. E. and G. E. Jones. 1985. Microbial biogeochemistry and bioturbation in the sediments of Great Bay, New Hampshire. Estuarine Coastal Shelf Science 20: 729-742.

Howes, B.L., R. W. Howarth, J. M. Teal, and I. Valiela. 1981. Oxidation-reduction potentials in a salt marsh: Spatial patterns and interactions with primary production. Limnology and Oceanography 26 (2): 350-360.

Howarth, R. W. 1993. Microbial processes in saltmarsh sediments, pp 239-259. In: T. E. Ford (ed.), Aquatic Microbiology: An Ecological Approach. Blackwell Scientific: Oxford.

Howarth, R. W. and J. M. Teal. 1979. Sulfate reduction in a New England salt marsh. Limnology and Oceanography 24 (6): 999-1013.

Hughes, C. E., P. Binning, and G. R. Willgoose. 1998. Characterization of the hydrology of an estuarine wetland. Journal of Hydrology 211: 34-49.

Huettel, M., W. Ziebis, S. Forster, and G. W. Luther, III. 1998. Advective transport affecting metal and nutrient distributions and interfacial fluxes in permeable sediments. Geochimica et Cosmochimica Acta 62 (4): 613-631.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69 (3): 373-386.

Katz, L. C. 1980. Effects of burrowing by the fiddler crab, *Uca pugnax* (Smith). Estuarine and Coastal Science 11: 233-237.

Koch, M. S. and I. A. Mendelssohn. 1989. Sulphide as a soil phytotoxin: Differential responses in two marsh species. Journal of Ecology 77 (2): 565-578.

Koch, M. S., I. A. Mendelssohn, and K. L. McKee. 1990. Mechanism for the hydrogen sulfide-induced growth limitation in wetland macrophytes. Limnology and Oceanography 35 (2): 399-408.

Koretsky, C. M., C. M. Moore, K. L. Lowe, C. Meile, T. J. Dichristina, and P. van Cappellen. 2003. Seasonal oscillation of microbial iron and sulfate reduction in saltmarsh sediments (Sapelo Island, GA, USA). Biogeochemistry 64 (2): 179-203.

Krebs, C. T. and I. Valiela. 1978. Effects of experimentally applied chlorinated hydrocarbons on the biomass of the fiddler crab, *Uca pugnax* (Smith). Estuarine and Coastal Marine Science 6: 375-386.

Krekeler, D., A. Teske, and H. Cypionka. 1998. Strategies of sulfate-reducing bacteria to escape oxygen stress in a cyanobacterial mat. FEMS Microbiology Ecology 25 (2): 89-96.

Lord, C. J., III and T. M. Church. 1983. The geochemistry of salt marshes: Sedimentary ion diffusion, sulfate reduction, and pyritization. Geochimica et Cosmochimica Acta 47: 1381-1391.

Luther, G.W., III, P. J. Brendel, B. L. Lewis, B. Sundby, L. Lefrancois, N. Silverberg, and D. B. Nuzzio. 1998. Simultaneous measurement of O_2, Mn, Fe, I^-, and S^{2-} in marine pore waters with a solid-state voltammetric microelectrode. Limnology and Oceanography 43 (2): 325-333.

Marschall, C., P. Frenzel, and H. Cypionka. 1993. Influence of oxygen on sulfate reduction and growth of sulfate-reducing bacteria. Archives of Microbiology 159 (2): 168-173.

Mendelssohn, I. A. and K. L. McKee. 1988. *Spartina alterniflora* die-back in Louisiana: Time-course investigation of soil waterlogging effects. Journal of Ecology 76 (2): 509-521.

Mendelssohn, I. A., K. L. McKee, and W. H. Patrick, Jr. 1981. Oxygen deficiency in *Spartina alterniflora* roots: Metabolic adaptation to anoxia. Science 214: 439-441.

Mitsch, W. and J. Gosselink. 1993. Wetlands. Van Nostrand Reinhold: New York.

Montague, C. L. 1980. A natural history of temperate western Atlantic fiddler crabs (Genus *Uca*) with reference to their impact on the salt marsh. Contributions in Marine Science, University of Texas 23: 25-55.

Montague, C. L. 1982. The influence of fiddler crab burrows and burrowing on metabolic processes in salt marsh sediments, pp 283-301. In: V. S. Kennedy (ed.), Estuarine Comparisons. Academic Press: New York.

Morris, J. and B. Haskin. 1990. A 5-year record of aerial primary production and stand characteristics of *Spartina alterniflora*. Ecology 71(6): 2209-2217.

Nielsen, O. I., E. Kristensen, and D. J. Macintosh. 2003. Impact of fiddler crabs (*Uca* spp.) on rates and pathways of benthic mineralization in deposited mangrove shrimp pond waste. Journal of Experimental Marine Biology and Ecology 289 (1): 59-81.

Nomann, B. E. and S. C. Pennings. 1998. Fiddler crab-vegetation interactions in hypersaline habitats. Journal of Experimental Marine Biology and Ecology 225: 53-68.

Otte, M. L. and J. T. Morris. 1994. Dimethylsulphoniopropionate (DMSP) in *Spartina alterniflora* Loisel. Aquatic Botany 48 (3-4): 239-259.

Parsons, T. R., Y. Maita, and C. M. Lalli. 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. Pergamon Press: Oxford.

Peterson, B. J. and K. L. Heck, Jr. 1999. The potential for suspension feeding bivalves to increase seagrass productivity. Journal of Experimental Marine Biology and Ecology 240: 37-52.

SAS Institute, Inc. 1999-2001. SAS User's Guide. SAS Institute, Inc.: Cary, NC.

Schubauer, J. P. and C. S. Hopkinson. 1984. Above- and belowground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. Limnology and Oceanography 29 (5): 1052-1065.

Shinn, E. 1968. Burrowing in recent lime sediments of Florida and the Bahamas. Journal of Paleontology 42(4): 879-894.

Shuttleworth, S.M., W. Davison, and J. Hamilton-Taylor. 1999. Two-dimensional and fine structure in the concentrations of iron and manganese in sediment pore-waters. Environmental Science & Technology 33 (23): 4169-4175.

Sigalevich, P., E. Meshorer, Y. Helman, and Y. Cohen. 2000. Transition from anaerobic to aerobic growth conditions for the sulfate-reducing bacterium *Desulfovibrio oxyclinae* results in flocculation. Applied and Environmental Microbiology 66 (11): 5005-5012.

Silliman, B. R., and J. C. Zieman. 2001. Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. Ecology 82 (10): 2830-2845.

Strickland, J. D. H. and T. R. Parsons. 1972. A Practical Handbook of Seawater Analysis. Fisheries Research Board of Canada: Ottawa.

Thomas, C. R. 2003. Salt marsh biogeochemistry and sediment organic matter accumulation. Ph.D. dissertation, University of Virginia, Charlottesville.

Valiela, I. and J. M. Teal. 1974. Nutrient limitation in salt marsh vegetation, pp. 547-563. In: R. J. Reimold and W. H. Queen (eds.), Ecology of Halophytes. Academic Press: New York.

Valiela, I., J. M. Teal, and N. Y. Persson. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: Belowground biomass. Limnology and Oceanography 21 (2): 245-252.

Valiela, I, J. M. Teal, and W. G. Deuser. 1978. The nature of growth forms in the salt marsh grass *Spartina alterniflora*. The American Naturalist 112 (985): 461-470.

Walsh. J. P. 1998. Low marsh succession along an overwash salt marsh chronosequence. Ph.D. dissertation, University of Virginia, Charlottesville.

Westrich, J. T. and R. A. Berner. 1984. The role of sedimentary organic matter in bacterial sulfate reduction: The G model tested. Limnology and Oceanography 29 (2): 236-249.