Physical and biological controls on sediment and nutrient fluxes in a temperate lagoon

Sarah Elizabeth Lawson
Decatur, GA

B.A., Eckerd College, 2000
M.S., University of Virginia, 2004

A Dissertation presented to the Graduate Faculty
of the University of Virginia in Candidacy for the Degree of
Doctor of Philosophy

Department of Environmental Sciences

University of Virginia
May, 2008

Peter

Abstract

The lack of riverine inflow and shallow depths in coastal lagoons make the fluxes of nutrients and sediment across the sediment-water interface important controls on primary productivity in these systems. However, the physical-biological coupling that controls these fluxes is not fully understood. Experiments using a Gust microcosm were conducted on samples from Hog Island Bay, a shallow lagoon on the Delmarva Peninsula to determine the physical and biological controls on sediment and nutrient fluxes. Two of the dominant benthic primary producers, seagrass and macroalgae, have traditionally been considered sediment stabilizers. However, at low densities, these primary producers can increase sediment suspension by as much as 97% through flow diversion around isolated shoots or abrasion of the bed by saltating macroalgae. This increased sediment suspension during forcing events may make developing seagrass beds particularly susceptible to light limitation. These primary producers also affect erodibility of the sediment bed, with increased measured erodibility in the summer months attributed to trapping of fine material by dense macroalgal mats, as well as bioturbation by benthic fauna. While these benthic primary producers affect the physical process of sediment suspension, their growth and productivity may be affected by the interaction of physical forcing and nutrient flux. During forcing events, two mechanisms, desorption and porewater advection balanced by biological uptake, create ammonium fluxes an order of magnitude greater than those measured under low-flow conditions. However, these fluxes are likely not sustained and decrease quickly (on the order of hours). This pulsed increase in nutrient availability may create a competitive advantage for fast-growing species capable of surge uptake of nutrients, such as macroalgae and phytoplankton. In this sense, the timing of nutrient fluxes may be as important as the cumulative magnitude.

Table of contents

List of figures

List of tables

Acknowledgements

This work would not have been possible without the support, patience and inspiration of many people. I am indebted to three great field assistants Rachel Hippert, Rachel Baker, and Jason Turner for invaluable and cheerful lab and field help. The National Science Foundation, through the Virginia Coast Reserve- Long Term Ecological Research site provided funding for many summer days on the water and on the lab. The staff of the VCR-LTER, past and present, was extraordinary in helping access field sites and providing much-needed humor on early morning sampling days. The McG lab group was a constant source of inspiration for all of their dedication to scientific understanding and scientific camaraderie. My committee, especially my advisors, has taught and will continue to teach me far more than I realize. I will always be grateful for their advice, patience and support. Finally, I would like to thank my family, the one I was born in to and all the family I have acquired over the years, for everything.

Chapter 1: Introduction

Background

Understanding the controls on primary productivity in coastal lagoons requires adequate characterization of material fluxes, particularly sediment and nutrients, across the sediment-water interface. While nutrients and suspended sediments in deep, river-fed estuaries are often controlled by freshwater inflow, coastal lagoons are typically characterized by a lack of riverine input (Boynton et al 1996). In addition, coastal lagoons have shallow depths (2-5 m) leading to high sediment surface area to water volume ratios (Boynton et al 1996), and as a result, benthic-pelagic coupling is an important control on nutrient and sediment dynamics in these shallow systems (Tyler et al 2003, Lawson et al 2007). Coastal lagoons are subject to the same stresses (increased nutrient loads, loss of seagrass) as deeper estuaries, controls on water column nutrient availability and suspended sediment in the absence of riverine inflow have received less attention.

Lagoons occur on all continents except Antarctica and are especially common on the eastern coast of the United States. Globally, these shallow systems account for about 13% of the world's coastline (Cromwell 1973, Kjerfve 1989). Because most of the sediment is in the photic zone, these systems are characterized by high benthic productivity, and relatively low pelagic productivity (Sand-Jensen and Borum 1991, McGlathery et al 2001). Perennial seagrasses, benthic microalgae and benthic macroalgae are the dominant primary producers in shallow, low nutrient systems because they have lower nutrient requirements than phytoplankton and better access to sediment nutrient pools (Sand-Jensen and Borum 1991). Unlike deeper estuaries, which typically respond to increased nutrient loading with an increase in pelagic productivity, shallow lagoons typically have increased growth of benthic macroalgae and epiphytes (Sand-Jensen and Borum 1991, Sfriso et al 1992, Duarte 1995). This increase in macroalgae can lead to shading and eventual decline of seagrass populations (Hauxwell et al 2001).

This shift from slow-growing, perennial seagrass to ephemeral macroalgae has important consequences for physical-biological coupling, particularly in relation to nutrient cycling and sediment transport. In their simplest forms, physical and biological processes in estuaries and lagoons are viewed separately (Fig. 1.1). However, recent research has shown that physical forcing affects nutrient cycling and benthic primary producers and fauna affect hydrodynamics and sediment transport. These processes will be modified by the type of primary producers and will affect the growth of primary producers.

Sediment suspension and erodibility can not be separated from the biological activity in the system. The role of macrophytes, particularly seagrass, in stabilizing sediment has long been recognized (e.g. Fonseca and Fisher 1986, Gambi et al 1990). Both benthic macroalgae and microalgae also stabilize sediment, though the mechanisms differ. Macroalgae stabilizes sediment through modification of hydrodynamics by deflecting flow around the macroalgal mats and decreasing shear stress at the sediment bed (Escartín and Aubrey 1995). Microalgae affect a bed's resistance to erosion by secreting extracellular polymeric substances (EPS) which can double sediment's resistance to erosion (de Brouwer et al 2000, Quaresma et al 2004). Benthic fauna can also affect sediment transport through bioturbation, ingestion of capping biofilms and modification of hydrodynamics by emergent features (Rowden et al 1998, Friedrichs et al 2000, Andersen 2001). Despite this extensive work on biotic effects on sediment suspension, the effects of low density populations of primary producers have not been studied. Because of the prominent role of sediment suspension in regulating light availability (Gallegos and Kenworthy 1996, Lawson et al 2007), a complete understanding of the controls on sediment suspension, including feedbacks with benthic primary producers, is necessary.

Nutrient cycling and transport also are significantly affected by physical forcing. However, most research on sediment-water column nutrient fluxes has been conducted in low-flow incubations that primarily capture the diffusive flux (e.g. Dollar et al 1991). Increased hydrodynamic activity increases the transport of nutrients between the sediment bed and water column through porewater advection and desorption (e.g. Huettel and Gust 1992, Morin and Morse 1999, Lawrence et al 2004). Porewater advection, the active pumping of porewater due to surface pressure differences, can increase the flux of porewater, and any associated nutrients, across the sediment-water interface to 7 times its normal value (Huettel and Gust 1992). Porewater advection also increases delivery of oxygen and organic material into the bed stimulating bacterial processes such as mineralization and nitrification (Forster et al 1996). Desorption from suspended particles can also significantly increase water column nutrient availability, with a 130 μM increase in NH_4^+ noted during a dredging event (Morin and Morse 1999). The effects of these hydrodynamically forced nutrient fluxes are non-trivial and can result in changes in ecosystem structure (Lawrence et al 2004).

The differences in life history and growth strategy between seagrass and macroalgae will affect the physical-biological coupling in coastal systems. Most notably, macroalgae has a "boom and bust" life cycle, depositing large quantities of organic matter to the sediment surface when the mat crashes. This organic matter can be quickly mineralized leading to a significant nutrient efflux from the sediment (Tyler et al 2001). Seagrasss and macroalgae also have different nutrient utilization strategies, with slower uptake and greater reliance on sediment nutrients for seagrass (Touchette and Burkolder 2000). Finally, though research has shown that both macroalgae and seagrass can stabilize sediment (e.g. Gambi et al 1990, Romano et al 2003) the comparative effects of these two types of primary producers and the effects of low-density populations are relatively unknown. Careful consideration of the effects of different primary producers and controls on nutrient and sediment transport will allow improved management of these systems and better prediction of ecosystem response to eutrophication.

This study was designed to examine the movement of sediment and nutrients across the sediment-water interface and the importance of physical and biological controls on this movement in a shallow coastal lagoon. We used a Gust erosion microcosm (Gust and Muller 1997) to expose sediment cores to controlled shear stresses representative of the flows in this system. Measurements were made over a growing season (mid-April to Mid-November) to reflect temporal variability in nutrient cycling and primary productivity. We also used controlled experiments on desorption and porewater advection, along with numerical modeling, to gain further insight into the controls on nutrient flux.

Site description

This study was conducted in the Virginia Coast Reserve- Long-Term Ecological Research site (VCR-LTER) on the eastern side of the Delmarva Peninsula (Fig. 1.2) The southern end of the Delmarva Peninsula is largely agricultural and has a string of shallow lagoons protected by barrier islands on the east side. The majority of the islands and much of the mainland marsh surrounding these lagoons are protected by the Nature Conservancy. Historically, the lagoons were dominated by *Zostera marina* until local extinction in the 1930's. Seagrass recolonization, both natural and anthropogenic, is on-going in the area.

Three sites (Creek, Shoal and Island) in the shallow subtidal of Hog Island Bay were chosen as the focus for this study (Fig. 1.1). These 3 sites represent a gradient from the fine-grained Creek site, to the relatively coarse-grained Island site. The sites also differ in primary productivity, with benthic microalgae dominant at the Creek and Island sites and large seasonal accumulations of macroalgae dominating primary productivity at the Shoal site. The Creek is relatively protected from wind activity and has low tide velocities, but the Shoal site has high wave exposure and the Island site has high current velocities (Lawson 2004).

Objectives

This study was designed to address four questions:

- How does the density of primary producers (seagrass and macroalgae) affect sediment and nutrient transport across the sediment-water interface?

- What is the relative importance of porewater advection and desorption across a range of fine to coarse-grained sediment at 3 sites in the lagoon?
- What controls sediment erodibility across a range of sites and seasons?
- How does nutrient flux from the sediment vary seasonally at the 3 sites?

Dissertation outline

The dissertation follows in four chapters, each prepared as a manuscript, and a concluding chapter. Chapter 2 addresses the influence of macroscopic benthic primary producers (seagrass and macroalgae) on sediment and nutrient fluxes across the sediment-water interface under controlled forcing conditions. Chapter 3 addresses the relative importance of 3 mechanisms of nutrient transport across the sediment-water interface: diffusion, porewater advection and desorption across a range of fine to coarse sediments and in the early and late growing season. Chapters 4 and 5 build together to examine seasonal variability and controls on the temporal and spatial variability in sediment erodibility (Chapter 4) and hydrodynamically-forced nutrient flux (Chapter 5). Both physical and biological controls on sediment erodibility and nutrient flux are considered. These chapters are followed by a concluding discussion of the interaction between physical and biological processes in controlling nutrient and sediment dynamics in shallow systems.

References

Andersen, TJ. 2001. Seasonal variation in erodibility of two temperate, microtidal mudflats. *Estuarine, coastal and shelf science*. 53(1):1-12.

Boynton, WR, JD Hagy, L Murray, C Stokes and W.M. Kemp. 1996. A comparative analysis of eutrophication patterns in a temperate coastal lagoon. *Estuaries*. 19(2B):408-421.

Cromwell, JE. 1973. Barrier coast distribution: a world-wide survey. In: *Barrier Islands*. M. L. Schwartz, (ed.), Dowden, Hutchinson & Ross:Stroudsburg, PA, pp.408.

de Brouwer, JFC and LJ Stahl. 2001. Short-term dynamics in microphytobenthos distribution and associated extracellualr carbohydrates in surface sediments of an intertidal mudflat. *Marine ecology progress series*. 218:33-44.

Dollar, SJ, SV Smith, SM Vink, S Obrebski and JT Hollibaugh. 1991. Annual cycle of benthic nutrient fluxes in Tomales Bay, California, and contribution of the benthoc to total ecosystem metabolism. *Marine ecology progress series*. 79(1-2):115-125.

Duarte, CM. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41**:**87-112.

Escartin J and DG Aubrey. 1995. Flow structure and dispersion within algal mats. *Estuarine coastal and shelf science*. 40(4):451-472.

Fonseca MS and JS Fisher. 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Marine ecology progress series*. 29: 15–22.

Forster, S, M Huettel and W Ziebis. 1996. Impact of boundary layer flow velocity on oxygen utilsation in coastal sediments. *Marine ecology progress series*. 143:173-185.

Friedrichs M, G Graf and B Springer. 2000. Skimming flow induced over a simulated polycheate tube lawn at low population densities. *Marine ecology progress series*. 192:219-228.

Gallegos, CL and WJ Kenworthy. 1996. Seagrass depth limits in the Indian River Lagoon (Florida, U.S.A.): Application of an optical water quality model. *Estuarine, coastal and shelf science* 42:267-288.

Gambi MC, ARM Nowell and PA Jumars. 1990. Flume observations on flow dynamics in *Zostera-marina* (eelgrass) bed. *Marine ecology progress series*. 61(1-2):159-169.

Gust, G and V Müller. 1997. Interfacial hydrodynamics and entrainment functions of currently used erosion devices. In: *Cohesive sediments*. Burt N, R Parker and J Watts (Eds). John Wiley and Sons. .

Hauxwell, J, J Cebrian, C Furlong and I Valiela. 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology*. 82(4):1007-1022.

Huettel, M and G Gust. 1992. Impact of bioroughness on interfacial solute exchange in permeable sands. *Marine ecology progress series*. 89(2-3):255-267.

Kjerfve, BJ. 1989. Estuarine geomorphology and physical oceanography. In: *Estuarine Ecology.* JW Day, CAS Hall, WM Kemp and AYanez-Arancibia (eds.). John Wiley & Sons:New York, pp. 47-78.

Lawrence, D, MJ Dagg, H Liu, SR Cummings, PB Ortner and C Kelble. 2004. Wind events and benthic-pelagic coupling in a shallow suptropical bay in Florida. *Marine ecology-progress series.* 266:1-13.

Lawson SE, PL Wiberg, KJ McGlathery and DC Fugate. 2007. Wind-driven sediment suspension controls light availability in a shallow coastal lagoon. *Estuaries and coasts.* 30(1):102-112.

McGlathery KJ, IC Anderson and AC Tyler. 2001. Magnitude and variability of benthic and pelagic metabolism in a temperate coastal lagoon. *Marine ecology progress series*. 216:1-15.

Morin, J and JW Morse. 1999. Ammonium release from resuspended sediments in the Laguna Madre estuary. *Marine chemistry*. 65(1-2):97-110.

Quaresma, VD, CL Amos and M Flindt. 2004. The influences of biological activity and consolidation time on laboratory cohesive beds. *Journal of sedimentary research*. 74(2):184-190

Romano, C, J Widdows, MD Brinsley and FJ Staff. 2003. Impact of *Enteromorpha intestinalis* mats on near-bed currents and sediment dynamics: flume studies. *Marine ecology progress series*. 256:63-74.

Rowden, AA, CF Jago and SE Jones. 1998. Influence of benthic macrofauna on the geotechnical and geophysical properties of surficial sediment, North Sea. *Continental shelf research*. 18(11):1347-1363.

Sand-Jensen, K and J Borum. 1991. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwater and estuaries. *Aquatic Botany.* 41:137-175.

Sfriso, A, B Pavone, A Marcomini and AA Orio. 1992. Macroalgae, nutrient Cycles, and pollutants in the Lagoon of Venice. *Estuaries.* 15(4)**:**517-528.

Touchette, BW and JM Burkholder. 2000. Review of nitrogen and phosphorus metabolism in seagrass. *Journal of experimental marine biology and ecology*. 250:133-167.

Tyler AC, KJ McGlathery and IC Anderson. 2001. Macroalgal mediation of dissolved organic nitrogen fluxes in a temperate coastal lagoon. *Estuarine coastal and shelf science*. 53:155-168.

Figures

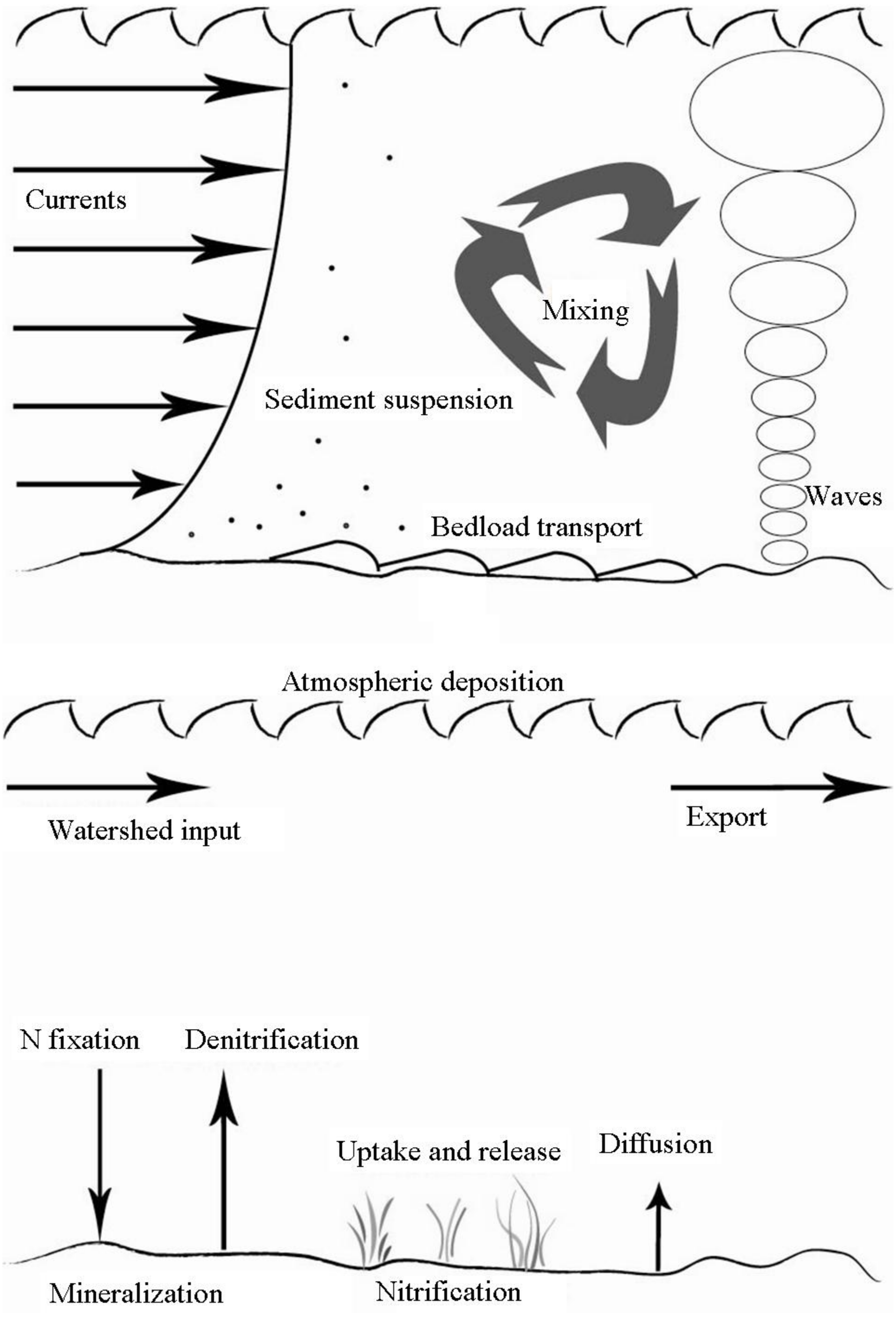

Figure 1.1. Diagrams of physical (top) and biological (bottom) processes in coastal systems. These processes are often considered separately, but are closely linked by processes such as porewater advection.

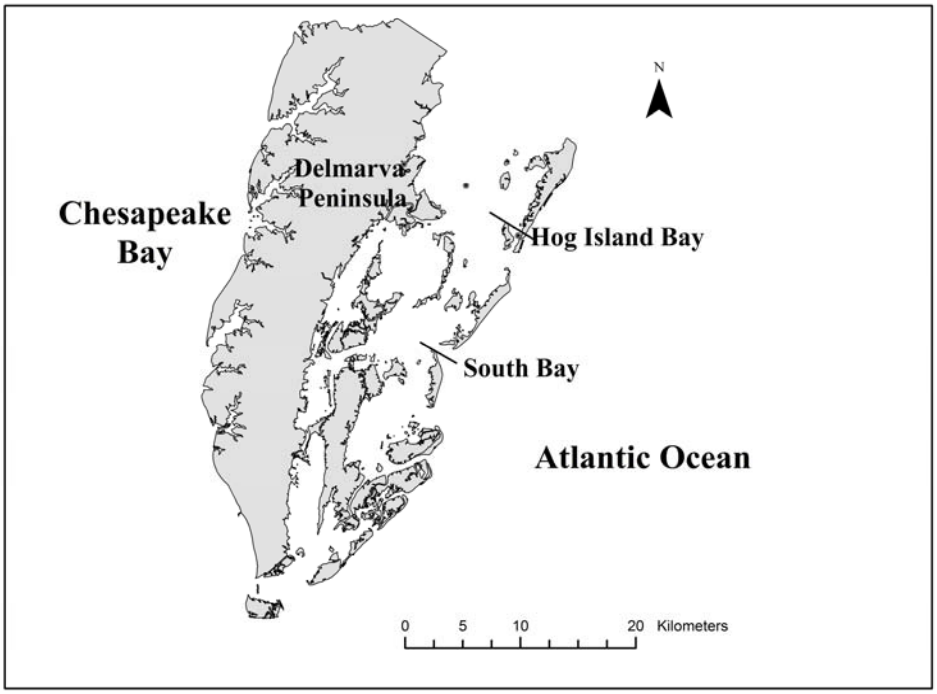

Figure 1.2. Study site in Northampton County, VA on the Delmarva Peninsula. This study was conducted primarily in Hog Island Bay, with the work in Chapter 2 conducted in neighboring South Bay. Both are shallow back-barrier lagoons mostly surrounded by *Spartina alterniflora* marshes.

Chapter 2: Effects of low-density seagrass and macroalgae on sediment suspension and nutrient flux

Abstract

Extensive research on fully-developed, dense seagrass meadows and high biomass populations of macroalgae has characterized these benthic primary producers as sediment stabilizers. However, low density/biomass populations are common in coastal systems and likely have a different effect on the hydrodynamic processes that influence sediment and nutrient fluxes. We used indoor microcosms consisting of core tubes containing bare sediment, sediment and seagrass, or sediment and macroalgae that were exposed to controlled shear stresses to determine the effects of benthic primary producers on sediment and nutrient fluxes during a forcing event. Low densities of seagrass and macroalgae increased sediment suspension by as much as 97%, while high density macroalgae decreased sediment suspension by 30%. If phosphate is used to represent nutrient flux with minimal effects of uptake, the physical effects of low-density macroalgae also increased nutrient efflux from the sediment. For both ammonium and nitrate, however, the uptake by the macroalgae masked this effect and resulted in an influx to the sediment. The transition from destabilizing to stabilizing effects of primary producers is density-dependent and likely requires the generation of skimming flow. Sediment destabilization by low-density seagrass meadows may make newly established seagrass meadows especially vulnerable to light limitation during wind events.

Introduction

Benthic primary producers play a critical role in regulating benthic-pelagic coupling in coastal ecosystems through modification of near-bed hydrodynamics. Extensive research has shown that the seagrass canopy reduces current velocity (Peterson et al 2004) and dampens wave energy (Fonseca and Cahalan 1992), leading to decreased sediment resuspension and increased particle deposition (Heiss et al 2000, Peterson et al 2004). The seagrass root structure also helps to stabilize sediments (Ginsburg and Lowenstam 1958, Greve et al 2005). Dense macroalgal mats may have similar stabilizing effects, as studies have shown that thick mats decrease sediment suspension (Sfriso and Marcomini 1997, Romano et al 2003) and shear flow at the sediment surface (Escartín and Aubrey 1995). Compared to these high-density populations, we know little about the effects of lower densities of benthic macrophytes on sediment and nutrient fluxes during forcing events, even though it is common for seagrasses and macroalgae to occur in low densities or to be patchy in distribution. For example, multiple stressors including sediment and nutrient runoff, algal blooms, and physical disturbances from storms, boat traffic and some fishing practices can cause thinning and/or patchiness in seagrass populations in addition to wholesale losses of seagrass habitat (Duarte 2002, Orth et al 2006). Macroalgae may also have patchy distributions, largely dependent on available substratum for attachment (Thomsen et al 2006).

At low density, the effect of benthic macrophytes on hydrodynamics and the resulting sediment/nutrient fluxes may be different than at high density. Dense seagrass meadows typically displace velocity vertically, which results in low current speeds and shear stress within the canopy, and an area of high shear stress and velocity at the top of the canopy (Gambi et al 1990). Thick macroalgal mats (equivalent to 3.5 to 6.2 kg m^{-2}) also behave similarly, and can deflect 90% of the flow over the mat, with only 10% of the flow traveling through the mat (Escartín and Aubrey 1995). Research on other types of emergent features in coastal systems, such as polycheate worm tubes, has shown that low density stands typically displace velocity horizontally rather than vertically, leading to increased erosion around the features (Friedrichs et al. 2000). Eckman et al (1981) found that erosion around tubeworms increased for densities that are considered to be relatively low (<7,000 individuals m^{-2}). Similarly, Widdows et al (2002) found that scour around mussels in beds with 25% and 50% coverage resulted in increased sediment erosion, while beds with 100% cover stabilized sediment. When flow is diverted around rather than over isolated, low-density features, the total cross-sectional area of the flow is decreased, and the higher velocities that result can cause areas of scour to develop around the features. This deflection of flow also creates areas of increased turbulence further increasing erosion during forcing events.

Modification of the near-bed flow by benthic macrophytes is also likely to influence sediment-water column nutrient fluxes. Field and modeling studies have shown that increased hydrodynamic activity and sediment suspension influenced nutrient flux in areas such as Lake Okeechobee, FL (Chen and Sheng 2003, Chen and Sheng 2005), the Satilla River Estuary, GA (Zheng et al 2004), and the Mediterranean Shelf (Gremare et al 2003). Benthic primary producers are well known to indirectly affect nutrient cycling rates, including effects on nitrogen fixation, nitrification, and nitrification/denitrification (e.g. Viaroli et al 1996, Hansen et al 2000, McGlathery et al 2004). These processes alter the availability and form of nutrients in the sediment and water column, which in turn affects their transport across the sediment-water interface. Benthic primary producers also directly affect nutrient flux by taking up nutrients mineralized in the sediment, which effectively decouples sediment nutrient cycling from water column productivity (Thybo-Christensen et al 1993, Sundback et al 2000, McGlathery et al 2004, McGlathery et al 2007). The total impact of benthic primary producers on the flux of nutrients between the sediment and water column is the result of both the physical modification and the biotic influences, yet these have rarely been studied in tandem.

This study was designed to compare the effects of low-density populations of two functional groups of primary producers, macroalgae and seagrass, on sediment suspension and nutrient flux under hydrodynamic conditions similar to field conditions during a wind or other forcing event. The invasive bloom-forming macroalga, *Gracilaria vermiculophylla*, and the seagrass, *Zostera marina*, were used as test species. To mimic natural variation in the biomass of the bloom-forming macroalgae, we categorized 3 macroalgal treatments to represent low, medium and high biomass accumulations. Replicate seagrass cores reflected natural shoot density in the field. The laboratory experiments were conducted using a Gust erosion microcosm (Gust and Müller 1997, microcosm, hereafter, Fig. 2.1), to mimic natural hydrodynamic conditions. We asked 2 questions: (1) During a forcing event, how do seagrass and macroalgae affect sediment suspension at different biomass levels? (2) Is the effect on sediment suspension also reflected in the nutrient flux? We then developed a conceptual model to describe the ecosystem-level consequences of sediment and nutrient fluxes in response to hydrodynamic events in low-density macrophyte populations.

Methods

Study site

This study was conducted with samples collected from a restored *Z. marina* meadow in South Bay, VA, a coastal lagoon on the eastern side of the Delmarva Peninsula, at the Virginia Coast Reserve Long Term Ecological Research site (VCR-LTER, Fig. 2.2) from June 18 to 22, 2007. South Bay is bordered by *Spartina alterniflora* (smooth cordgrass) marshes on the mainland and barrier island boundaries. It is a shallow coastal lagoon (average depth < 1 m at MLW) and has a semi-diurnal tidal range of ~ 1.5 m. The watershed of approximately 6000 ha is primarily agricultural (72% of total land use), and there is no significant river input, so groundwater is the dominant source of freshwater to the system. The lagoon, like neighboring lagoons to the north and south, was dominated historically by *Z. marina* until the 1930's, when a large hurricane decimated populations already weakened by the 'wasting disease', the marine slime mold *Labyrinthula zosterae*. Seagrass has begun recolonizing the coastal bays, both through natural recolonization and large-scale restoration efforts (Orth et al 2006). Ongoing restoration efforts began in South Bay in 2001 by seeding large areas (0.5 – 1.0 acres) that developed into sparse meadows by 2003 (Orth et al 2006). Although few data are available on macroalgal biomass in South Bay, in a neighboring lagoon (Hog Island Bay), seasonal accumulations of macroalgae reach an average summer biomass of 54 g DW m^{-2}, with the coarsely-branched invasive macroalga, *G. vermiculophylla*, accounting for 74% of the total biomass by weight (Thomsen et al 2006). This value was used to define realistic biomass levels for the macroalgae treatments in the microcosm experiments. Five plots with patchy distributions of seagrass were selected randomly within the South Bay seagrass meadows for this study. Each plot was sampled on 1 day and all treatments were tested at each site (except no medium algae treatment was done on Day 3 due to the loss of 1 sediment core). The study was designed as a randomized complete block design, blocked by day and plot.

Site characterization

Samples were taken at each plot to characterize porewater nutrients, sediment grain size, exchangeable ammonium (NH_4^+) and benthic chlorophyll. Five replicate samples for grain size and NH_4^+ were taken to 2 cm depth with a 60 ml syringe and 5 replicate samples for benthic chlorophyll were taken to 1 cm depth with a 5 ml syringe. Three replicate polycarbonate cores with an internal diameter of 8 cm and a height of 23 cm were collected for laboratory sampling of porewater. All samples were kept at 4 °C during transport to the lab. Samples for benthic chlorophyll and extractable NH_4^+ were immediately frozen; grain size samples were maintained at 4 °C until analysis. Porewater samples were extracted from the sediment cores at 2 cm depth intervals to 10 cm depth using a stainless steel probe (Berg and McGlathery 2001) and were immediately filtered (0.45 μm) and frozen. Exchangeable NH_4^+ was extracted for 1 h with an equal volume of 1N KCl solution. Porewater samples (for NH_4^+, phosphate (PO_4^{3-}), and nitrate+nitrite (NO_3^-)) and exchangeable NH_4^+ samples were analyzed on a Lachat QuickChem 8500 using standard methods (Hach Co., Loveland, CO). Benthic chlorophyll was determined spectrophotometrically following extraction with a 45% acetone, 45% methanol, 10% deionized water solution using the equations of Lorenzen (1967). Sediment grain size was analyzed as 1 bulk sample per plot, from 5 pooled samples, using a combination of wet sieving for sands and analysis on a Sedigraph 5100 particle size analyzer for silt and clay.

Shear stress experiments

Sample collection, storage and preparation

Sediment samples for the experiments were taken by hand on a falling tide, within 1 h of predicted low tide, using polycarbonate core tubes with an internal diameter of 10.8 cm and a height of 22.5 cm, with a 10 cm water column preserved. Core tubes were sealed using rubber plumbing end caps and kept in the dark at 4 °C for transport back to the lab. Ambient water was collected in 20 l carboys for use as the replacement water during the experiments and for core storage until analysis. Upon arrival at the lab, within 1 h of core collection, the cores were submerged in a cooler of ambient water oxygenated by an aquarium bubbler and maintained in low light at ambient temperatures. Macroalgae were collected in South Bay and maintained in a container of ambient water at 4 °C for transport to the lab, then kept in oxygenated ambient water until use. Immediately prior to the experiment, the overlying water in each sediment core was gently replaced with the same water used as the replacement water during the experiment.

Four bare sediment cores and 1 core with seagrass were taken at each plot on a single day. Analysis order was assigned randomly and bare sediment cores were assigned randomly to 1 of 4 treatments (control, low macroalgae, medium macroalgae, and high macroalgae). Macroalgae treatments were defined as 2 (low), 4 (medium), or 6 (high) g WW of macroalgae, standardized by blotting excess water with a paper towel. Macroalgae were added to a bare sediment core immediately before the start of the experiment. At the end of the experiment, the macroalgae were collected and dried at 60 ºC to a constant weight to determine DW biomass. Height limitations of the microcosm required seagrass to be trimmed to a maximum height of 8 cm. The potential artifact from trimming the seagrass is considered in the discussion section. The trimmed seagrass was dried at 60 ºC and weighed. At the end of the experiment, all remaining seagrass aboveground biomass was cut and also dried and weighed so that total biomass and biomass during the experiment could be calculated for each core.

Shear stress manipulation

The microcosm used in these experiments consists of an erosion head with a rotating plate and a push-through water system fitted over a polycarbonate core tube. The combination of the rotation of the plate and the suction of the water system in the center of the core generates a near-uniform bed shear stress and diffusive boundary layer thickness, though not a uniform pressure distribution (Tengberg et al 2004). Because sediment conditions and hydrodynamic forcing were controlled in this study, changes in sediment suspension should be a direct result of alterations to the near-bed hydrodynamics. Across treatments, any increase in the mass of sediment eroded from the bed should reflect an increase in near-bed velocity and/or bed shear stress.

Immediately prior to the experiment, a water sample was pumped from the replacement water to provide reference/background concentration values. The cores were then exposed to a low shear stress of 0.01 Nm^{-2} for 20 min as a flushing step, then a shear stress of 0.32 Nm^{-2} for 40 min. This shear stress is similar to peak shear stresses in a coastal lagoon adjacent to the one where the samples were collected (Hog Island Bay;

Lawson et al 2007). Effluent water was collected in 1 l Nalgene bottles exchanged every 5 min for the higher shear stresses. All effluent water from the erosion tests was collected, subsampled and filtered for total suspended solids (TSS), NH_4^+, PO_4^{3-}, and NO_3^-.

Laboratory analysis

All sediment and water samples were analyzed using standard methods. TSS (sample volumes 150-550 ml) was analyzed by weight difference after filtration onto pre-combusted, pre-weighed Whatmann GF/F filters (nominal particle retention 0.7 µm). Subsamples for nutrients (20 ml) were filtered (0.45 µm) and frozen until analysis. NH_4^+, PO_4^{3-}, and NO_3^- were analyzed using standard methods on a Lachat QuikChem 8500 (as described in the site characterization). NO_3^- and nitrite (NO_2^-) were not separated because NO_2^- values were frequently below the detection level. The combined value is presented as NO_3^- throughout this study.

To correct for the mass of measured components carried in the replacement water, all fluxes were corrected with a background concentration. For all nutrient measurements, the background concentration was defined as the daily average of sub-samples pumped from the carboy of replacement water immediately before the experiments. Nutrient background values were treated differently than sediment because of the possibility of nutrient uptake by the primary producers. To account for the sediment carried in the input water, the lowest TSS recorded during the experiments for each site was used as a background correction. Data from the flushing step were discarded and only data from the higher shear stress step were analyzed. Nutrient data from Day 2 were not included in the analysis, because all nutrient data points from this day were outliers and greater current and wind speeds were observed during sampling. One macroalgal treatment was reclassified (from low to medium) at the end of the experiment based on the measured DW of the macroalgae.

Results

Site characterization

There were no significant differences in the initial conditions at the 5 plots in South Bay (Table 2.1). Extractable NH_4^+ ranged from 0.065 to 0.087 µmols g DW^{-1} with an average of 0.08 (±0.00 SE) µmols g DW $^{-1}$. Porewater NH_4^+ concentrations ranged from 0 to 152 µM, PO_4^{3-} concentrations ranged from 0 to 16 µM, and NO_3^- concentrations ranged from 1.2 to 6 µM. The sediment in all plots was very fine sand, with between 5-11% mud (average grain size=71 µm). Water column nutrient concentrations, as measured from the replacement water, were 0.5 (±0.1 SE) µM NH_4^+, 0.4 (±0.1 SE) µM PO_4^{3-}, and 0.3 (±0.1 SE) µM NO_3^-, similar to values measured in a neighboring lagoon (McGlathery et al 2001).

The macroalgae treatments, based on the average field biomass of 54 g DW m^{-2}, resulted in a range of dry biomass with averages of 18 (±0.83 SE) g DW m^{-2} (low), 37 (±2.1 SE) g DW m^{-2} (medium) and 66 (±4.4 SE) g DW m^{-2} (high). For the seagrass, total aboveground biomass before trimming in the cores ranged from 64 to 201 g DW m^{-2}. This is comparable to 238 to 1743 shoot m^{-2}, based on field measurements of biomass per shoot (0.269 ± 0.022 SE) from South Bay in 2007 (unpublished data). The aboveground biomass of the trimmed seagrass (i.e. the 8 cm tall blades kept in the core for the experiment) ranged from 41 to 184 g DW m^{-2}. Because of the trimming, all future comparisons are based on shoot density. The use of shoot density, rather than biomass, to describe the seagrass effects on hydrodynamics in the microcosms also allows us compare our data with that for other seagrass species and other emergent features, such as polycheate worms.

Sediment flux

During the 40 min high-stress experiment, an average of 0.26 (± 0.03 SE) g of sediment was eroded for all treatments, which is equivalent to an erosion depth of 2.9 x 10^{-3} m (assuming a bulk density of 1) or 29 g m^{-2} (Figs. 2.3 and 2.5). Macroalgal biomass had a significant effect on sediment suspension, with an initial increase above control values for the low biomass treatment, followed by a decrease for the medium and high biomass treatments (ANOVA, p=0.03, n=14, Fig. 2.3). If we take into account the variability in macroalgal biomass for each replicate and consider the macroalgal biomass as a continuous variable, the mass of sediment eroded was strongly negatively dependent on biomass (exponential decay, R^2=0.60, p=0.001, n=14, Fig. 2.4a). The relationship was fit with a non-linear relationship because the amount of sediment eroded can not be negative and should have a lower limit near zero. The control treatment was excluded from this regression analysis because of the initial increase in sediment erosion from the control to low biomass treatments.

There was no significant effect of seagrass presence on sediment suspension compared to bare sediments when exposed to forcing at the shoot densities represented in the microcoms (paired t-test, p=0.42, Fig. 2.5). However, lumping the seagrass cores as a single treatment masks the significant effect that the seagrass density has on sediment suspension, as seen in Fig. 2.4b. When the variation in seagrass density in the replicate cores is taken into account, the data show that there was an initial increase in sediment suspension at low densities (238 –747 shoots m^{-2}) and then a decrease in erosion at high density (~1750 shoots m^{-2}). This unimodal relationship can be described by a Gaussian curve ($R^2 = 0.99$, p=0.01, n=5, Fig. 2.4b). The location of the transition point is only approximated in this fit, and would be best described by more data in the mid-density range. The potential effect of trimming of the seagrass blades on this fit is explored in the discussion.

Nutrient flux

For the macroalgae treatments, the PO_4^{3-} fluxes showed a similar pattern to sediment fluxes, with an increase in flux between the control and low biomass treatment, followed by a decrease for the medium and high biomass treatments (Fig. 2.3). There was a net consumption of PO_4^{3-} from the water column for both the control and high macroalgal treatments. The pattern was different for both NH_4^+ and NO_3^- , with a decrease in flux with increasing macroalgal biomass. For NH_4^+ there was always a net consumption from the water column, and for NO_3^- there was a net consumption only at the high macroalgal treatment. If we again take into account the variability in macroalgal biomass between the individual replicates that were lumped into the categorical treatments and consider the macroalgal biomass as a continuous variable, we can see that the NH_4^+ and NO_3^- fluxes were inversely related to the macroalgal biomass (for NH_4^+ p=0.03, R=0.57, one outlier removed; for NO_3^- p=0.04, R=0.54, Fig. 2.6), whereas the

PO_4^{3-} flux was not (p=0.67, Fig. 2.6). The PO_4^{3-} and NO_3^- fluxes were positively correlated with the mass of sediment eroded (for PO_4^{3-}, p=0.03, R=0.57, one outlier removed; and for NO_3^-, p=0.06, R=0.50, Fig. 2.6). For these relationships, an outlier is defined as a single point with a pronounced effect on the fit, when no other single point has a similar influence. These correlations suggest different mechanisms are responsible for controlling the inorganic N and P nutrient fluxes from the sediment to the overlying water column. Unlike the macroalgal treatments, we did not find a significant effect between seagrass treatments and bare sediments, which may in part be due to the high variability in shoot density between the different replicates and the small sample size (p=0.26, NH_4^+; p=0.23, PO_4^3; p=0.11, NO_3^-; Fig. 2.5).

Discussion

Our study provides evidence that low-density seagrass meadows and low biomass populations of unattached, bloom-forming macroalgae have different hydrodynamic effects than those that have been shown previously for high-density populations. At low densities, both seagrass and macroalgae destabilized sediment, and macroalgae also increased the nutrient efflux from the sediment when exposed to a forcing event. Previous work on high-density populations of these benthic macrophytes has shown that both seagrasses and macroalgae effectively reduce hydrodynamic activity at the sediment surface (e.g. Gambi et al 1990, Fonseca and Cahalan 1992, Peterson et al 2004) and prevent the efflux of sediments and nutrients to the overlying water column (e.g. Thybo-Christensen et al 1993, Sundback et al 2000, McGlathery et al 2004, McGlathery et al 2007). The available literature on the effects of density on hydrodynamics for other emergent features in these shallow coastal systems, such as worm tubes or mussel beds, provides insight into the mechanisms that likely account for the macrophyte density effects on sediment and nutrient fluxes that we observed.

Sediment flux

Effects of seagrass

Seagrass density has been cited as a controlling factor in the effects of seagrass on hydrodynamics, but all previous studies have shown that seagrass decreases sediment suspension. Peterson et al (2004) found a decrease in flow velocity in 10 of 13 cases of seagrass meadows of different morphology and density exposed to a range of velocity conditions, with flow reduction directly related to seagrass density. However, Fonseca and Fisher (1986) found no consistent relationship between seagrass density and canopy friction or sediment movement. The majority of previous studies have been conducted in meadows with higher shoot density and/or significantly taller plants than used in this study (Table 2.2).

Fully-developed seagrass meadows deflect flow vertically creating a protected area next to the sediment surface (Gambi et al 1990), but low-density, short seagrass meadows may displace velocity horizontally rather than vertically, leading to increased erosion around the features (Fig. 2.7). Friedrichs et al (2000) studied the transition from destabilizing to stabilizing effects of polycheate tubes and found that densities below 8.8% surface coverage caused sediment destabilization, while higher densities resulted in the development of skimming flow and decreased erosion. The development of skimming flow is dependent on the ratio of distance between the emergent features to height of the emergent features (Vogel 1994). When the distance between the features is much greater than the height of the features, the flow wakes are independent, while skimming flow develops when the distance between features is less than the height (Vogel 1994).

This characterization shows that the transition from stabilizing to destabilizing effects will depend on both the plant density and height. The trimming of seagrass blades in this study may have shifted the relationship between density and sediment erosion. However, the pattern should remain the same (Fig. 2.4). This relationship between height and density may explain why tubeworms, which are generally much shorter than seagrass shoots, can increase erosion at densities much higher than seagrasses do (< 7000 individuals m^{-2}, Eckman et al 1981). Recently, Hasegawa et al (2008) showed that the reduction of current velocity by an eelgrass meadow varied seasonally with seagrass biomass and canopy height, with a higher canopy and greater biomass corresponding to a greater reduction in current velocity. In this study, seagrass plants with relatively low density and plant height were used to reflect developing or declining meadows and characterize sediment suspension in relatively understudied meadows. Further research is needed to further elucidate the relationship between height and density and the threshold values at which seagrass meadows transition from destabilizing to stabilizing.

The current study also provides greater insight into the behavior of edge areas. Previous studies have shown consistently the reduction of flow velocity by seagrass increases with distance into the meadow (Fonseca and Fischer 1986, Gambi et al 1990). The microcosm has a surface area of only 9.2×10^{-3} m^2, meaning that the entire surface would be within the edge of a typical seagrass meadow. Few studies have measured the effects on flow velocity in the first few cm of a seagrass meadow, with measurements frequently beginning about 0.1 m into the meadow (e.g. Fonseca and Fischer 1986, Gambi et al 1990). While this may represent a small portion of the meadow in well-developed meadows, in disturbed or recolonizing meadows, much of the area may be small patches, with these smaller patches (< 32 shoots) showing greater mortality (Olesen and Sand-Jensen 1994). These small patches may be especially susceptible to sediment suspension and subsequent light attenuation during forcing events.

Effects of macroalgae

The mechanism that explains the higher sediment suspension in low density macroalgal populations relative to bare sediments is likely the well-documented phenomenon of saltating or abrading particles increasing erosion in cohesive beds (e.g. Houser and Nickling 2001, Thompson and Amos 2002, Thompson and Amos 2004). In cohesive beds, the critical stress required to initiate erosion is often greater than the stress required to maintain the sediment in suspension. Under these conditions, the impact of a particle or other object, in this study the macroalgae, may dislodge particles and significantly increase sediment suspension/erosion (Fig. 2.8). In a study determining the effects of kelp on understory species, Kennelly (1989) noted that stopping scour from short-stiped kelp caused an increase in microscopic silt compared to areas with short-stiped kelp in which scour was allowed to continue. Observations made during the current study indicated that sediment erosion was higher in cores in which the macroalgae was in motion than in cores in which the macroalgae was stationary. While some of the thresholds of motion in this study may be influenced by the microcosm design, macroalgae transport as bedload is a documented phenomenon. Flindt et al (1997) found that most macroalgae are transported within 30 cm of the sediment bed. Measured transport rates in the Lagoon of Venice of *Ulva* approached 300 g DW m^{-2} h^{-1} during peak tidal flows (Flindt et al 2004). These studies suggest that transport of macroalgae may cause significant sediment suspension. This increase in sediment suspension will affect both light availability and nutrient flux, two important controls on the growth and productivity of benthic primary producers.

The current study shows that at high density macroalgae stabilize sediment, with a 30% decrease in sediment suspension between the high biomass and control treatments. The ability of macroalgae to suppress sediment suspension challenges the assumption that seagrass die-off during eutrophication will be accompanied by sediment destabilization as macroalgae typically replace seagrass as the dominant benthic primary producer. A decrease in light availability caused by increased sediment suspension is frequently cited as a factor hindering seagrass recolonization (e.g. Morris and Virnstein 2004). While this assumption may hold true when seagrass die-off is a result of disease or sudden disturbance (e.g. prop scour, dredging, storms, etc.), when seagrass is replaced by macroalgae, the macroalgae may provide sufficient stabilization to retain high light availability. Macroalgae can decrease sediment resuspension, particularly with great spatial coverage (> 5 kg WW m^{-2}, Sfriso aand Marcomini 1997). Sediment suspension was also lower in Venice Lagoon during times of high macroalgal biomass than during a period of very low biomass and intense clam harvesting (Sfriso et al 2005). The mat-forming macroalgae *Enteromorpha intestinalis* can reduce sediment suspension by as much as 90% at 60% areal cover (Romano et al 2003). Algal mats have also been shown to significantly affect shear flow at the sediment surface (Escartín and Aubrey 1995). The results of this study similarly showed that macroalgae, at biomasses similar to low and average bloom densities, suppresses sediment suspension.

Similarities between functional groups

Though seagrass and macroalgae have very different morphology, both appear to stabilize sediment by deflecting flow over the meadow or mat (Fig 2.7 and 2.8). Results are presented here in terms of biomass or shoot density, but the controlling feature may be whether the flow interacts with the primary producers as one solid feature (i.e. the meadow or mat) or isolated, individual structures (shoots or fronds). For seagrass, the ability of the canopy to open or close may control how it interacts with the flow. This ability will depend on the morphology of the blades and the density, as well as the forcing conditions (Koch and Gust 1999). Similarly, suppression of sediment suspension was seen when flow was deflected around the macroalgae, while scouring of the sediment bed was seen when flow was through the macroalgae, actually causing movement of the algae. Further research may enable development of a metric, such as cross-sectional area of primary producer per volume of water (as used by Peterson et al 2004), which can be used to compare functional groups and even species with different morphologies within a functional group. Such a metric would incorporate the effects of both density and height, facilitating comparisons between trimmed seagrass blades, such as in this study, and multiple species of seagrasses of different heights.

While the relationship between biomass/density and sediment erosion appears to show different forms for macroalgae and seagrass, they may simply be different parts of the same curve. The macroalgae relationship needs further data to explore the rising arm of the distribution (from zero to the low treatment), while the seagrass relationship needs greater clarification in the descending arm. This range of seagrass densities has been studied in numerous other studies, but no study has covered a range of enhancement and suppression of sediment suspension by seagrass. For both seagrass and macroalgae, low density/biomass can be viewed as destabilizing up to a threshold beyond which it become stabilizing. Further research is needed to clarify the location of this threshold and whether or not it is dependent on forcing conditions.

Nutrient flux

The current study shows that the effect of primary producers on nutrient flux during a forcing event is a balance between uptake and the physical modification of the flow. Previous still water incubations have shown that benthic primary producers can prevent efflux of nutrients from the sediment (Cerco and Seitzinger 1997, Sundback et al 2000, Tyler et al 2001) with the balance between benthic autotrophy and heterotrophy having a significant influence on nutrient efflux (Eyre and Ferguson 2002). In dense macroalgal mats, nutrients from the water column often support growth in the upper layers of the mats while nutrients from the sediment support growth in the lower layers (McGlathery et al 1997). This process effectively decouples nutrient cycling in the sediment and the water column (Kristensen et al 2000, Anderson et al 2003). However, based on the results of the current study, low biomass accumulations of primary producers may enhance nutrient flux to the water column, through modification of physical forcing.

Because phosphorus is not likely limiting in this system, it can be considered a conservative tracer, along with sediment, reflecting the physical effects of suspension and transport, without significant uptake. Phosphorus flux was directly related to sediment suspension and higher for the low macroalgae treatment than the control. This increase shows that low density primary producers are able to increase nutrient flux from the sediment. Many studies have shown that primary producers can decrease the sediment efflux of nutrients; however, to the authors' knowledge, none have shown an increase in the efflux of nutrients from the sediment (given consistent sediment and water column nutrient starting conditions) due to primary producers.

The increased nutrient flux at low biomass may be intensified by the boom and bust cycle of a macroalgal mat. As a developed mat begins to shade itself, the lower layers begin to decay, depositing organic rich material on the sediment surface increasing mineralization (McGlathery et al 1997, Astill and Lavery 2001). Based on our current results, as biomass continues to decrease, the mat may transition from stabilizing sediment and suppressing nutrient flux at high biomass, to eroding sediment and increasing nutrient flux at low biomass. The increased nutrient stock in the sediment from the decaying organic matter may enhance the nutrient flux, potentially leading to an increase in phytoplankton biomass, similar to the response seen in McGlathery et al 2001. The impact may be different for a developing mat, as low biomass of macroalgae increases sediment suspension and nutrient flux, increasing nutrient flux to the water column, and therefore nutrient availability to the macroalgae.

The lack of signal in NH_4^+ fluxes indicates that macroalgae is capable of rapid uptake of increased nutrients, even at low light levels. Most studies on enhanced nutrient flux due to hydrodynamic activity have shown nitrogen and phosphorus both increasing with hydrodynamic forcing (e.g. Ward et al 1984). However, the results of this study showed that NH_4^+ was more controlled by macroalgae biomass. This finding suggests that macroalgal nutrient demand is greater than the enhancement of nutrient flux. In low-flow incubations, macroalgal nutrient demand is often greater than the efflux of nutrients from the sediment, resulting in a net flux of nitrogen directed towards the sediment (e.g. Sundback et al 2000, Tyler et al 2003). In this study, hydrodynamic forcing likely increased the efflux from the sediment, but NH_4^+ flux was still directed towards the sediment bed. The NO_3^- flux was related to both sediment and macroalgal biomass, indicative of the balance between uptake and transport.

Implications for management and future research

Faced with a global decline in seagrass populations (Duarte 2002), the need to understand the role of macroalgae and low density meadows of seagrass in structuring coastal ecosystems is apparent. Most conceptual models and many case studies (e.g. Sand-Jensen and Borum 1991, Boynton et al 1996) describe shallow coastal systems as dominated by slow-growing, persistent macrophytes, such as seagrasses, until eutrophication or disturbance results in a die-off and subsequent colonization by ephemeral macroalgae. Many systems have been slow to return to a seagrass state, even after a reduction in nutrient loading or removal of the disturbance. This hysteresis indicates that the change in primary producers may lead to changes in the overall ecosystem, resulting in conditions more favorable to macroalgae. Based on the results of this study, a conceptual model which may explain this hysteresis is proposed (Fig. 2.9).

While nutrient fluxes and sediment suspension showed a greater dependence on biomass than functional group, the ecosystem consequences will be primary producer dependent.

When exposed to a forcing event, low density accumulations of primary producers may increase sediment suspension and nutrient flux. Because seagrass has high light requirements and limited reliance on water column nutrients, this effect may be detrimental to continued growth of the meadow or may hasten the decline of a meadow. The relationship between density and stabilizing effects may affect transplant survival as low density transplant meadows have significantly higher mortality rates in intermediate to high exposure sites than high density transplant meadows (Bos and van Katwijk 2007). These transplanted meadows may be vulnerable to sediment suspension and subsequent light limitation until plant density is high enough to stabilize the sediment. Macroalgae, which are often nutrient limited, may show the opposite response, with increased growth in response to increased nutrient availability. While further research is needed to develop these relationships, this feedback may explain some of the continued development of macroalgae following a reduction in nutrient load and the high mortality of transplanted seagrass meadows. These relationships may be intensified by the pulsed nature of hydrodynamically-forced nutrient and sediment fluxes. While this study did not give insight into how long these enhanced fluxes could be continued, the duration of light limitation and nutrient enrichment will both have significant impacts on the ecosystem response. The faster growth rate of macroalgae may make it better able to utilize brief periods of increased nutrient concentrations.

Conclusion

Though low density accumulations of macroalgae and low density seagrass meadows have received less research attention, they are important features of many coastal ecosystems. This study clearly shows that the effects of low density stands of primary producers can be profoundly different from high density stands. The global loss of seagrass beds has led to an increased need to understand declining and developing seagrass meadows. This loss has also lead to increased proliferation of macroalgae, which experiences two phases of low density, during the development and decline of a typical mat. Successful management of coastal systems will require an understanding of low density seagrass and macroalgae.

References

Anderson, IC, KJ McGlathery and AC Tyler. 2003. Microbial mediation of 'reactive' nitrogen transformations in a temperate lagoon. *Marine ecology progress series.* 246:73-84.

Astill, H and PS Lavery. 2001. The dynamics of unattached benthic macroalgal accumulations in the Swan-Canning Estuary. *Hydrological processes*. 15(13):2387-2399.

Berg, P and KJ McGlathery. 2001. A high-resolution pore water sampler for sandy sediments. *Limnology and Oceanography*. 46:203-210.

Boynton, WR, JD Hagy, L Murray, C Stokes and WM Kemp. 1996. A comparative analysis of eutrophication patterns in a temperate coastal lagoon. *Estuaries*. 19(2B):408-421.

Bos, AR and MM van Katwijk. 2007. Planting density, hydrodynamic exposure, and mussel beds affect survival of transplanted intertidal eelgrass. *Marine ecology progress series*. 336:121-129.

Chen, XJ and YP Sheng. 2003. Modeling phosphorus dynamics in a shallow lake during an episodic event. *Lake and reservoir management*. 19(4):323-340.

Chen, XJ and YP Sheng. 2005. Three-dimensional modeling of sediment and phosphorus dynamics in Lake Okeechobee, Florida: Spring 1989 simulation. *Journal of environmental engineering- ASCE*. 131(3):359-374.

Cerco, CF and SP Seitzinger. 1997. Measured and modeled effects of benthic algae on eutrophication in Indian River Rehoboth Bay, Delaware. *Estuaries*. 20(1):231-248.

Duarte, CM. 2002. The future of seagrass meadows. *Environmental conservation*. 29(2)192-206.

Eckman, JE, ARM Nowell and PA Jumars. 1981. Sediment destabilization by animal tubes. *Journal of marine research*. 39(2):361-374.

Escartin, J and DG Aubrey. 1995. Flow structure and dispersion within algal mats. *Estuarine coastal and shelf science*. 40(4):451-472.

Eyre, BD and AJP Ferguson. 2002. Comparison of carbon production and decomposition, benthic nutrient fluxes and denitrfication in seagrass, phytoplankton, benthic microalgae and macroalgae-dominated warm-temperate Australian lagoons. *Marine ecology progress series*. 229:43-59.

Flindt, M, J Salomonsen, M Carrer, M Bocci and L Kamp-Nielsen. 1997. Loss, growth and transport dynamics of *Chaetomorpha aerea* and *Ulva rigida* in the Lagoon of Venice during an early summer field campaign. *Ecological modelling*. 102(1):133-141.

Fonseca, MS and JS Cahalan. 1992. A preliminary evaluation of wave attenuation by 4 species of seagrass. *Estuarine coastal and shelf science*. 35(6):565-576.

Fonseca, MS and JS Fisher. 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Marine ecology progress series*. 29: 15–22.

Friedrichs, M, G Graf and B Springer. 2000. Skimming flow induced over a simulated polycheate tube lawn at low population densities. *Marine ecology progress series*. 192:219-228.

Gambi, MC, ARM Nowell and PA Jumars. 1990. Flume observations on flow dynamics in *Zostera-marina* (eelgrass) bed. *Marine ecology progress series*. 61(1-2):159-169.

Ginsburg, RN and HA Lowenstam. 1958. The influence of marine bottom communities on depositional environment of sediments. *Journal of geology*. 66:310-318.

Gremare, A, JM Amouroux, G Cauwet, F Charles, C Courties, F De Bovee, A Dinet, JL Devenon, XD De Madron, B Ferre, P Fraunie, F Joux, F Lantoine, P Lebaron, JJ Naudin, A Palanques, M Pujo-Pay and L Zudaire. 2003. The effects of a strong winter storm on physical and biological variables at a shelf site in the Mediterranean. *Oceanologica acta*. 26(4):407-419.

Greve, TM, D Krause-Jensen, MB Rasmussen, and PB Christensen. 2005. Means of rapid eelgrass (*Zostera marina L.*) recolonisation in former dieback areas. Aquatic botany. 82(2):143-156.

Gust, G and V Müller. 1997. Interfacial hydrodynamics and entrainment functions of currently used erosion devices. In: *Cohesive sediments*. Burt N, R Parker and J Watts (Eds). John Wiley and Sons. .

Hansen, JW, JW Udy, CJ Perry, WC Dennison and BA Lomstein. 2000. Effect of the seagrass *Zostera capricorni* on sediment microbial processes. *Marine ecology progress series*. 199:83-96.

Hasegawa, N, M Hori and H Mukai. 2008. Seasonal changes in eelgrass functions: current velocity reduction, prevention of sediment resuspension, and control of sediment-water column nutrient flux in relation to eelgrass dynamics. *Hydrobiologia*. 596:387-399.

Heiss, WM, AM Smith and PK Probert. 2000. Influence of the small intertidal seagrass *Zostera novazelandica* on linear water flow and sediment texture. *New Zealand journal of marine and freshwater research*. 34:689-694.

Houser, CA and WG Nickling. 2001. The factors influencing the abrasion efficiency of saltating grains on a clay-crusted playa. *Earth surface processes and landforms*. 26(5):491-505.

Kennelley, SJ. 1989. Effects of kelp canopies on understory species due to shade and scour. *Marine ecology progress series*.50:215-224.

Koch, EW and G Gust. 1999. Water flow in tide and wave dominated beds of the seagrass *Thalassia testudinum*. *Marine ecology progress series*.184: 63–72.

Kristensen, E, FO Andersen, N Holmboe, M Holmer and N Thongtham. 2000. Carbon and nitrogen mineralization in sediments of the Bangrong mangrove area, Phuket, Thailand. *Aquatic microbial ecology*. 22(2):199-213.

Lawson, SE, PL Wiberg, KJ McGlathery and DC Fugate. 2007. Wind-driven sediment suspension controls light availability in a shallow coastal lagoon. *Estuaries and coasts*. 30(1):102-112.

Lorenzen, C. 1967. Determination of chlorophyll and phaeopigments: spectrophotometric equations. *Limnology and oceanography*. 12:343-346.

McGlathery, KJ, IC Anderson and AC Tyler. 2001. Magnitude and variability of benthic and pelagic metabolism in a temperate coastal lagoon. *Marine ecology progress series*. 216:1-15.

McGlathery, KJ, D Krause-Jensen, S Rysgaard and PB Christensen. 1997. Patterns of ammonium uptake within dense mats of the filamentous macroalga *Chaetomorpha linum*. *Aquatic botany*. 59:99-115.

McGlathery, KJ, K Sundback and IC Anderson. 2004. The importance of primary producers for benthic N and P cycling. In: *The influence of primary producers on estuarine nutrient cycling*. Nielsen SL, GM Banta and MF Pedersen (Eds). Kluwer Academic.

McGlathery KJ, K Sundback and IC Anderson. 2007. Eutrophication in shallow coastal bays and lagoons: the role ofplants in the coastal filter. *Marine ecology progress series*. 348: 1-18.

Morris, LJ and RW Virnstein. 2004. The demise and recovery of seagrass in the northern Indian River Lagoon, Florida. *Estuaries*. 27(6)915-922.

Olesen, B and K Sand-Jensen. 1994. Patch dynamics of eelgrass *Zostera-marina*. *Marine ecology progress series*. 106(1-2):147-156.

Orth, RJ, ML Luckenbach, SR Marion, KA Moore and DJ Wilcox. 2006. Seagrass recovery in the Delmarva Coastal Bays, USA. *Aquatic botany*. 84:26-36.

Peterson, CH, RA Luettich, F Micheli and GA Skilleter. 2004. Attenuation of water flow inside seagrass canopies of differing structure. *Marine ecology progress series*. 268:81-92.

Romano, C, J Widdows, MD Brinsley and FJ Staff. 2003. Impact of *Enteromorpha intestinalis* mats on near-bed currents and sediment dynamics: flume studies. *Marine ecology progress series*. 256:63-74.

Sand-Jensen, K and J Borum. 1991. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquatic botany*. 41(1-3):137-175.

Sfriso, A, C Facca, and A Marcomini. 2005. Sedimentation rates and erosion processes in the lagoon of Venice. *Environment international*. 31:983-992.

Sfriso, A and A Marcomini. 1997. Macrophyte production in a shallow coastal lagoon 1. Coupling with chemico-physical parameters and nutrient concentrations in waters. *Marine environmental research*. 44(4):351-375.

Sundback, K, A Miles and E Goransson. 2000. Nitrogen fluxes, denitrification and the role of microphytobenthos in microtidal shallow-water sediments: an annual study. *Marine ecology progress series*. 200:59-76.

Tengberg, A, H Stahl, G Gust, V Muller, U Arning, H Andersson and POJ Hall. 2004. Intercalibration of benthic flux chambers I. Accuracy of flux measurements and influence of chamber hydrodynamics. *Progress in oceanography*. 60:1-28.

Thompson, CEL and CL Amos. 2002. The impact of mobile disarticulated shells of *Cerastoderma edulis* on the abrasion of a cohesive substrate. *Estuaries*. 25(2):204-214.

Thompson, CEL and CL Amos. 2004. Effect of sand movement on a cohesive substrate. *Journal of hydraulic engineering- ASCE*. 130(11):1123-1125.

Thomsen, MS, KJ McGlathery and AC Tyler. 2006. Macroalgal distribution patterns in a shallow, soft-bottom lagoon, with emphasis on the nonnative *Gracilaria vermiculophylla* and *Codium fragile*. *Estuaries and coasts*. 29:470-478.

Thybo-Christensen, M, MB Rasmussen and TH Blackburn. 1993. Nutrient fluxes and growth of *Cladophora sericea* in a shallow Danish Bay. *Marine ecology-progress series*. 100(3):273-281.

Tyler, AC, KJ McGlathery and IC Anderson. 2001. Macroalgal mediation of dissolved organic nitrogen fluxes in a temperate coastal lagoon. *Estuarine coastal and shelf science*. 53:155-168.

Tyler, AC, KJ McGlathery and IC Anderson. 2003. Benthic algae control sediment-water column fluxes of organic and inorganic nitrogen compounds in a temperate lagoon. *Limnology and oceanography*. 48:2125-2137.

Viaroli, P, M Bartoli, C Bondavalli, RR Christian, G Giordani and M Naldi. 1996. Macrophyte communities and their impact on benthic fluxes of oxygen, sulphide and nutrients in shallow eutrophic environments. *Hydrobiologia*. 329(1-3):105-119.

Vogel, S. 1994. *Life in moving fluids*. Pergamon, New York.

Ward, LG, WM Kemp and WR Boynton. 1984. The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Marine geology.* 59: 85–103.

Widdows, J, JS Lucas, MD Brinsley, PN Salkeld and FJ Staff. 2002. Investigation of the effects of current velocity on mussel feeding and mussel bed stability using an annular flume. *Helgoland marine research*. 56(1):3-12.

Figures and Tables

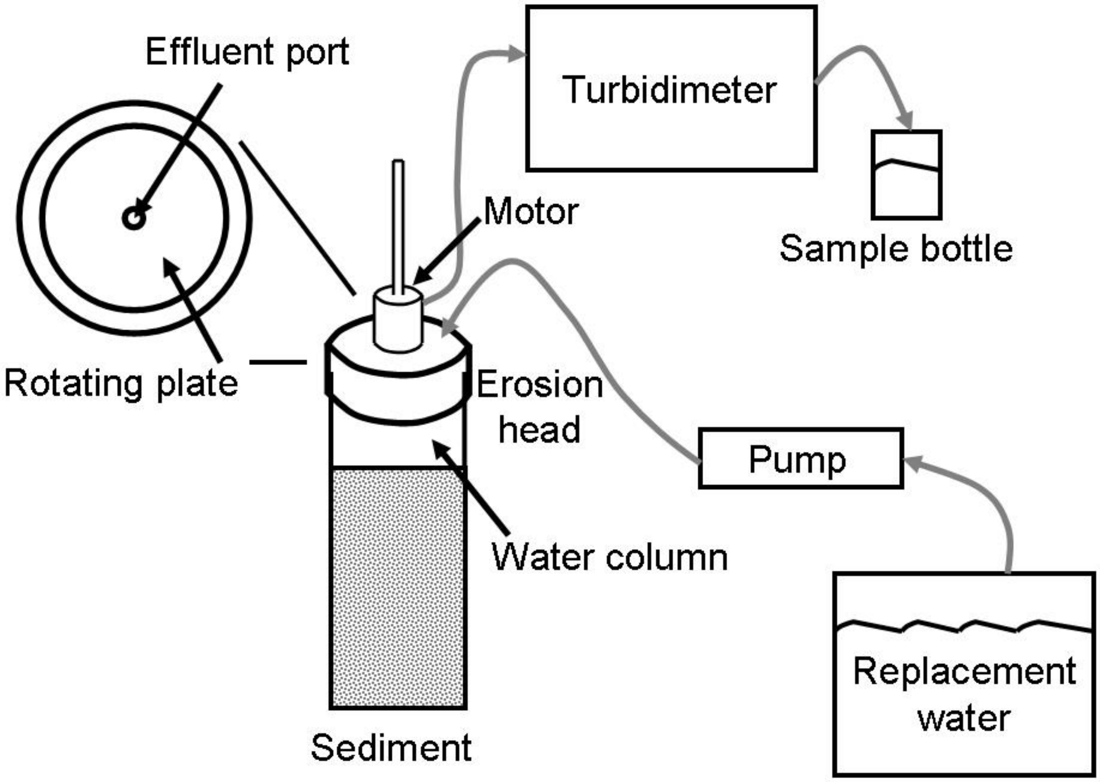

Figure 2.1. Gust erosion microcosm. The erosion head is a spinning disk that generates a uniform shear stress on the sediment surface of a core. The rate of rotation of the erosion head and the pumping rate are controlled by a datalogger. The turbidity from the effluent is continuously recorded on the turbidimeter.

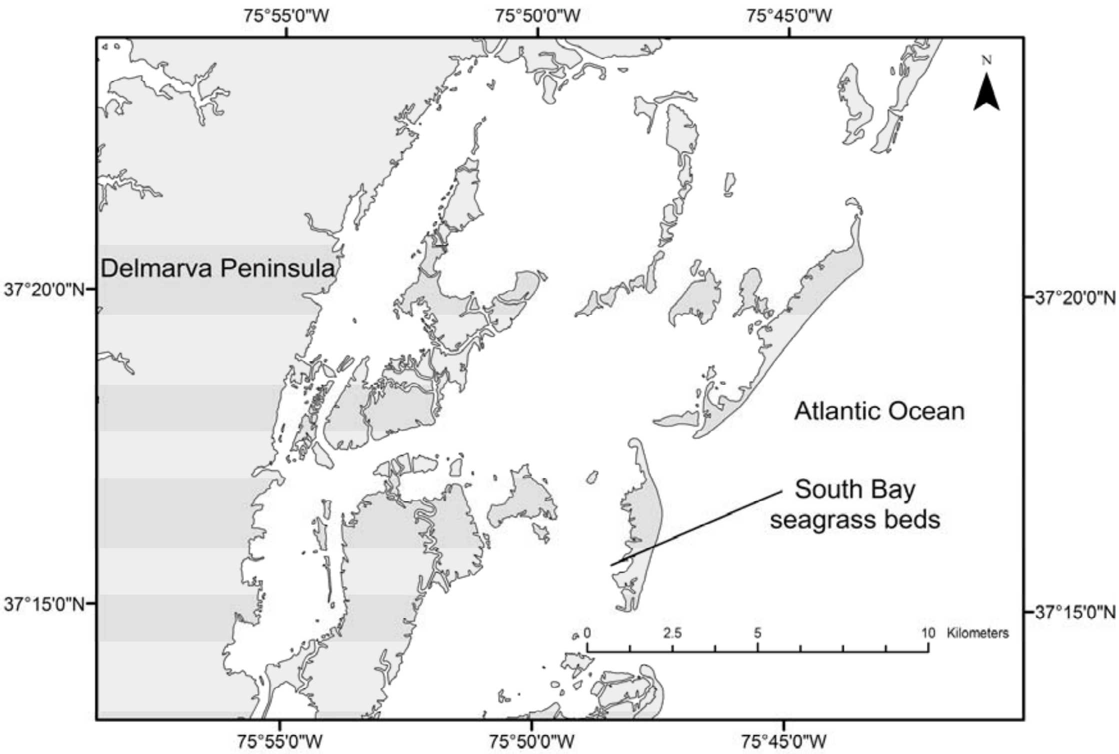

Figure 2.2. Map of the study site. South Bay is a shallow coastal lagoon on the east side of the Delmarva Peninsula. Seagrass transplant efforts have led to the development of patchy seagrass beds in the area.

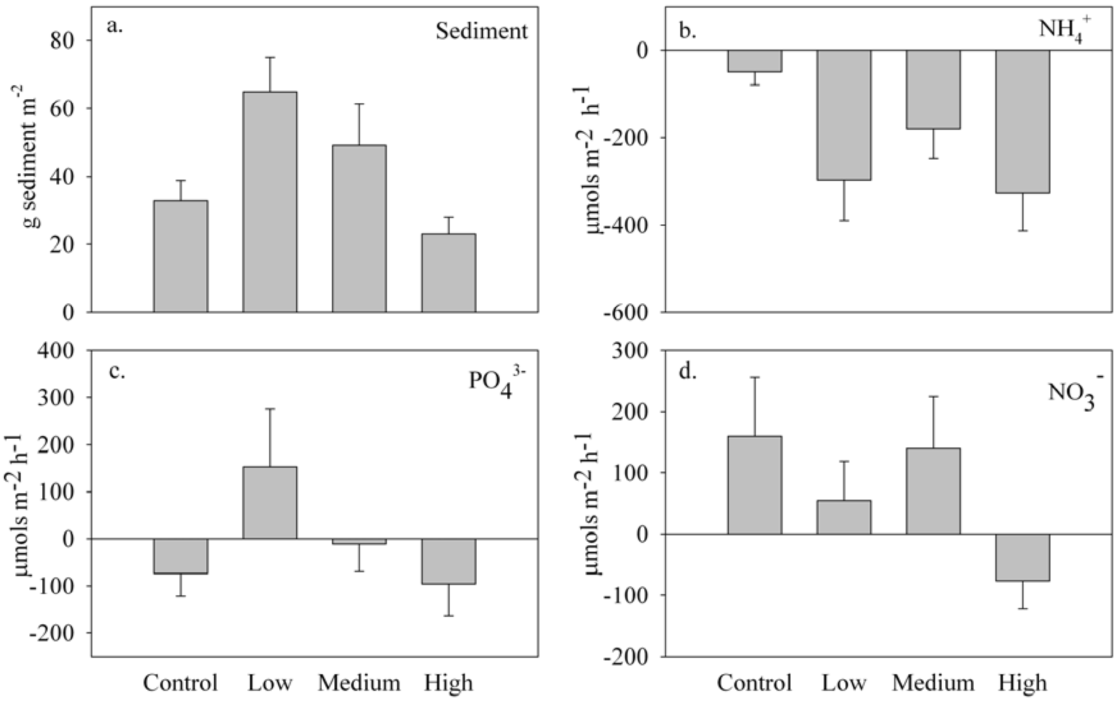

Figure 2.3. Summary of sediment and nutrient fluxes for macroalgae. The panels depict fluxes of sediment (a.), NH_4^+ (b.), PO_4^{3-} (c.) and NO_3^- (d.). Nutrient fluxes generally mirrored the sediment flux.

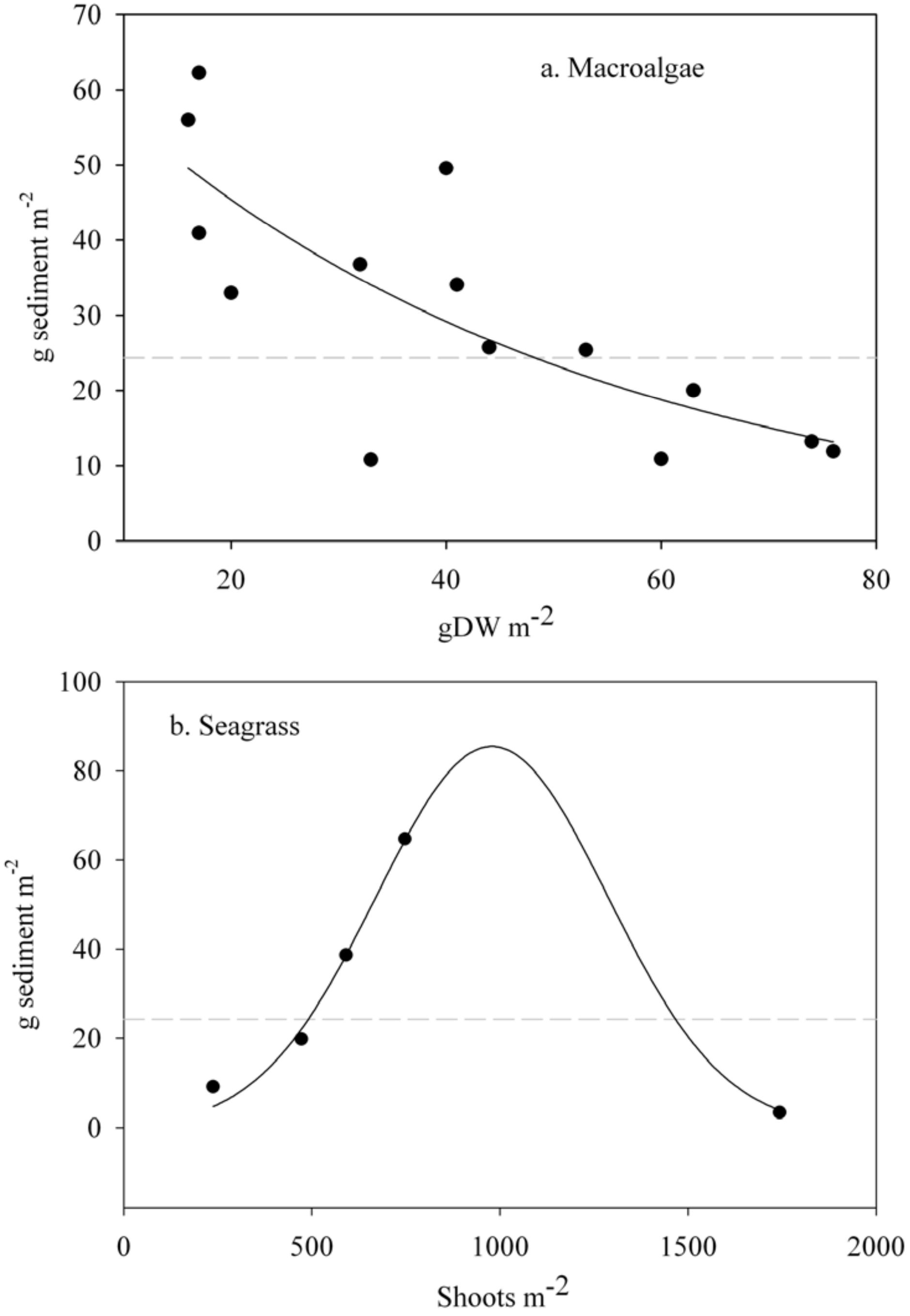

Figure 2.4. The relationship between sediment eroded and primary producer biomass. Macroalgae (a) and seagrass (b) show different effects on erosion, but may simply be showing different sections of the same curve. The gray dashed line represents the average of all control cores.

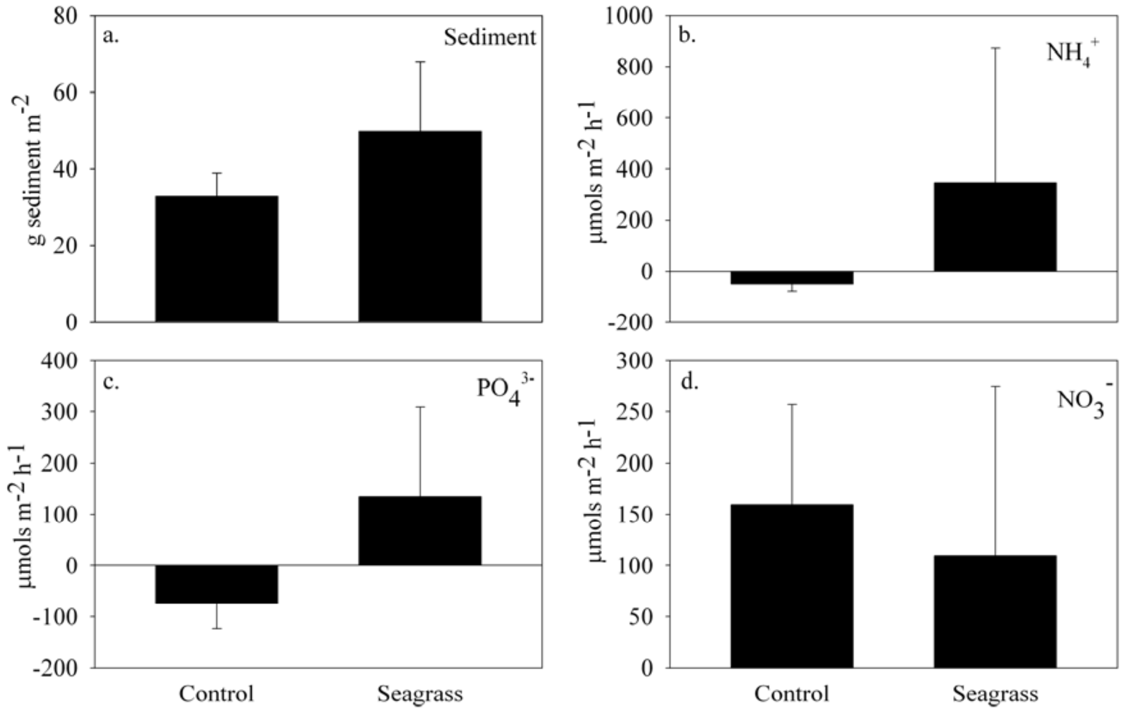

Figure 2.5. Summary of sediment and nutrient flux for seagrass. The panels depict fluxes of sediment (a.), NH_4^+ (b.), PO_4^{3-} (c.) and NO_3^- (d.). Nutrient fluxes generally mirrored the sediment flux though standard errors were large.

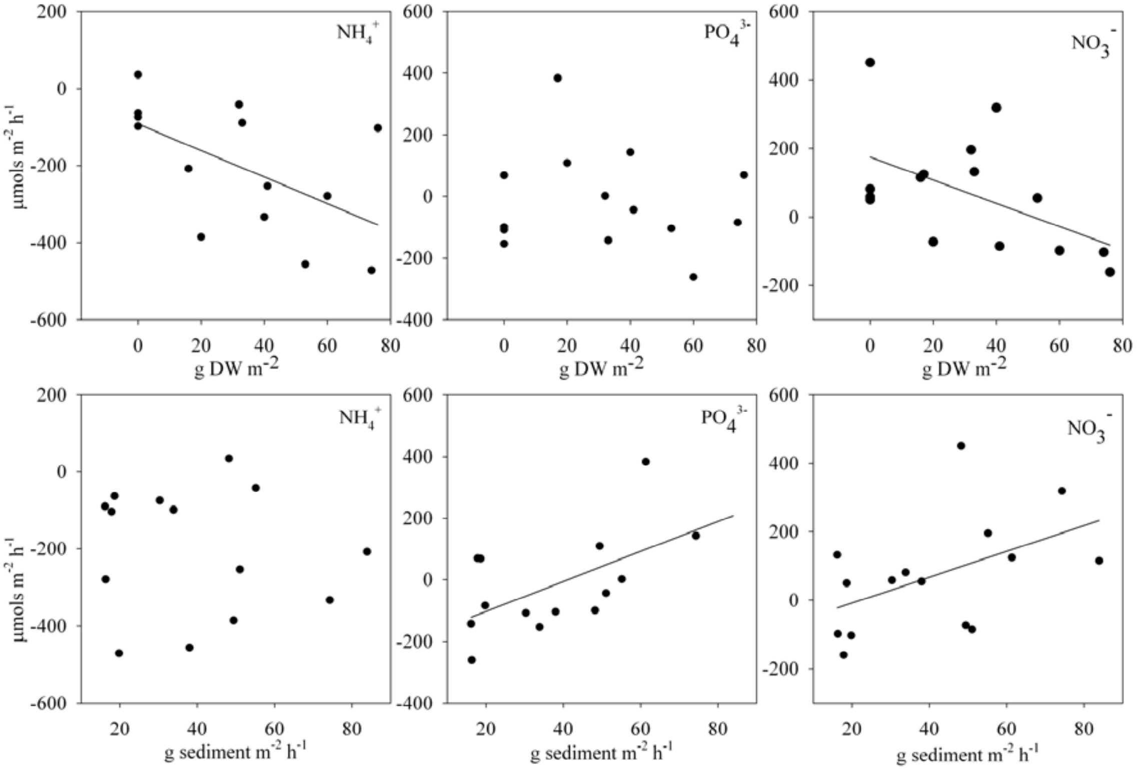

Figure 2.6. Relationships between nutrient flux and macroalgal biomass (top row) and sediment (bottom row). NH_4^+ and NO_3^- were negatively related to biomass and PO_4^{3-} and NO_3^- were positively related to sediment. Because sediment and macroalgal biomass are correlated, results have to be interpreted cautiously, but suggest that uptake controls NH_4^+ dynamics and transport controls PO_4^{3-} dynamics.

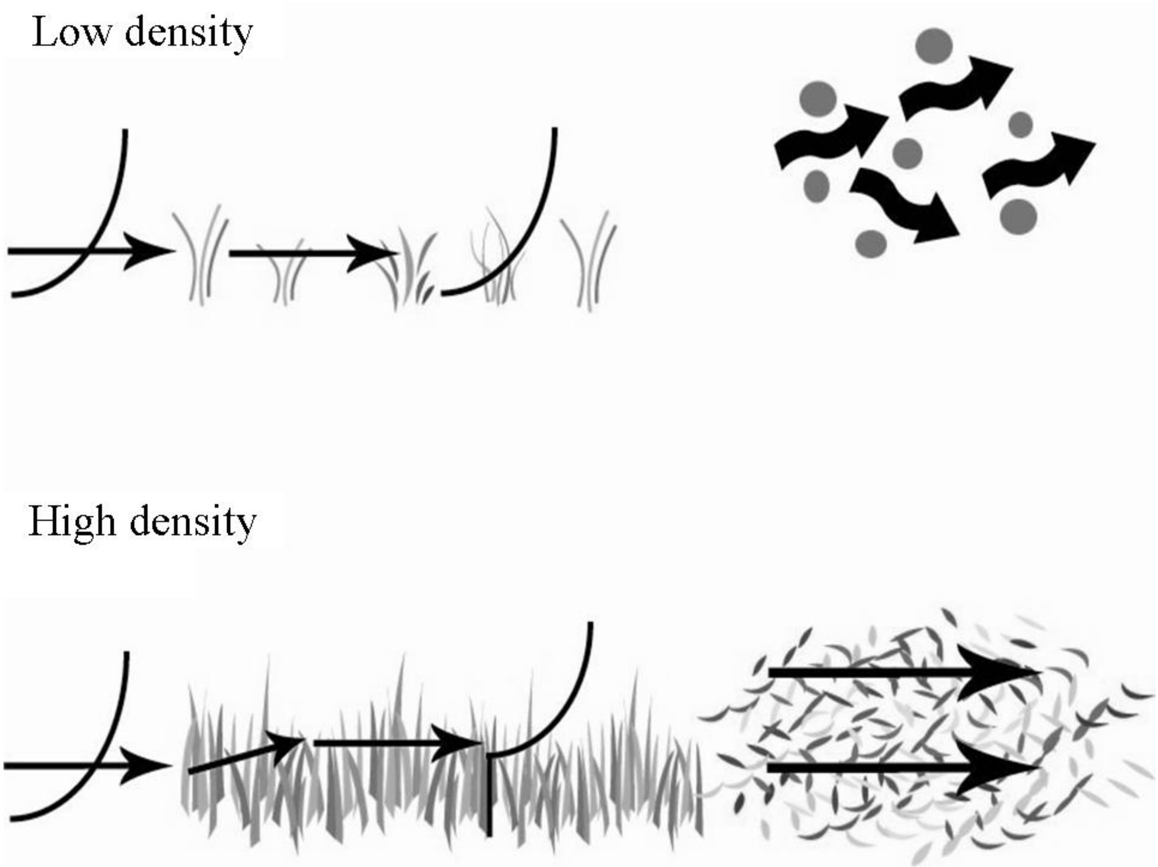

Figure 2.7. Schematic drawing of the effect of seagrass on water flow. A high density meadow will displace the flow over the top of the meadow protecting the sediment bed, while a low density meadow increases sediment suspension by diverting flow around the seagrass shoots.

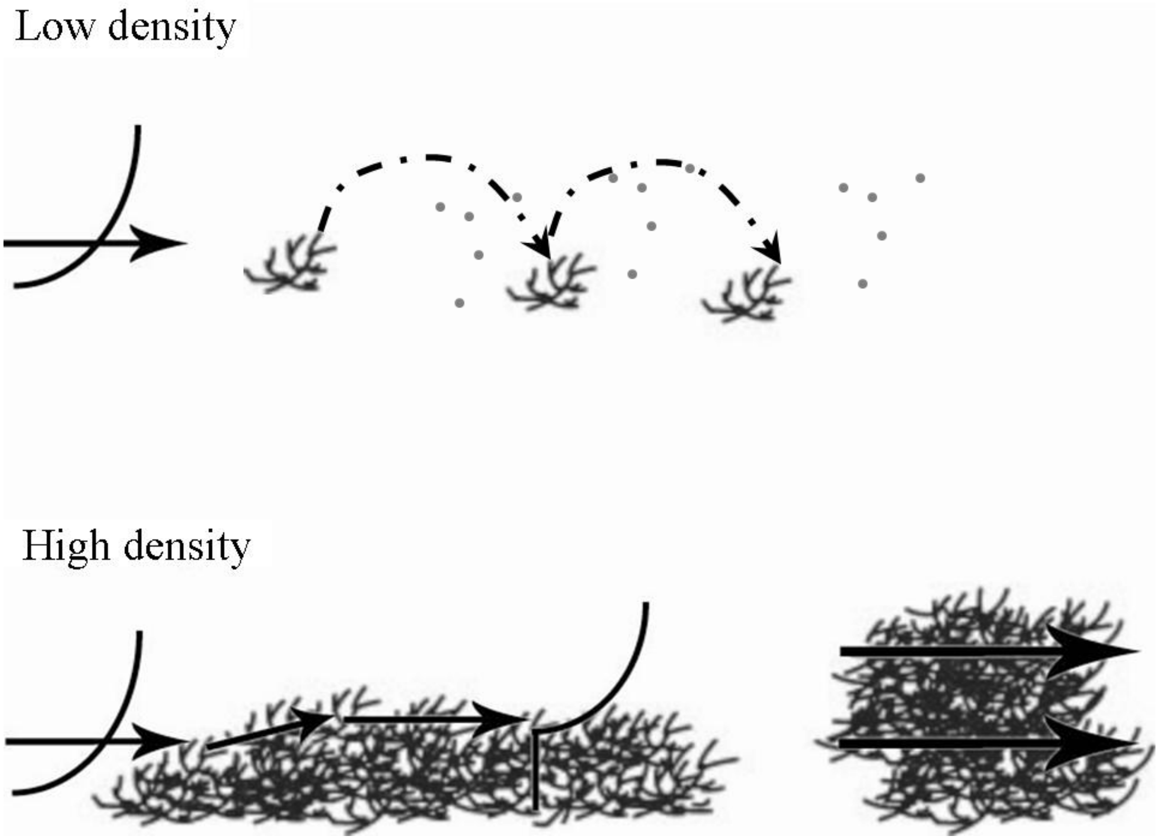

Figure 2.8. Schematic of the effects of macroalgae on flow. Dense macroalgal mats will deflect flow over the top of the mat, while isolated pieces of macroalgae may be transported as bedload leading to increased particle dislodgement.

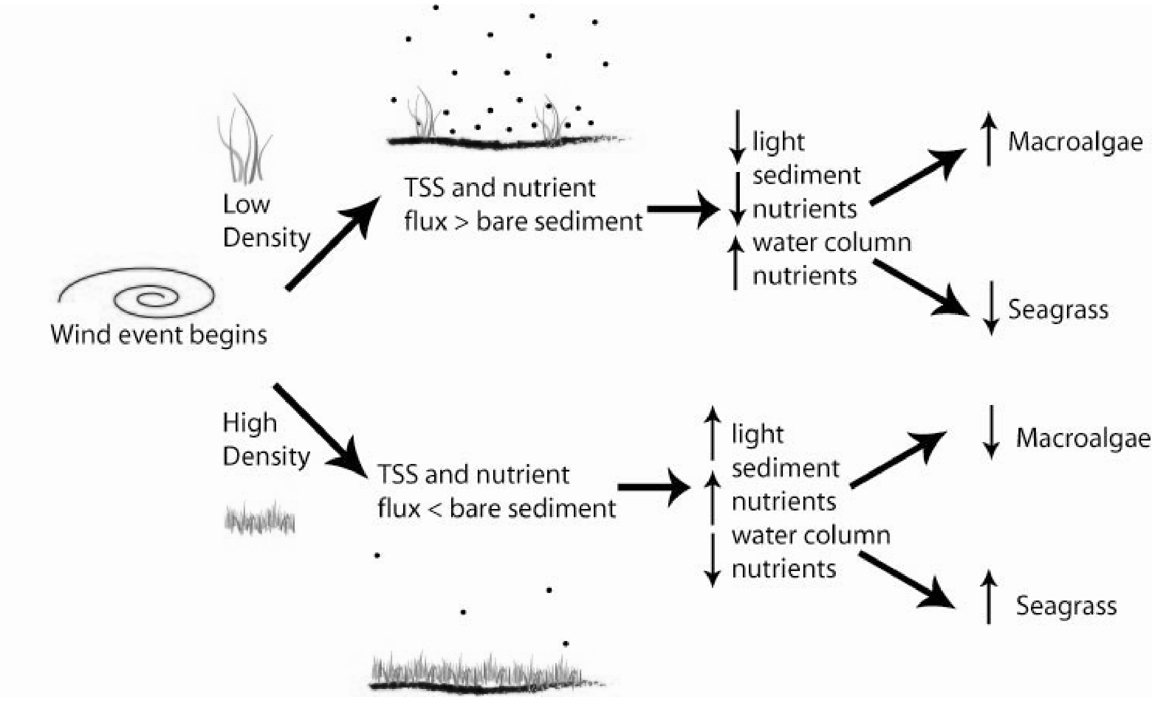

Figure 2.9. Conceptual model of the ecosystem impacts of the different effects of low and high density primary producers on sediment suspension and nutrient flux. The ecosystem response depends on the nutrient and light demands of the primary producers.

Table 2.1. Summary of site characteristics for each plot in South Bay. All plots showed similar sediment and nutrient conditions. Values are averages of samples as described in the methods and numbers in parentheses are standard error.

	Day 1	**Day 2**	**Day 3**	**Day 4**	**Day 5**
Average grain size (microns)	76	70	76	67	66
Benthic chlorophyll (mg m^{-2}*)*	4.7(0.8)	5.2(0.2)	5.6(0.9)	4.5(0.6)	6.1(0.8)
Ammonium (μM)	0.4(0.2)	0.2(0.1)	0.6(0.2)	0.6(0.1)	0.7(0.1)
Phosphate (μM)	0.3(0.1)	0.2(0.0)	0.4(0.2)	0.4(0.0)	0.5(0.2)
Nitrate (μM)	0.5(0.1)	----	0.2(0.1)	0.3(0.1)	0.3(0.2)
Extractable ammonium	0.06 (0.00)	0.09 (0.00)	0.08 (0.00)	0.07 (0.00)	0.08 (0.02)
Porewater ammonium (μM)	62(5)	43(5)	82(7)	34(9)	42(3)
Porewater phosphate (μM)	4.3(0.5)	3.5(0.6)	5.7(0.4)	4.7(0.2)	3.4(0.5)
Porewater nitrate (μM)	2.2(0.2)	1.7(0.3)	2.0(0.1)	2.6(0.3)	2.6(0.3)

Table 2.2. Summary of studies on the effects of seagrass meadows on hydrodynamics and sediment suspension. Most studies have been conducted in meadows with higher shoot densities than South Bay (average 246 shoots m^{-2}, Reynolds and Cole unpublished data, though values used in this study were often greater) and have all found decreased hydrodynamic activity and sediment suspension in seagrass beds.

Primary producer	**Density (shoots m^{-2})**	**Measured response**	**Study**
Zostera marina and Halodule wrightii	544-3740	Decreased near-bed velocity	Peterson et al 2004
Thalassia testudinum	784	Decreased sediment suspension	Koch 1999
Thalassia testudinum	850, 1050, 1500	Decreased sediment movement	Fonseca and Fisher 1986
Halodule wrightii	1900, 2260, 2870	Decreased sediment movement	Fonseca and Fisher 1986
Zostera marina	485, 750, 1000	Decreased sediment movement	Fonseca and Fisher 1986
Syringodium filiforme	230, 570, 1350	Decreased sediment movement	Fonseca and Fisher 1986
Zostera marina	400, 600, 800, 1000, 1200	Decreased near-bed velocity	Gambi et al 1990
Posidonia oceanica L	204-350	Decreased particle resuspension	Terrados and Duarte 2000

Chapter 3: Scales of variability of hydrodynamically-forced ammonium fluxes in a shallow coastal lagoon

Abstract

Under moderate to high flow conditions, porewater advection and desorption from suspended particles can increase nutrient fluxes above the levels supported by diffusion alone but the temporal and spatial variability of these fluxes is not fully understood. In this study, diffusion, porewater advection and desorption of ammonium (NH_4^+) were all examined through controlled experiments at 3 sites, ranging in average sediment grain size from 28 to 120 µm, and two times (late spring and early fall). Numerical simulations of porewater advection and diffusion were also conducted to gain greater temporal resolution and to determine the effects of permeability and initial porewater profile. Though desorption created the highest calculated fluxes, no single mechanism was clearly dominant (averages across all sites 11(±5(SE)) µmols m^{-2} h^{-1} from diffusion, 4(±1(SE)) µmols m^{-2} h^{-1} from porewater advection, and 33(±25(SE)) µmols m^{-2} h^{-1} from desorption). The calculated desorption fluxes were based on a shorter time series than the porewater advection and diffusive fluxes and may therefore be more representative of peak fluxes than a sustained flux. Fluxes from desorption were highest at the fine-grained Creek site (158 µmols m^{-2} h^{-1} late spring, 13 µmols m^{-2} h^{-1} early fall), while the volume of porewater advected was highest at the coarse-grained Island site (1.2 l m^{-2}). Numerical simulations of porewater advection and diffusion show that in permeable sediments, porewater advection creates a large, short duration peak flux (> 20 times the highest modeled diffusive flux) that rapidly diminishes. Because of the short duration, the magnitude of this peak flux, controlled by initial porewater profile and permeability, has relatively minor effects on

average flux over a 12 hour simulation. To determine possible ecosystem effects of these NH_4^+ fluxes, both the average fluxes and the timing of the fluxes must be considered, as primary producers such as phytoplankton may be better able to utilize pulse nutrient fluxes than slower growing macrophytes.

Introduction

Nutrient cycling in shallow coastal lagoons is fundamentally different from that in deep estuaries. These lagoons are characterized by shallow depth, a well-mixed water column and low freshwater input (Boynton et al 1996). The shallow depth creates a high sediment surface area to water volume ratio and allows the sediment to be subject to frequent wave-driven resuspension, two characteristics that increase the importance of benthic-pelagic coupling. The significance of the diffusive nutrient flux between the sediment and water column has been demonstrated in laboratory mesocosms and field experiments using enclosed chambers (e.g. Hopkinson et al 1999, Thouzeau et al 2007), and recent research has shown that hydrodynamic activity can greatly increase nutrient flux (e.g. , Huettel et al 1998, Morin and Morse 1999). However, this effect has not been well-characterized in shallow coastal systems.

Waves and currents can enhance transport of nutrients from the sediment to the water column through sediment resuspension with associated desorption, and porewater advection (as described by Huettel and Webster 2001), both of which may be important in shallow coastal systems. When sediment with sorbed nutrients is suspended in the water column, the change in surrounding aqueous nutrient concentration (the typically lower concentration in the water column compared to the porewater) results in desorption of the nutrients from the sediment (Fig. 3.1). For a given nutrient, the magnitude of this flux depends on the quantity of the exchangeable nutrient, the solid to solution ratios, and the redox conditions (Morin and Morse 1999, Morse and Morin 2005). The quantity of exchangeable nutrients is largely dependent on sediment grain size, with fine-grained sediment with high organic content having greater quantities of sorbed nutrients (Boatman and Murray 1982, Mackin and Aller 1984). Porewater advection is generated by pressure gradients at the sediment surface and significantly enhances nutrient flux in areas with coarse, permeable sands, such as portions of the continental shelf (Huettel et al 1998), but has not been studied extensively in shallow, more fine-grained environments (Fig. 3.2). This previous research indicates that desorption may be more important in areas with fine-grained sediments while porewater advection may be dominant in areas with coarse-grained sediments. These fluxes may also occur on very different time scales than diffusion.

Nutrient availability and flux must be viewed in the context of the dominant primary producers, particularly in light of increased nutrient loads leading to coastal eutrophication. Most models predict a progression of 3 functional groups of primary producers with different nutrient utilization strategies during eutrophication: seagrass, macroalgae, and phytoplankton. Seagrass growth relies primarily on nutrients drawn from the sediment through its roots (Touchette and Burkholder 2000). Macroalgae are unable to utilize nutrients directly from the sediment but can form a mat over the sediment surface that can take up nutrients and intercept the flux of nutrients from the sediment to the water column (Tyler et al 2001). Phytoplankton also depend on the availability of water column nutrients. Macroalgae and phytoplankton both exhibit surge uptake of nutrients, a high rate of uptake sustainable only for a short period of time (Cochlan and Harrison 1991, Pedersen and Borum 1997, Tyler et al 2005), while seagrass shows sustained uptake of nutrients at a slower rate (Touchette and Burkholder 2000). These spatial and temporal differences in nutrient utilization suggest that the processes that control the spatial and temporal distribution of nutrients may be as important as bulk nutrient availability in supporting the demand of primary producers in these shallow systems.

This study was designed to examine the relative importance of desorption, porewater advection and diffusion on ammonium (NH_4^+) flux at 3 sites in a shallow coastal lagoon on the

Eastern Shore of Virginia (Hog Island Bay, Fig. 3.3) using both experimental (desorption and porewater advection) and modeling (diffusion and porewater advection) approaches. The 3 sites chosen for this study represent a gradient of grain size, background nutrient concentrations, and primary productivity which should impact the relative importance of the mechanisms of nutrient transport (Table 3.1). The experimental studies included a sediment addition experiment with constant mixing to characterize desorption and measurements of rhodamine dye transport under both still-water conditions and high-flow conditions in a Gust erosion microcosm (microcosm hereafter, Gust and Müller 1997, Fig. 3.4) to characterize porewater advection. The mathematical determination of diffusion was based on Fick's Law using the tortuosity correction of Boudreau (1996). These values were then compared to values measured under low-flow conditions at the same sites. Predicted rates of porewater advection were calculated based on the methods of Rutherford et al (1995). Numerical simulation of porewater advection and diffusion provides higher temporal resolution than afforded by the measurements and allows manipulation of controlling variables to examine the importance of the shape of the initial porewater profile and sediment permeability on these fluxes. The experiments and numerical simulations were all done considering only one mechanism of nutrient transport (e.g. desorption, diffusion or porewater advection). While multiple processes may be occurring in natural sediments at once, they were considered separately here to illustrate the potential effect from each process and their relative importance.

Methods

Site description

This study was conducted at 3 shallow subtidal sites in Hog Island Bay, VA on the Delmarva Peninsula (Fig. 3.3, Table 3.1). Hog Island Bay was historically dominated by seagrass, *Zostera marina*, until a hurricane wiped out populations already decimated by a wasting disease. Seagrass has been replaced with benthic microalgae and benthic macroalgae as the dominant primary producers (McGlathery et al 2001). The Creek site is characterized by organic rich, fine-grained sediment (mostly silt and clay). The site is next to a *Spartina alterniflora* marsh in a tidal creek with very little freshwater input. The Shoal site is next to relic oyster reefs and has the highest seasonal accumulations of macroalgae, reaching over 700 g DW m^{-2}. Previous research has shown that when this mat "crashes", the added organic matter is quickly remineralized and transferred to the water column as dissolved organic and dissolved inorganic compounds (Tyler et al 2001). The Island site is located on the western side of a barrier island, between the island and a smaller marsh island. This site is characterized by the coarsest sediment of the 3 sites and relatively low organic content. Macroalgal biomass is lowest at this site with typical peak annual biomasses of only 10 – 20 g m^{-2}. Current velocities in this area are higher than at the Creek or Shoal site, but the site is relatively protected from wave forcing (Lawson et al 2007).

Experiments

Desorption

The NH_4^+ flux from sediment suspended in the water column was examined by adding surface sediment to samples of ambient water that was then continuously mixed in a modification the methods of Morin and Morse (Morin and Morse 1999, Morse and Morin 2005). A 20 liter water sample was collected at each site, then subdivided into 8 1-liter bottles that were assigned randomly to zero (control) or high sediment treatments corresponding to the addition of 0 or 1.2 cm^3 of sediment and porewater from the top 1 cm of the sediment bed. Water was sampled for initial concentration and then sediment was added to each treatment bottle. The bottles were placed into a BigCat cement mixer to provide constant mixing of the bottles. The bottles were sub-sampled at 5, 15, 30, 60, 180 and 360 min after addition of sediment. Mixing was only stopped for sampling, less than 5 minutes for each time step. Water sub-samples were filtered with a 0.45 µm syringe filter then frozen until analysis for NH_4^+ using standard methods for brackish water on a Lachat QuickChem 8500 (Hach Company, Loveland, CO).

At the completion of the experiment, the remaining water in each bottle was filtered onto pre-combusted Whatmann GF/F filters (nominal retention size of 0.7 µm). Filters were then dried at 105 ºC and weighed to determine total suspended solids (TSS). The experiment was repeated twice in May 2006 and once in September 2006. For one of the May experiments, water and sediment were autoclaved for 20 min at 120 °C before the experiment to eliminate any effects of biological nutrient transformation and uptake. Sediment from each site and each date was also analyzed for extractable NH_4^+ using a standard 1 N KCl extraction.

Nutrient desorption (µmols g^{-1}) was calculated for each treatment bottle and time step as:

$$\text{Desorption}_t = (\Delta C_{\text{treatment}} - \Delta C_{\text{control}})/\text{TSS} \tag{1}$$

where $\Delta C_{treatment}$ is the change in concentration of the treatment bottle and $\Delta C_{control}$ is the average change in concentration of the control treatments, both compared to initial concentrations and TSS is the concentration of total suspended solids of the treatment minus the average for the control bottles. To calculate the total potential flux from desorption at the site, the total mass of sediment eroded during a 100 minute erosion test at the site (see Chapter 4) during April 2006 or September 2006 was multiplied by the per-mass desorption calculated above. This value was changed to an hourly rate by multiplying by 0.6 (from 100 to 60 minutes).

Porewater advection

The radial pressure gradient in the microcosm was used to determine the effects of increased flow on porewater advection. The microcosm consists of a sediment core and a top fitting with a rotating plate and a push-through system for water replacement (Fig. 3.4). The combination of the rotation of the plate and suction from the water exiting the system creates a near-uniform bed shear stress but a non-uniform pressure distribution, with higher pressure at the edge of the core and low pressure near the center of the core. Because of the relatively low permeability of the sediment in Hog Island Bay, the porewater advection experiment was done with a pressure gradient that is much larger than typical field pressure gradients to determine a maximum possible effect from porewater advection (see Tengberg et al 2004 for discussion of the pressure gradients in the microcosm, Huettel and Webster 2001 for discussion of typical pressure gradients in natural systems). The greater pressure gradients will affect the depth of porewater advection and the rate. In this study, the depth of porewater advected was limited by the height of the sediment column, limiting the total magnitude of the porewater advection flux. Because the total magnitude is limited, the increased pressure gradient likely affected the rate of porewater advection but not the total quantity.

Eight cores per site were taken within 1 h of low tide and transported to the lab, where the cores were equilibrated for at least 24 h in an ambient water bath oxygenated by an aquarium bubbler. Cores were then analyzed for 8 h in pairs of one control core and one treatment core. Five ml of a rhodamine WT solution were added to the overlying water in each core. The control core was allowed to sit undisturbed for the duration of the experiment. The treatment core was exposed to a boundary shear stress of 0.01 Nm^{-2} for 15 min to thoroughly mix the dye; the shear stress was then increased to 0.32 Nm^{-2} for the duration of the experiment. Water column samples taken throughout the experiment were used to determine the background rhodamine concentration. Porewater samples were taken at 1,3,5,7, and 9 cm depth at the completion of the experiment. For the more coarse-grained sites (Shoal and Island) a porewater probe (Berg and McGlathery 2001) was used and samples were taken midway between the edge of the core and the center of the core. This location likely represented the maximum depth of porewater influence because the pressure was highest at the edge of the core and lowest in the center. The muddy sediments at the Creek site clog the porewater probes , so porewater at the Creek site was extracted by centrifuging sections of the core representing 2cm in height. The rhodamine concentration was determined using a RF-5301PC spectrofluorophotometer.

The effects of porewater advection were defined as the difference in porewater rhodamine concentration (standardized to the background concentration) between the control and treatment cores. The porewater rhodamine concentrations were used to calculate an equivalent volume of water exchanged per 2 cm depth, based on mixing between dyed and un-dyed water as

$$V_o = (V_p C_p)/C_o \qquad (2)$$

where V_o is the volume of overlying water exchanged (equal to the volume of porewater advected), V_p is the volume of porewater in a layer (area * depth * porosity), C_p is the rhodamine concentration measured in the porewater and C_o is the concentration of rhodamine in the overlying water. This calculated exchange volume was then combined with measured porewater profiles (Chapter 5, Table 3.2) to calculate NH_4^+ flux. Depths for which the normalized concentration from the control cores was greater than the normalized concentration for the treatment cores were not used to calculate flux.

Diffusion

Because of the differences in diffusion coefficient between rhodamine and NH_4^+ and also the high rhodamine concentrations used (possibly creating an artificially high concentration gradient), a bulk diffusion calculation was used to represent the diffusive flux of NH_4^+ instead of the experimental results. A lack of published values of the diffusion coefficient for rhodamine also decreased the usefulness of the still-water measurements for predicting the diffusive flux of NH_4^+. Diffusion was calculated using Fick's first law with a tortuosity correction as:

$$F= - (\varphi / \theta^2) D (\Delta C / \Delta x)$$

(3)

where F is the nutrient flux, φ is porosity, θ is tortuosity, D is the diffusion coefficient, C is concentration and x is depth in the sediment (Boudreau 1996). Tortuosity was calculated following Boudreau (1996) as

$$\theta^2 = 1- \ln(\varphi^2) \qquad (4)$$

The diffusive boundary layer thickness was set as 0.0001m which adds Δx, but not significantly. Diffusion to the water column was calculated based on measured concentrations in the water column just above the sediment surface and at 1 cm depth in the sediment (Table 3.2). A diffusion coefficient for NH4+ of 1.4×10^{-9} m^2 s^{-1} (Lavery et al 2001) was used. Diffusion was assumed to be constant for the entire 8 hour time period.

Numerical simulations

Numerical simulations of advection and diffusion were done to determine the effects of sediment permeability and the shape of the initial porewater profile on nutrient fluxes. Two sample porewater profiles were selected: (1) a linear increase in concentration from the sediment surface (representative of diffusive transport of nutrients from a deep source) and (2) a region of low concentration near the sediment surface increasing to a region of higher concentration with depth (representative of a well-mixed bed with frequent flushing of nutrients from the upper centimeters of the sediment bed) (Fig. 3.5). Both profiles were created to give the same total mass of NH_4^+ in the modeled area. Sediment porosity was held constant (0.5) for all simulations and the starting water column NH_4^+ concentration was 4 μM, similar to conditions at the Shoal and Island sites (Tables 3.1 and 3.2).

Porewater advection

Porewater advection was calculated based on the subsurface flow driven by pressure gradients produced by a surface flow over a bedform, assuming the pressure distribution is sinusoidal (Rutherford et al 1995). Advection was modeled along streamtubes in the sediment with no exchange between tubes. Calculations were done on a semicircular grid with trapezoidal cells representing the area under a single bedform. The concentration was assumed to be constant in each trapezoid and NH_4^+ flux was calculated as the discharge from a streamtube times the concentration in the final cell. Forcing, and therefore discharge, was constant with respect to time, so differences in flux were based on the evolving porewater concentrations. Vertical (v) and horizontal velocity (u), respectively, were calculated as

$$v(x,y) = v_{max} \sin(\gamma x)\exp(-\gamma y) \tag{5}$$

$$u(x,y) = -v_{max} \cos(\gamma x)\exp(-\gamma y) \tag{6}$$

where x is distance along the main flow direction, y is depth in the sediment and $\gamma = 2\pi/L$, where L is the bedform wavelength (Rutherford et al 1995). Velocity decays with depth and the maximum depth of advection is L/2 (Rutherford et al 1995). The maximum velocity (v_{max}) was calculated from the half amplitude of the pressure head distribution at the bed surface (h_{max}) based on flow and bedform characteristics as

$$h_{max} = (0.28 * (U^2/2g) * (H/0.34Y)^{3/8} \quad \text{for } H/Y<0.34 \qquad (7)$$

$$v_{max} = \gamma(k\rho g/\mu) * H_{max} \qquad (8)$$

where k is permeabililty, ρ is the density of water, μ is dynamic viscosity, U is mean water velocity, g is gravitation acceleration and H is bedform height (Rutherford et al 1995). For the simulation, $U=0.25$ m s^{-1}, $L= 0.1$ m, and $H=0.03$ m. The net flux of NH_4^+ across the sediment-water interface per bedform was calculated as the efflux minus any nutrient influx to the sediment. This influx was calculated as the volume of water exchanged across the sediment-water interface multiplied by the water column concentration of NH_4^+. Two values of k used were $5x10^{-11}$ and $5x10^{-12}$ m^2, representative of sandy and silty sediments respectively.

Diffusion

Diffusion was calculated as above using equations 3 and 4, with a time step of 5 min, a depth interval in the sediment of 1×10^{-3} m (Δx), water depth of 1 m (Y), and a sediment surface area of 1 m^2. Diffusion was calculated throughout a 5 cm porewater profile. Unlike in the above diffusion calculation, the porewater profile, and therefore the diffusive flux, varied through time. The depth limit for the calculation was set to coincide with the advection simulation (L/2) though this did not significantly affect the results.

Results

Experiments

Desorption

Nutrient release to the water column from desorption from the Hog Island Bay sediments averaged over all dates (autoclaved and non-autoclaved) for each site was greatest at the Creek site (2.4±0.5(SE) µmols g^{-1} Creek, 0.3±0.1(SE) µmols g^{-1} Shoal, 0.4±0.1(SE) µmols g^{-1} Island, Table 3.3). Nutrient increases averaged over all sites were highest in the late spring (0.7±0.4(SE) µmols g^{-1} non-autoclaved early fall; 1.3±1.0(SE) µmols g^{-1} non-autoclaved late spring, Table 3.3). Nutrient desorption for the non-autoclaved experiments (1.0±0.5(SE) µmols g^{-1}) was similar to the autoclaved experiments (1.2±0.7(SE) µmols g^{-1}) indicating the biological processing did not have a significant effect on these peak results. Desorption during the experiment was dependent on exchangeable NH_4^+ (R^2=0.80, p<0.01), though desorption always exceeded the amount of NH_4^+ from a single KCl extraction. A similar trend has been noted in other desorption experiments (Morin and Morse 1999, Morse and Morin 2005) leading to criticism of the single extraction method for nutrients. Multiple studies have found that a single extraction significantly underestimates the total amount of sorbed NH_4^+ (e.g. Laima et al 1992, Morin and Morse 1999). This extraction method was used in this study for consistency with other data available from Hog Island Bay. All measurements presented are the greatest increase from initial concentration (corrected for the control as described in methods) to represent the increase in NH_4^+ due to desorption before nutrient uptake. This approach was used because biological processing can not be completely discounted in the non-autoclaved experiments, even though the experiment was conducted in the dark.

Porewater advection

Dye concentrations in the porewater were higher in the treatment cores than in the control cores at the conclusion of the experiment, though the differences were non-significant (Fig. 3.6). Porewater rhodamine concentrations, normalized to the average water column concentration, were highest at the Shoal site, though the difference between the control and treatment was highest at the Island site. Dye was detected at all measured depths (up to 9 cm) at the Island site, to 6 cm depth at the Shoal site during both experiments and to 6 cm in early fall and 4 cm in late spring at the Creek site. The measured rhodamine concentration at 3 cm was often greater than the measured concentration at 1 cm for the control cores at the Island site, indicating that surface water was pulled in to these samples, possibly by entering the hole in which the porewater probe was inserted. To correct for this, the concentration at 3 cm in the control cores was calculated as the average of the concentration at 1 and 5 cm. Scaled to a 1 m^2 area, the volumes of porewater flushed were 1.2, 1.1, and 0.4 liters for Island, Shoal and Creek respectively.

Comparison of fluxes

Sediment addition (desorption), diffusion and porewater advection, all as determined above for an 8 hour period, were compared to examine the relative importance of these mechanisms across the 3 sites (Table 3.4). Averaged across all sites and times, desorption created the highest flux of any mechanism (33±25(SE) µmols m^{-2} h^{-1} desorption, 4±1(SE) µmols m^{-2} h^{-1} advection, 11±5(SE) µmols m^{-2} h^{-1} diffusion) with the highest flux from desorption at the Creek site (160 µmols m^{-2} h^{-1} late spring), which has the finest sediment and the highest organic content. Diffusion (6 µmols m^{-2} h^{-1}) and advection (7 µmols m^{-2} h^{-1}) at the Shoal site were relatively equal in the late spring, but much smaller than desorption (15 µmols m^{-2} h^{-}1), while desorption (3 µmols m^{-2} h^{-1}) and advection (4 µmols m^{-2} h^{-1}) were similar in the late fall and smaller than diffusion (6 µmols m^{-2} h^{-1}). At the Island site, with the coarsest grained sediment, desorption (3 µmols m^{-2} h^{-1} late spring, 7 µmols m^{-2} h^{-1} early fall) was the dominant process, with porewater advection (0 µmols m^{-2} h^{-1} late spring, 4 µmols m^{-2} h^{-1} early fall) and diffusion (0 µmols m^{-2} h^{-1} late spring, 3 µmols m^{-2} h^{-1} early fall) similar during both time periods. The calculated fluxes were generally greater than the measured fluxes made in low-flow (stirred) laboratory incubations under dark conditions for sediments from the same sites (Tyler 2002, Tyler et al 2003, Table 3.4). For all sites, diffusion and advection did not differ by more than a factor of 3. Given the coarseness of the calculations (the higher pressure gradient used in determining advection, the single time step used in diffusion calculations, and the compounding error in the porewater advection and desorption fluxes), this difference does not indicate a clear dominance by one process. The numerical simulations were used to further differentiate these processes.

Numerical simulations

The numerical simulations produced similar effluxes of NH_4^+ as the experiments, though diffusion was always lower than advection (Table 3.5). Diffusion and advection both showed a peak in efflux at the start of the simulation, but advection, particularly in the high permeability simulations, showed a rapid decline in flux (Fig. 3.7). The peak flux from the high permeability simulations was an order of magnitude higher than the peak flux from the low permeability simulations, likely reflecting the order of magnitude difference in permability. For both high permeability simulations, the flux reached zero net efflux within 3 hours of the start of the simulation.

Discussion

Importance of hydrodynamically-forced nutrient fluxes

Porewater advection and desorption are essentially the movement of a limited quantity of nutrients available at a given shear stress, not a sustained flux. Porewater advection is generally considered depth-limited as a function of permeability (e.g. Huettel and Gust 1992) and forcing (Rutherford et al 1995). In a study of particle transport into the sediment bed, Rusch and Huettel (2000) calculated a flushing rate of 14 l h^{-1} m^{-2} resulting in particle transport down to 5 cm. For a bed with a porosity of 0.5, 14 l m^{-2} is equivalent to the total volume of porewater in a bed layer 2.8 cm thick. Based on this rough calculation, the entire volume of water exchanged (to 5 cm) could be exchanged in 2 h. While this calculation is an over-simplification because porewater velocities are higher near the surface (Rutherford et al 1995), in the numerical simulation in this study, the effects of porewater advection declined greatly in the first hours. Continued flushing will have limited effects dependent on the rate of replenishment of nutrients in the flushed area by diffusion. In this sense, the total amount of nutrients that can be transferred to the water column is limited by the depth of porewater affected. The limit on desorptive flux from suspended sediment stems from the type of sediment erosion. In cohesive sediment beds, a relatively finite quantity of sediment can be eroded at a given shear stress (see Chapter 4). The erosion rate peaks soon after this shear stress is applied, then rapidly declines. The total mass of nutrients than can be transferred to the water column for a given shear stress is equal to this mass of available sediment multiplied by the mass-concentration of sorbed nutrients.

Because of these limits on desorption and porewater advection and the much higher flux rates expected in the first hours, duration must be considered when making comparisons. In this study, desorption was calculated from a peak exchange value and erosion rates measured during a 100 minute experiment. Because of this, the presented hourly flux in this study is more appropriately a representation of the amount of desorption possible when these sites are exposed to a 0.32 N m^{-2} shear stress (the maximum stress used in the erosion experiments Chapter 4) regardless of duration than an hourly flux. Care should be taken in extrapolating this measurement to time periods longer than one hour, however, there was not sufficient information for a more appropriate scaling. In addition, the porewater advection measurements were made using an artificially high pressure gradient. Because the total quantity of porewater available was limited by the depth of the core, the high pressure gradient likely affected the rate of porewater advection more than the total magnitude (limited by depth). Because the calculated rates of porewater advection were lower than seen in many other studies (e.g. Huettel and Gust 1992), the high pressure gradient did not likely cause an over-estimation of porewater advection because the values were essentially integrated for 8 hours. The numerical simulations of porewater advection indicate that errors could be made with short measurements of porewater advection because of the high initial flux, particularly in high permeability sediments. For both of these desorption and porewater advection, the time scale for measurement and comparison must be chosen carefully. For bulk nutrient flux, both processes may be best presented as integrated over a forcing event. However, in terms of effects on primary producers, the flux rate is also important.

Hydrodynamically-forced nutrient fluxes play an important role in nutrient availability in shallow coastal systems. Porewater advection and desorption from suspended sediments, with the exception of the Creek site in late spring, both produced fluxes similar to diffusion and those measured in low-flow incubations (Table 3.4). On the surface, this finding is incongruent with the much higher fluxes presented later in Chapter 4. However, the fluxes presented in this chapter are integrated over 8 hours, while the fluxes presented in Chapter 4 represent only a 100 minute experiment. Given the high initial peak and quick decline of nutrient fluxes from porewater advection and desorption, the apparent incongruity stems only from the averaging period. The similarity in magnitude does not mean that hydrodynamically-forced nutrient fluxes are unimportant. The combined flux from desorption and porewater advection ranged from 0.6 to 30 times the calculated diffusive flux. Previous research has shown that increases in water column NH_4^+ concentrations of this scale can significantly affect productivity and community structure. Gremare et al (2003) found that an increase in water column nutrient concentrations, including a 2x increase in NH_4^+ concentration, following passage of a winter storm resulted in increased bacterial production and biomass. Similarly, an increase in water column NH_4^+ concentrations from about 6 μM to 8 μM following a wind event in Florida Bay led to increased water column phytoplankton biomasss, growth and production (Lawrence et al 2004). In Hog Island Bay, an increase in inorganic nitrogen in the water column caused by mineralization of the macroalgal mat after its crash stimulates phytoplankton porduction (McGlathery et al 2001). In all of these cases, relatively small increases in nutrient concentrations resulted in changes in primary productivity and ecosystem structure. In addition to magnitude, the spatial (between sites) and temporal (seasonal and hours to minutes) variability in hydrodynamically-forced nutrient fluxes must be considered to determine the importance of these fluxes.

Spatial variability

Both the overall magnitude and relative importance of desorption, porewater advection and diffusion varied across the 3 sites. To the author's knowledge, no other study has examined all 3 mechanisms across a range of sediment and nutrient conditions within a single site. The spatial variation in NH_4^+ fluxes across Hog Island Bay is largely controlled by sediment grain size and standing stock nutrient concentrations.

Sediment grain size is a control on how much of the available stock of nutrients is sorbed to particles and a control on the quantity of particle suspended, necessary for desorption. Both the high organic and clay content of sediment at the Creek site, and similar fine-grained sites, can increase adsorption of nutrients due to increased surface area and particle charges (Boatman and Murray 1989, Laima 1992), as reflected in the higher extractable NH_4^+ and desorption fluxes (Table 3.3). The clay content also affects transport as clay contents as low as 5% can cause cohesion in a sediment bed raising the critical shear stress needed to initiate transport (van Ledden et al 2004).

Permeability, which generally increases with increasing grain size, controls the volume of porewater advected while nutrient concentrations control the mass of nutrients carrried in this porewater. The volume of porewater advected was greatest at the Island site (Table 3.2), likely due to increased permeability. Forster et al (1996) found that increased flow velocity over small mounds increased oxygen consumption in a permeable ($k=5 \times 10^{-11}$ m^2) sediment, but not in a less permeable sediment ($k=5 \times 10^{-12}$ m^2). Huettel and Gust (1992) similarly proposed that porewater advection is only important in sediments with permeability greater than 10^{-12} m^2 and the depth of sediment dominated by porewater advection (as opposed to diffusion or bioturbation) approaches 10 cm only with permeability of 10^{-11} m^2. Based on the measured grain size and porosity (calculated from bulk density), permeability at all sites in Hog Island Bay is roughly 2.5×10^{-11} m^2 (2.5×10^{-11} m^2 Creek, 2.4×10^{-11} m^2 Shoal, 3.0×10^{-11} m^2 Island) as calculated by the Kozeny-Carman equation (presented in Huettel and Webster 2001). The higher calculated permeability at the Island site supports the greater volume of porewater advected. A similar effect of permeability was seen in the numerical simulations with greater average and peak fluxes in the higher permeability simulations than in low permeability simulations (Table 3.5). The lower concentrations at the Island site lead to lower NH_4^+ fluxes from porewater advection despite higher permeability.

Temporal variability

Seasonal

The differences between the late spring and early fall fluxes may be a combination of seasonal and episodic effects. While seasonal mineralization of organic matter will affect porewater NH_4^+, porewater concentrations are also subject to episodic forcing. Just as oxygen penetration depth can increase with increasing flow velocity (Forster et al 1996, Lohse et al 1996), the penetration depth of low-nutrient overlying water can increase. High preceding forcing conditions can result in a well-mixed "water-sediment column" consisting of the water column and the upper centimeters of the sediment bed, all with similar aqueous nutrient concentrations. This effect was seen in this study in the high permeability simulations when porewater advection resulted in complete flushing of high nutrient porewater from the top 5 cm of the sediment bed below the bedform crest in less than 3 hours (Fig. 3.7). While migrating bedforms would increase the time required for complete flushing, by increasing the horizontial area affected, porewater could still be flushed in a relatively short time, leaving much slower diffusion to replenish nutrients in this area. A subsequent forcing event would produce a minimal nutrient flux from porewater advection, regardless of season, because of the previous flushing of the bed. This effect may explain the low porewater advection flux at the Island site in late spring. Porewater NH_4^+ concentrations were low (5.37 to 5.74 μM) and similar to the water column concentration (4.92 μM) resulting in a low NH_4^+ flux (Tables 3.2 and 3.4). Resuspension and deposition may result in similar variability in sorbed NH_4^+ and preceding events may affect sediment erosion. As explained further in Chapter 4, preceding forcing can directly affect erodibility and may deplete the supply of erodible sediment.

<u>Within a forcing event</u>

While the hydrodynamically-forced fluxes were comparable to diffusion over 8 hours, hydrodynamically-forced nutrient fluxes may be much higher over short time periods. Both fluxes from diffusion and porewater advection decreased with time in the numerical simulations (Fig. 3.7), but this effect was more notable for porewater advection. In the high permeability sediment, porewater advection resulted in a zero flux of NH_4^+ in under 3 hours, indicating that the sediment bed was flushed quickly resulting in a high short duration peak flux. This temporal variability was not captured in the porewater experiment and few studies have examined explicitly the temporal variability in porewater advection. Most studies displaying time series show asymptotic growth of the cumulative mass flux (e.g. Huettel and Gust 1992, Hutchinson and Webster 1998), which indicates that instantaneous flux decreased with time in these studies as well. However, little attention has been given to changes in the instantaneous flux (changes on the order of minutes). Desorption similarly occurs on a short time scale with the majority of sorbed nutrients released in under 2 hours (Morin and Morse 1999).

Ecological significance

The majority of research examining hydrodynamic effects on nutrient flux across the sediment-water interface has focused on a single mechanism of transport and to the author's knowledge none have considered the relative importance of both porewater advection and desorption across a gradient of sites in a small geographic area. These mechanisms are of the same order of magnitude as diffusive fluxes in Hog Island Bay when averaged over 8 hours. However, differences in the timing and duration of porewater advection and desorption fluxes versus diffusive fluxes is important. Porewater advection and desorption both result in a rapid increase in available nutrients, on the scale of one hour (Morin and Morse 1999, Morse and Morin 2005 for time scales of desorption), which may benefit rapidly-growing, ephemeral species, such as macroalgae and microalgae, while slower growing species, such as seagrass, may not be less able to use the rapid efflux of nutrients (Fig. 3.8). This difference in timing may explain some of the effects on community structure seen in field studies following forcing events (Gremare et al 2003, Lawrence et al 2004). In Hog Island Bay and similar shallow nearshore systems, hydrodynamically-forced nutrient fluxes may be important as a control on community structure by providing pulsed nutrient fluxes. Our results highlight that nutrient fluxes between the sediment and water column should be viewed in the context of the time scales in which the local primary producers are able to use these fluxes as well as the overall magnitude of the fluxes.

References

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

Boatman, CD and JW Murray. 1982. Modeling exchangeable NH_4^+ adsorption in marine sediments: Processes and controls of adsorption. *Limnology and oceanography*. 27(1):99-110.

Boudreau, BP. 1996. The diffusive tortuosity of fine-grained unlithified sediments. *Geochimica et cosmochimica acta*. 60(16):3139-3142.

Boynton WR, JD Hagy, L Murray, C Stokes and WM Kemp. 1996. A comparative analysis of eutrophication patterns in a temperate coastal lagoon. *Estuaries*. 19(2B):408-421.

Cochlan, WP and PJ Harrison. 1991. Uptake of nitrate, ammonium, and urea by nitrogen-starved cultures of *Micromonas-pusilla* (prasinophyceae)- transient responses. *Journal of phycology*. 27(6):673-679.

Forster, S, M Huettel and W Zeibis. 1996. Impact of boundary layer flow velocity on oxygen utilisation in coastal sediments. *Marine ecology progress series*.143:173-185.

Gremare, A, JM Amouroux, G Cauwet, F Charles, C Courties, F De Bovee, A Dinet, JL Devenon, XD De Madron, B Ferre, P Fraunie, F Joux, F Lantoine, P Lebaron, JJ Naudin, A Palanques, M Pujo-Pay and L Zudaire. 2003. The effects of a strong winter storm on physical and biological variables at a shelf site in the Mediterranean. *Oceanologica acta*. 26(4):407-419.

Gust, G. and V. Müller. 1997. Interfacial hydrodynamics and entrainment functions of currently used erosion devices. In *Cohesive sediments*. Burt N., R. Parker, and J. Watts (eds). John Wiley and Sons. 149-174.

Hopkinson, CS, AE Giblin, J Tucker, and RH Garritt. 1999. Benthic metabolism and nutrient cycling along an estuarine salinity gradient. *Estuaries*. 22(4):863-881.

Huettel, M and IT Webster. 2001. Porewater flow in permeable sediments. In *The benthic boundary layer*. BP Boudreau and BB Jørgensen (eds). Oxford University Press, New York. 144-179.

Huettel, M and G Gust. 1992. Impact of bioroughness on interfacial solute exchange in permeable sands. *Marine ecology progress series*. 89(2-3):255-267.

Huettel, M, W Ziebis, S Forster and GW Luther. 1998.Advection transport affecting metal and nutrient distributions and interfacial fluxes in permeable sediments. *Geochimica et cosmochimica acta*. 62(4):613-631.

Hutchinson, PA and IT Webster. 1998. Solute uptake in aquatic sediments due to current-obstacle interactions. *Journal of environmental engineering-ASCE*. 124(5):419-426.

Laima, MJC. 1992. Extraction and seasonal variation of NH_4^+ pools in different types of coastal marine sediments. *Marine ecology progress series*.82:75-84.

Lawrence, D, MJ Dagg, H Liu, SR Cummings, PB Ortner, and C Kelble. 2004. Wind events and benthic-pelagic coupling in a shallow suptropical bay in Florida. *Marine ecology progress series*. 266:1-13.

Lawson, SE, PL Wiberg, KJ McGlathery and DC Fugate. 2007. Wind-driven sediment suspension controls light availability in a shallow coastal lagoon. *Estuaries and coasts*. 30(1):102-112.

Lavery, PS, CE Oldham and M Ghisalberti. 2001. The use of Fick's First Law for predicting porewater nutrient fluxes under diffusive conditions. *Hydrological processes*. 15:2435-2451.

Lohse, L, EHG Epping, W Helder and W van Raaphorst. 1996. Oxygen pore water profiles in continental shelf sediments of the North Sea: Turbulent versus molecular diffusion. Marine ecology progress series. 145(1-3):63-75.

Mackin, JE and RC Aller. 1984. Ammonium adsorption in marine sediments. *Limnology and oceanography*. 29(2):250-257.

McGlathery, KJ, IC Anderson and AC Tyler. 2001. Magnitude and variability of benthic and pelagic metabolism in a temperate coastal lagoon. *Marine ecology progress series*. 216:1-15.

Morin, J and JW Morse. 1999. Ammonium release from resuspended sediments in the Laguna Madre estuary. *Marine chemistry*. 65(1-2):97-110.

Morse, JW and J Morin. 2005. Ammonium interaction with coastal marine sediments: influence of redox conditions on K*. *Marine chemistry*. 95(1-2):107-112.

Pedersen, MF and J Borum 1997. Nutrient control of estuarine macroalgae: growth strategy and the balance between nitrogen requirements and uptake. *Marine ecology progress series*. 161:155-163.

Rusche, A and M Huettel. 2000. Advective particle transport into permeable sediments – Evidence from experiments in an intertidal sandflat. *Limnology and oceanograpy*. 45(3):525-533.

Rutherford, JC, JD Boyle, AH Elliot, TVJ Hatherell and TW Chiu. 1995. Modeling benthic oxygen uptake by pumping. *Journal of environmental engineering*. 121(1):84-95.

Tengberg, A, H Stahl, G Gust, V Muller, U Arning, H Andersson and POJ Hall. 2004. Intercalibration of benthic flux chambers I. Accuracy of flux measurements and influence of chamber hydrodynamics. *Progress in oceanography*. 60:1-28.

Thouzeau, G, J Grall, J Clavier, L Chauvaud, F Jean, A Leynaert, S ni Longphuirt, E Amice, and D Amouroux. 2007. Spatial and temporal variability of benthic biogeochemical fluxes associated with macrophytic and macrofaunal distributions in the Thau lagoon (France). *Estuarine coastal and shelf science*. 72(3):432-446.

Touchette, BW and JM Burkholder. 2000. Review of nitrogen and phosphorus metabolism in seagrass. *Journal of experimental marine biology and ecology*. 250:133-167.

Tyler, AC. 2002. Impact of benthic algae on dissolved organic nitrogen in a temperate coastal lagoon. PhD Dissertation. University of Virginia, Charlottesville, VA.

Tyler AC, KJ McGlathery and IC Anderson. 2001. Macroalgal mediation of dissolved organic nitrogen fluxes in a temperate coastal lagoon. *Estuarine coastal and shelf science*. 53:155-168.

Tyler, AC, KJ McGlathery and IC Anderson. 2003. Benthic algae control sediment-water column fluxes of organic and inorganic nitrogen compounds in a temperate lagoon. *Limnology and oceanography*. 48:2125-2137.

Tyler, AC, KJ McGlathery and SA Macko. 2005. Uptake of urea and amino acids by the macroalgae *Ulva lactuca* (Chlorophyta) and *Gracilaria vermiculophylla* (Rhodophyta). *Marine ecology progress series*. 294:161-172.

van Ledden, M, WGM van Kesteren and JC Winterwerp. 2004. A conceptual framework for the erosion behaviour of sand-mud mixtures. *Continental shelf research*. 24:1-11.

Figures and Tables

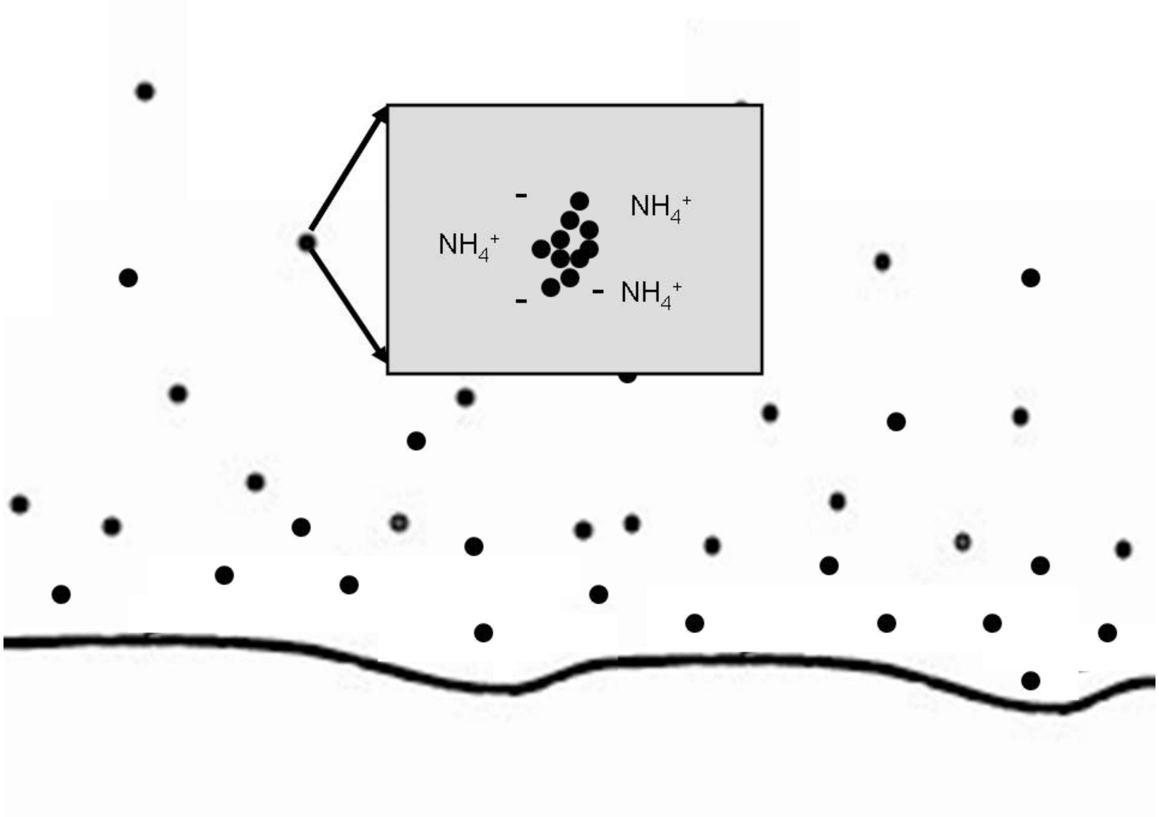

Figure 3.1. Desorption. Suspended particles often carry sorbed nutrients. When the surrounding nutrient concentration changes, as it does when sediment is moved from the bed to the water column, these nutrients can desorb.

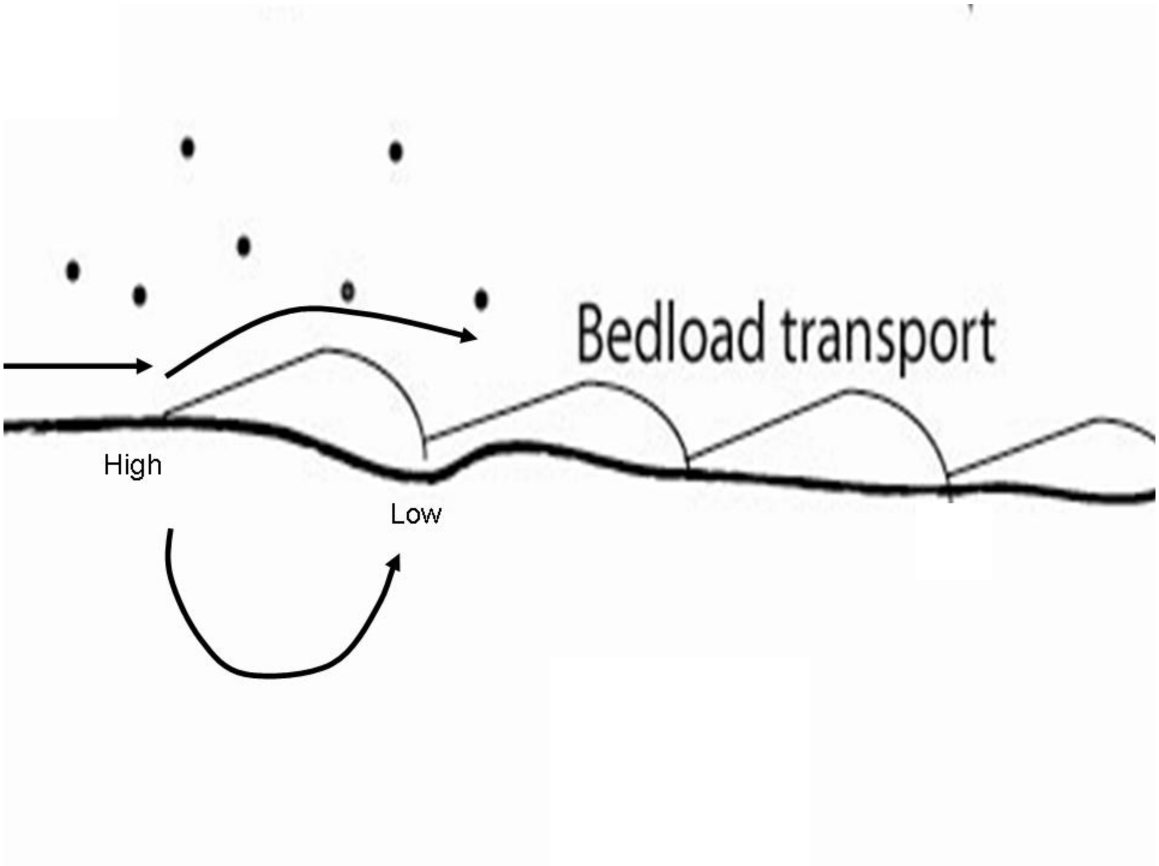

Figure 3.2. Porewater advection. When water flow is diverted around an object, such as a bedform, animal tube or burrow, areas of high and low pressure can be generated leading to porewater advection.

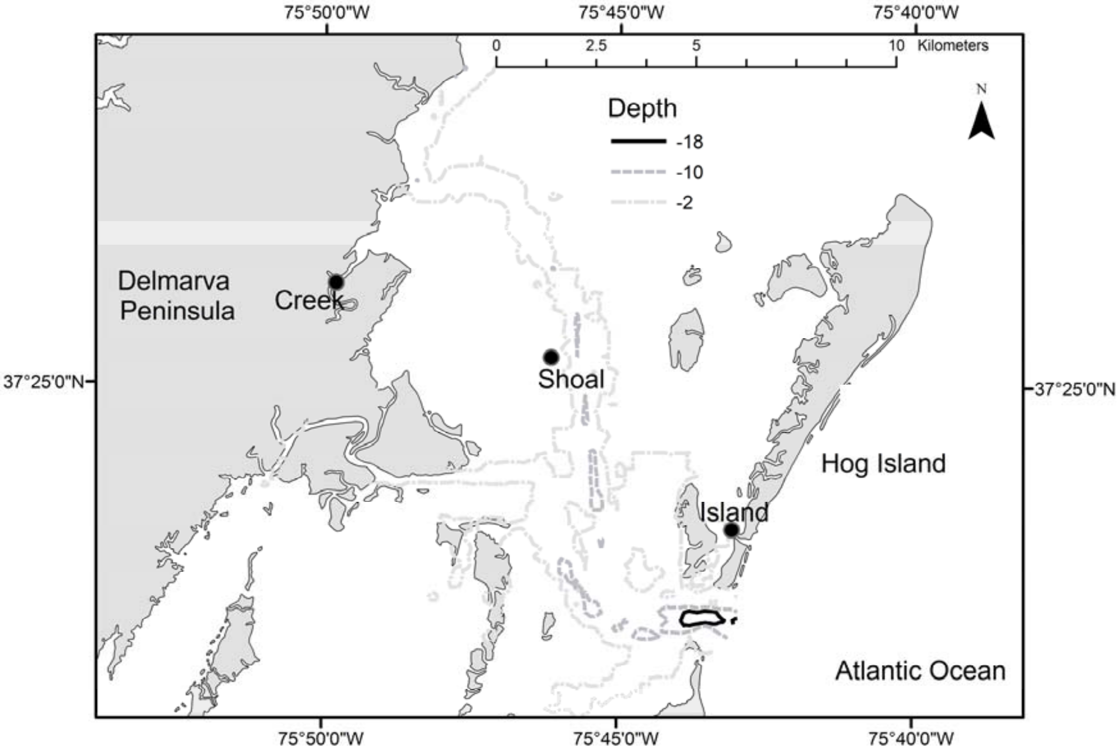

Figure 3.3. Map of study sites. The 3 selected sites in Hog Island Bay represent a gradient of nutrient availability and sediment characteristics.

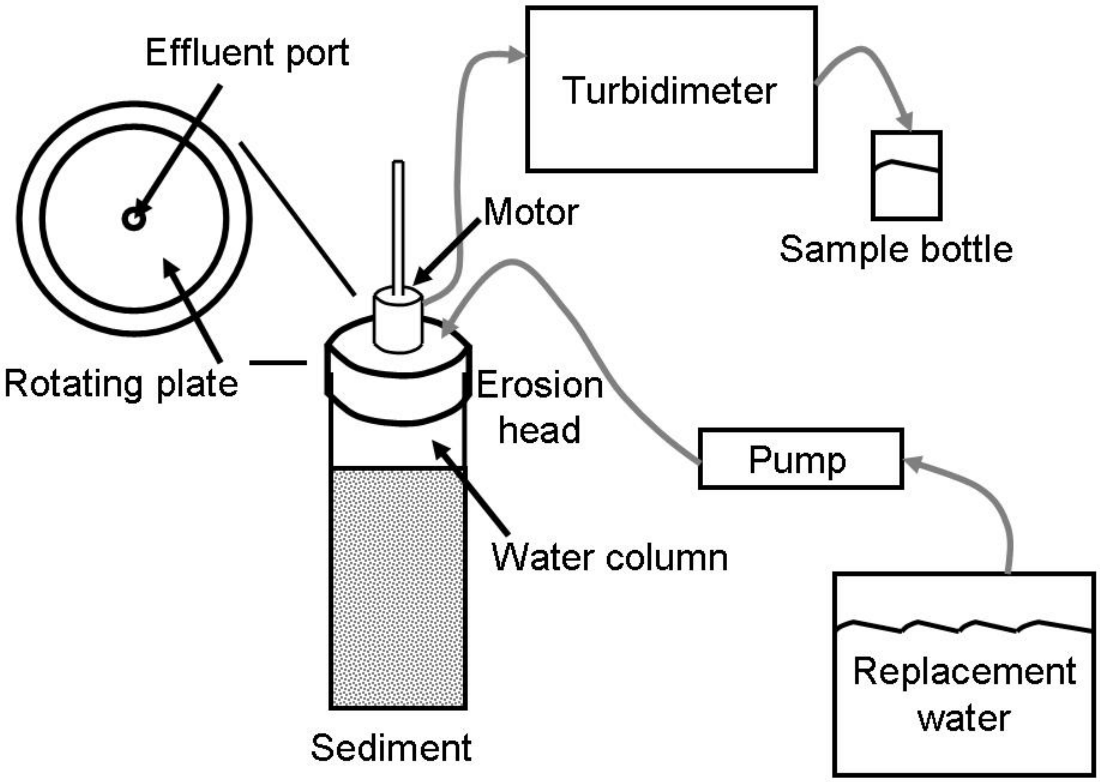

Figure 3.4. Gust erosion microcosm. The erosion head is a spinning disk that generates a uniform shear stress on the sediment surface of a core. The action of the erosion head and the suction from water leaving the core creates a pressure gradient from the outside of the core to the center which was used to force porewater advection in this study.

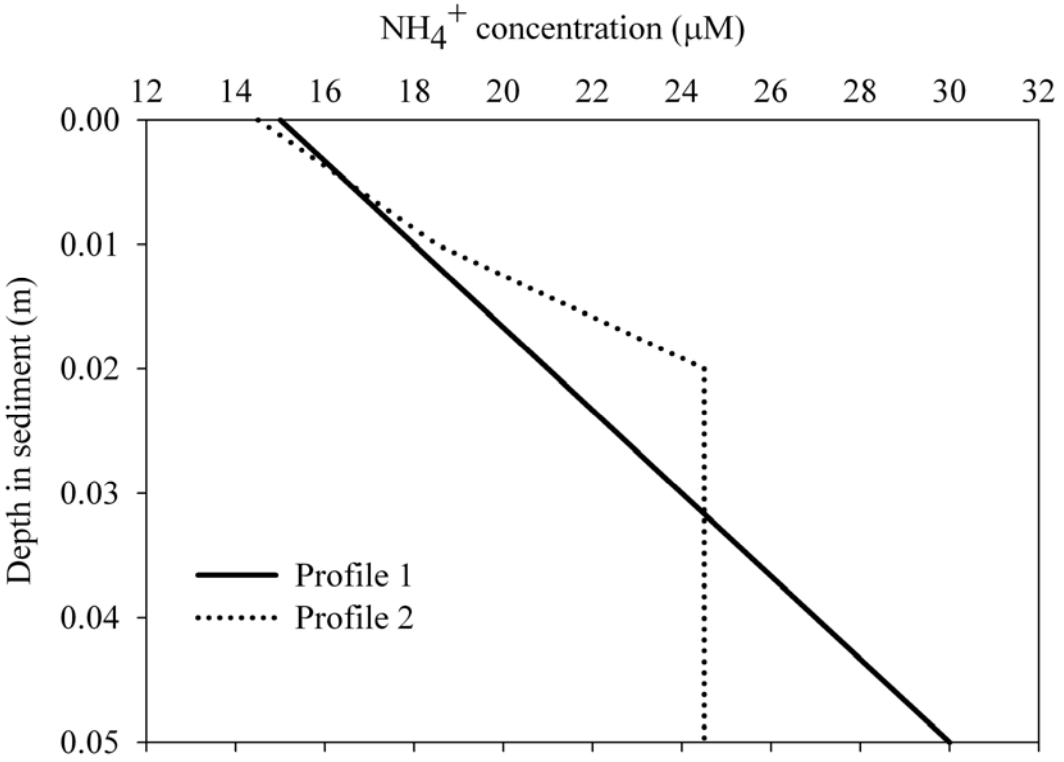

Figure 3.5. Starting porewater profiles for the numerical simulations. Two profiles were used (1) a linear increase in concentration from the sediment surface (representative of diffusive transport of nutrients from a deep source) and a region of low concentration near the sediment surface increasing to a region of higher concentration with depth (representative of a well-mixed bed with frequent flushing of nutrients from the upper centimeters of the sediment bed). The profiles were created to have the same total quantity of nutrients in the upper 0.05 m of the bed.

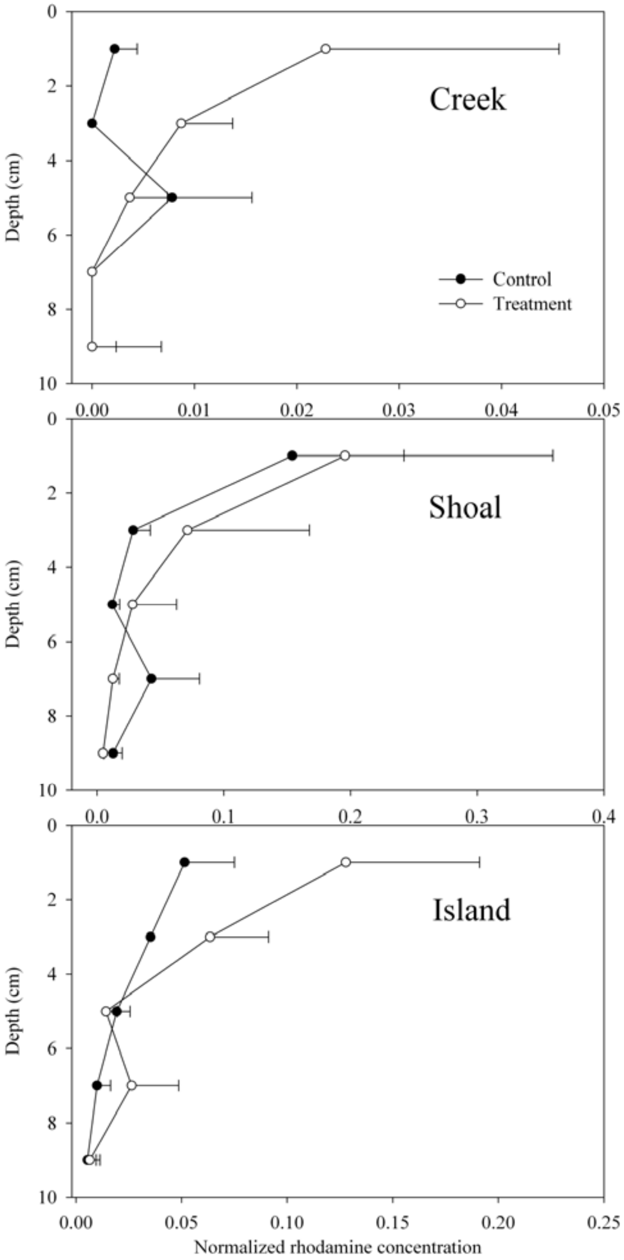

Figure 3.6. Results of porewater experiment. The concentration of rhodamine dye was higher in the porewater of the treatment cores (exposed to pressure gradients) than the control cores at all sites.

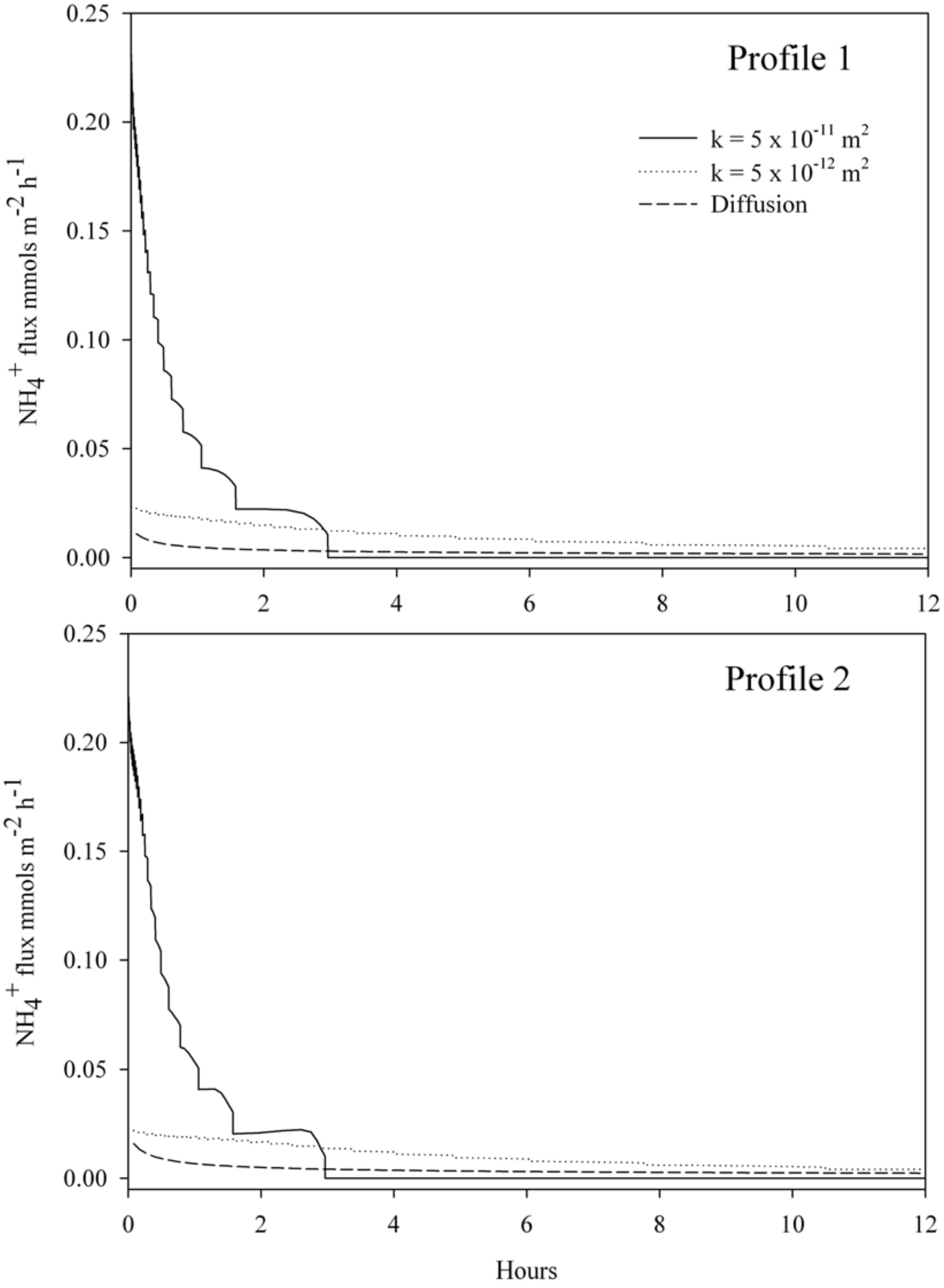

Figure 3.7. Simulation results for porewater profile 1 (a) and profile 2 (b). Porewater advection always caused higher fluxes than diffusion, particularly at the start of the simulation. The high permeability sediments had greater fluxes but short duration than the low permeability sediments. The two profiles produced similar fluxes averaged for the model period.

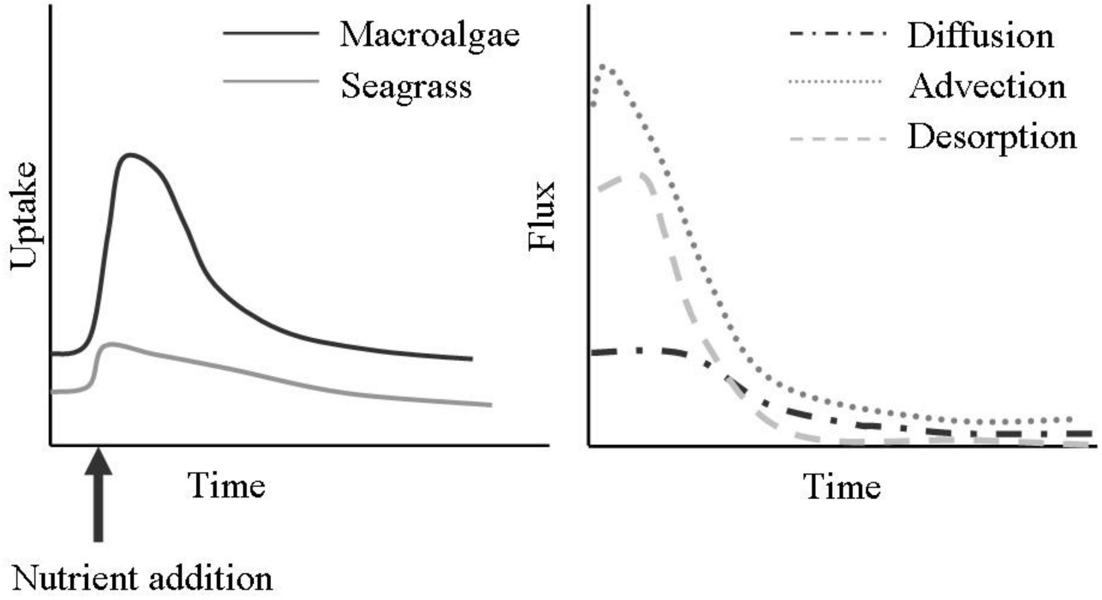

Figure 3.8. Comparison of time scales of nutrient uptake and flux. Benthic primary producers with high uptake rates may be better able to use nutrient fluxes from porewater advection and dsorption.

Table 3.1. Summary of site characteristics. Data with * are from McGlathery et al 2001, data with ** are from Thomsen et al 2006, and data with *** are Lawson from this dissertation. Numbers in parentheses are standard error.

	Creek	**Shoal**	**Island**
*Dissolved inorganic nitrogen (µM) **	4.4 (0.9)	2.3 (2.5)	1.2 (0.4)
*Dissolved organic nitrogen (µM) **	15.4 (1.9)	12.1 (3.7)	11.8 (1.6)
*Dissolved inorganic phosphorus (µM) **	1.4 (0.2)	0.8 (0.1)	0.5 (0.1)
Macroalgal biomass (g DW m^{-2}*) ***	19.4 (3.66)	128.44 (20.63)	4.58 (0.89)
Microalgal biomass (µg m^{-2}*) ****	6.5(0.8)	4.2(2.7)	11.7(0.7)
*Sediment grain size (µm) ****	28(9)	74(4)	120(2)
Organic content (%)	3.7(0.1)	1.1(0.1)	0.6(0.2)
Porosity	0.7(0.02)	0.5(0.01)	0.5(0.01)

Table 3.2. Summary of information used to calculate porewater advection mass transfer. The volume of porewater exchanged was calculated from the dye experiments and multiplied by the porewater NH_4^+ concentration to calculate a mass transfer (μmols m^{-2}).

		Creek					**Shoal**					**Island**			
		Late spring		**Early fall**			**Late spring**		**Early fall**			**Late spring**		**Early fall**	
Depth (m)	*Volume of porewater exchanged (l m^{-2})*	*NH_4^+ (μM)*	*Mass transfer*	*NH_4^+ (μM)*	*Mass transfer*	*Volume of porewater exchanged (l m^{-2})*	*NH_4^+ (μM)*	*Mass transfer*	*NH_4^+ (μM)*	*Mass transfer*	*Volume of porewater exchanged (l m^{-2})*	*NH_4^+ (μM)*	*Mass transfer*	*NH_4^+ (μM)*	*Mass transfer*
0	---	8(1.5)		12(10)		---	9(4)		4(0.3)		---	5(1)		1(0.5)	
0.00-0.02	0.31(0.34)	53(18)	14	124(22)	34	0.46(2.0)	44(16)	16	43(15)	18	0.74(0.65)	6(2)	0.6	22(19)	16
0.02-0.04	0.13(0.07)	140(66)	17	165(15)	20	0.47(1.1)	63(12)	26	33(9)	14	0.34(0.59)	6(0.2)	0.3	39(31)	13
0.04-0.06	0	127(65)	0	345(19)	0	0.18(0.38)	83(--)	13	34(10)	6	0	5(1)	0	56(27)	0
0.06-0.08	0	142(60)	0	398(126)	0	0	70(22)	0	49(11)	0	0.16(0.22)	5(3)	0.1	70(38)	11
0.08-0.10	0	145(79)	0	529(100)	0	0	50(--)	0	49(1)	0	0.01(0.06)	16(4)	0	59(24)	1
Total mass (8 h)			**31**		**55**			**55**		**38**			**1**		**40**

Table 3.3.Results of the desorption experiment. The maximum value was combined with the results of an erosion test (sediment eroded, Chapter 4) to determine the flux of NH_4^+ from a sediment suspension event. The NH_4^+ flux calculated from the experiment was always greater than that predicted by the single KCl extraction of NH_4^+.

Site	**Date**	**Autoclaved?**	**Sediment eroded (g/m²)**	**Ext NH_4^+ (µmols/g)**	**Maximum (µmols/g)**	**Mass transfer (µmol/m²)**
Creek	Early fall	No	14(3)	0.2(0.04)	1.5(1.0)	21(15)
Shoal	Early fall	No	49(10)	0.05(0.004)	0.1(0.2)	5(10)
Island	Early fall	No	30(10)	0.1(0.02)	0.4(0.4)	12(13)
Creek	Late spring	No	84(22)	0.3(0.01)	3.2(0.2)	260(70)
Shoal	Late spring	No	56(1)	0.1(0.02)	0.4(0.3)	25(19)
Island	Late spring	No	24(17)	0.2(0.01)	0.2(0.2)	5(6)
Creek	Late spring	Yes	84(22)	0.3(0.01)	2.5(0.8)	210(87)
Shoal	Late spring	Yes	56(1)	0.1(0.02)	0.4(0.2)	24(9)
Island	Late spring	Yes	24(17)	0.2(0.01)	0.7(0.2)	17(13)

Table 3.4 Comparison of the fluxes of NH_4^+ calculated from the experiments for the 3 study sites at 2 time periods. Desorption generally created the largest fluxes and porewater advection and diffusion produced fluxes of similar magnitudes at the Shoal and Island sites. The fluxes determined in this study were generally similar to those measured in the low-flow incubations of Tyler 2002 (presented here as low-flow). All values are in μmols m^{-2} h^{-1}.

Late spring	*Diffusion*	*Advection*	*Desorption*	*Low flow*
Creek	14	4	160	30
Shoal	6	7	15	6
Island	0	0	3	1
Early fall				
Creek	35	7	13	2
Shoal	6	5	3	0
Island	3	5	7	4

Table 3.5. Simulation results. Advection produced higher fluxes than diffusion, especially during the short peak fluxes at the beginning of simulations. The different porewater profiles had relatively minor effects on nutrient flux. All results are in µmols m^{-2} h^{-1}.

	Profile 1			**Profile 2**		
	Diffusion	*Advection(low)*	*Advection(high)*	*Diffusion*	*Advection(low)*	*Advection(high)*
Average	3	10	13	4	13	18
Peak	11	23	230	16	22	220

Chapter 4: Physical and biological controls on sediment erodibility

Abstract

Recent research has shown that the erodiblity of a muddy sediment bed is dependent on its depositional history and biotic influences, such as bioturbation and benthic primary producers, as well as sediment grain size and density, but the details of this dependence are not well-characterized. This study used controlled erosion experiments to determine changes in erodibility at 3 sites in a shallow coastal lagoon from early spring to late fall. These sites included a fine-grained mainland creek site, an intermediate-grain-size mid-lagoon shoal site, and a relatively coarse-grained back-barrier island site. To investigate controls on erodibility, sediment characteristics (bulk density, organic content and benthic chlorophyll a) at each site were measured and meteorological data (preceding wind speed, change in tidal amplitude and temperature) from NOAA were used to characterize preceding conditions. Two sites showed significantly greater sediment erosion during experiments on sediment cores collected during the summer months (0.07 kg m^{-2} Island, 0.15 kg m^{-2} Shoal) than the rest of the year (0.01 kg m^{-2} Island, 0.03 kg m^{-2} Shoal). Erosion at the Creek site showed no temporal variability (0.03 kg m^{-2} average for all time periods). Variations in erodiblity among sites were caused largely by differences in grain size. While the periods of high erodibility coincided with higher organic content, preceding wind speed, and temperature (Shoal only), the measured sediment characteristics and meteorological data did not explain the seasonal variability in erodibility well. Examination of further data available

for the sites indicated that the increased erodibility is likely due to trapping of fine material by seasonal accumulations of macroalgae and increased invertebrate density during the summer months.

Introduction

An understanding of and ability to predict sediment suspension is important for successful management of estuaries and lagoons. Sediment suspension and transport influence both water column nutrient availability (e.g. Chen and Sheng 2005, Zheng et al 2004) and light availability (e.g. Lawson et al 2007), two of the dominant controls on benthic primary productivity. Sediment transport also affects engineering efforts such as channel maintenance and the stability of structures such as piers. Two factors control the initiation of sediment transport: the forcing conditions acting on the sediment and the sediment's resistance to transport. Spatial and temporal variability in these factors combine to create variability in sediment erosion. Current technology allows high resolution measurements of most forcing conditions, such as wind, waves and currents, and well-validated, mechanistic equations have been developed to represent how these external forces are transformed into forces acting on the sediment bed. Sediment erodibility is, however, more difficult to measure, and therefore predict, because even minor disturbances to the sediment surface can have profound effects on measured erodibility (Tolhurst et al 2000b). In addition, comparative measurements of bed erodiblity require replication of field forcing conditions. The continued development of both in situ and laboratory devices to control shear stresses and mimic hydrodynamic forcing has allowed improved characterization of sediment erodibility (e.g. Virginia Institute of Marine Science Sea Carousel, Maa et al 1993; Gust microcosm, Gust and Müller 1997).

Sediment erodibility is characterized in a variety of ways. First, sediment erosion can be classified as Type I (depth-limited) or Type II (unlimited) erosion (as described in

Sanford and Maa 2001). In Type I erosion, the force necessary to transport/suspend sediment varies with depth, resulting in a relatively finite quantity of sediment that can be eroded at a given bed shear stress. Type II erosion occurs when there is no change in critical shear stress with depth, so the erosion rate remains constant through time for a constant bed shear stress. Type I erosion is often considered characteristic of fine-grained, cohesive sediments, while Type II erosion typically occurs in coarser, well-sorted, non-cohesive sediments. The identification of a critical shear stress, either constant or varying through time and depth, is implied in characterization of erosion as either Type I or Type II. However, the definition of critical shear stress, and its appropriate identification both in the field and in the lab, varies widely between studies (Sanford and Maa 2001). Some of this variability may stem from attempts to define a single shear stress for a sediment bed, neglecting variations with depth and time. Similar ambiguity has surrounded characterization of erosion rate. Type I erosion is characterized by a decay in erosion rate with time for a given stress, while the erosion rate is relatively constant in Type II erosion. Although erosion rate is consistently expressed as a mass of sediment per area per time, some studies of Type I erosion have defined it as the initial erosion rate following an increase in shear stress (e.g. Maa et al 1998), while others have defined it as an average rate over time (e.g. Tolhurst et al 2000a).

Changing physical characteristics, particularly consolidation, affect Type I erosion. Increasing consolidation with time since bed deposition has been experimentally shown to decrease erodibility in laboratory created beds (e.g. Lundkvist et al 2007) while frequent remobilization of sediment, due to suspension from high shear stresses, causes lower stability beds (Bale et al 2007). High shear stresses can also cause destruction of an overlying biofilm, decreasing bed stability (de Brouwer et al 2000). However, long duration exposure to shear stresses below the critical erosion threshold can cause particle rearrangement, resulting in increased stability of the bed (Paphitis and Collins 2005, Haynes and Pender 2007). In shallow coastal systems, these shear stresses will be generated by tides and wind-driven waves and currents.

Biotic factors can also affect bed stability, particularly for fine-grained sediment. Micropyhtobenthos, microscopic algae and cyanobacteria, can create a mat on the sediment surface, protecting it from erosion/resuspension. These mats can more than double bed stability by excreting extracellular polymeric substances (EPS) which binds sediment particles (de Brouwer et al 2000, Quaresma et al 2004). These polymers create high bed stability until the mat fails, due to high shear stresses or grazing, leading to high rates of sediment transport (Miller et al 1996). Similarly, patchiness of the biofilm may be as important as strength of the biofilm in determining the erodibility of the sediment bed (Neumeier et al 2006). In a controlled laboratory comparison, Lundkvist et al (2007) found that benthic diatoms and bacteria had a greater effect on sediment stability than bed consolidation.

Additionally, macrophytes (seagrass and macroalgae) and fauna can affect erodibility of the sediment bed through indirect means. By decreasing near-bed hydrodynamic activity, macrophytes can trap fine material and organic matter leading to significantly different sediment characteristics within a stand of benthic macrophytes than outside of it (Stamski and Fields 2006, Hasegawa et al 2008). This trapped material can then be resuspended or transported if macrophyte biomass declines, either due to seasonal variations in temperature and light or due to disturbances (Hasegawa et al 2007). Animals can also affect sediment erodibility, primarily through bioturbation and feeding behavior. Bioturbators can result in the stabilization or destabilization of a bed, by the addition or subtraction of mud (Paarlberg et al 2005). Bioturbators can also decrease bulk density, leading to increased erodiblity of the bed (Rowden et al 1998). Andersen et al (2002) showed that the presence of mud snails increased the sediment erosion rate 2 to 4 times over the control, likely because of increased deposition of fecal pellets and ingestion of biofilms (Andersen 2001). High densities of benthic grazers may prevent the development of sediment biofilms (Andersen 2001) or disturb surface sediments resulting in unconsolidated, easily eroded surface sediments (Orvain et al 2007).

This study is designed to examine changes in erodibility at 3 sites in a shallow coastal lagoon from early spring to late fall. These sites represent a gradient of grain size, primary producer biomass, and exposure, but experience similar tidal, temperature and wind conditions. The range of sites and times was chosen to examine both seasonal and spatial variation in erodibility and interactions between these two types of variability. Sediment suspension was measured during experiments with controlled forcing conditions, so that temporal and spatial variations in measured sediment suspension had to be caused by variations in erodibility. Six possible predictive variables were recorded for each site for each of six sampling events. These variables include 3 global, meteorologically forced variables: preceding wind speed, preceding tidal variation and water temperature, and 3 site specific bed characteristics: organic content, bulk density and benthic chlorophyll a concentration. These variables were chosen both for potential influence on sediment erodibility and because they are frequently measured in monitoring programs, making historical data on these variables easy to gather. These 6 variables also encompass common biotic and physical controls on sediment erodibility.

Methods

Study site

This study was conducted in Hog Island Bay, VA, on the eastern side of the Delmarva Peninsula (Fig. 4.1). Hog Island Bay is a shallow coastal lagoon with an average depth of about 1 m at MLW and no riverine input. Primary production in the lagoon is dominated by benthic microalgae and macroalgae. Restoration of seagrass (*Zostera marina*), the dominant primary producer until the 1930's, began in 2006 in some areas of the lagoon. Sediment in the lagoon ranges from fine silt to fine sand with increasing grain size with distance from the mainland (Lawson 2004). Because of the shallow depth, sediment suspension is closely related to wind forcing (Lawson et al 2007).

Three locations within the bay were used for this study representing a gradient from the muddy Creek site to the Island site with fine sands (Table 4.1). The Creek site is characterized by organic rich, fine-grained sediment (74% silt and clay). The site is next to a *Spartina alterniflora* marsh in a tidal creek with very little freshwater input. Current velocities are relatively low in this area and wave exposure is minimal (Lawson 2004). Macroalgal biomass was low at this site and benthic microalgae were the dominant primary producer. The Shoal site was next to relic oyster reefs and had seasonally high accumulations of macroalgae that reached over 700 g DW m^{-2} (McGlathery unpublished data). Previous research has shown that when this mat "crashes", the added organic matter is quickly remineralized and transferred to the water column as dissolved organic and dissolved inorganic compounds (Tyler et al 2001). This site had the greatest wind fetch and is therefore likely the most subject to wave suspension (Lawson 2004). Sediment at this site is very fine sand (19% silt and clay). The Island site was located on the lagoon side of a barrier island, between the island and a smaller marsh island. This site was characterized by the coarsest sediment of the 3 sites (120±2(SE) μm) and relatively low organic content. Macroalgal biomass is lowest at this site with typical peak annual biomasses of only 10 – 20 g DW m^{-2} (McGlathery unpublished data). Current velocities in this area are higher than at the Creek or Shoal site, but the large grain size results in little suspension and high light availability (Lawson et al 2007). Sampling was conducted at all 3 sites approximately every 6 weeks from mid-April to mid-November.

Erosion experiments

Sample collection, storage and preparation

Sediment samples for the erosion experiments were taken by hand on a falling tide, within 1 h of predicted low tide, using polycarbonate core tubes with an internal diameter of 10.8 cm and a total height of 22.5 cm; a 10 cm water column was preserved above the sediment surface. Core tubes were sealed using rubber plumbing end caps and kept in the dark at 4 °C for transport back to the lab. Ambient water was collected in 20 l carboys for use as the replacement water during the experiments and for core storage until analysis. Upon arrival at the lab, within 1 h of core collection, the cores were submerged in a cooler of ambient water oxygenated by an aquarium bubbler and maintained in low light at ambient temperatures.

Shear stress manipulation

A Gust erosion microcosm (Gust & Müller 1997, microcosm, hereafter, Fig. 4.2) was used to apply specified shear stresses to the sediment surface during the erosion tests. It consists of an erosion head with a rotating plate and a push through water system fitted over a polycarbonate core tube. The combination of the rotation of the plate and the suction from the water system in the center of the core generates a near-uniform bed shear stress and diffusive boundary layer thickness, though not a uniform pressure distribution (Tengberg et al 2004). Shear stress is controlled through a calibrated datalogger system that also records turbidity and motor RPM every second. Immediately prior to the experiment, a water sample was pumped from the replacement water to provide reference/background concentration values. The cores were then exposed to a low shear stress of 0.01 Nm^{-2} for 20 minutes as a flushing step, then incremental shear stress increases every 20 minutes to 0.08, 0.16, 0.24 and 0.32 Nm^{-2}, similar to the range of bed shear stresses in a shallow coastal lagoon (Lawson et al 2007). Shear stress increases were generated by calibrated increases in pumping rate and plate rotation rate.

Effluent water was collected in 1 l Nalgene bottles exchanged every 5-10 min, depending on the pumping rate. The effluent water was subsampled and filtered for total suspended solids (TSS), separated into particulate inorganic matter (PIM) and particulate organic matter (POM) based on loss on ignition. All experiments were conducted in low light conditions. Results of concurrent nutrient analysis are presented in Chapter 5. TSS (sample volumes 150-550 ml) was analyzed by weight difference after filtration onto pre-combusted, pre-weighed Whatmann GF/F filters (nominal particle retention 0.7 µm). To correct for the mass of measured components carried in the replacement water, all fluxes were corrected with a background concentration, set as the lowest TSS recorded during the experiment. This value was chosen to guarantee that all sediment fluxes were positive since sediment can not be consumed. Data from the flushing step were discarded and only data from the higher shear stress steps were analyzed. The experiments were repeated in triplicate for each site during six sampling campaigns from April to November 2006 (Table 4.2).

Site characterization

To account for differences in the sediment and water column characteristics on the dates of sampling, site characterizations were made for each sampling event. Syringe cores (1 cm depth) were taken for benthic chlorophyll a, frozen immediately, and later extracted with a 45% acetone, 45% methanol, 10% deionized water solution. Samples were then analyzed spectrophotometrically using the equations of Lorenzen (1967). Bulk density and organic content were determined by drying 2 ml samples taken with a syringe core to 105 °C (bulk density), then 500 °C (organic content by difference between dry and combusted weights). Sediment grain size was determined once at each site by a combination of wet sieving (sands) and analysis on a Sedigraph 5100 (silts and clays) of triplicate samples of the top 2 cm of the sediment bed. Water temperature, preceding wind speed (hourly averages for the 6 hours preceding sample collection) and tidal amplitude (hourly change in tidal elevation for the 6 hours preceding the experiment) were gathered from NOAA CO-OPS stations at Kiptopeke, VA (water temperature and wind speed), 36 km away from the site, and Wachapreague, VA (tidal amplitude), 21 km away from the site.

Results

Site characterization

There was significant variability in sediment and nutrient characteristics among the 3 sampling sites (Table 4.2). Bulk density increased with distance from the mainland and ranged from 0.6 to 1.4 g cm^{-3}. Organic content showed the opposite trend, with high values (3.5 to 4.0 %) at the Creek site and low values (0.3 to 1.4%) at the Island site. Sediment grain size was measured only in June and showed a trend of increasing grain size with distance from the mainland, similar to that seen in Lawson (2004). Benthic chlorophyll was highest at the Island site (7.8 – 14.5 μg m^{-2}) with similar values at the Creek (3.7 -14.3 μg m^{-2}) and Shoal (3.1 – 6.2 μg m^{-2}) sites.

While many of the site variables varied with time, only water temperature showed a clear seasonal trend (Table 4.3). Water temperature was highest from June to September. Wind speed was highly variable with no consistent seasonal trend. Because wind speed was determined only for the 6 hours preceding sampling, wind speed often showed high variability within a single sampling effort (Table 4.3). At all sites, organic content was highest in July, though timing of minimum values was not consistent across sites (Table 4.2).

Erosion tests

Sediment suspension in Hog Island Bay was predominantly Type I and showed seasonal variation. Erosion rates during the experiments ranged from 8-164 g m^{-2} h^{-1}. Erosion typically peaked quickly after each shear stress addition then decreased to close to background values (Fig. 4.3). The pattern of cumulative erosion as a function of shear stress at all sites also indicates Type I erosion owing to the non-linear relationship between cumulative mass eroded and time (Fig. 4.4). At both the Shoal and Island site, erodibility was greater during the summer months (June, July and August for the Shoal site, p =0.009; June and July each unique for the Island site, p=0.0001; no significant difference for the Creek site, p=0.18; all results from ANOVA). Erosion was generally highest at the Shoal site and similar at the Creek and Island sites. Organic matter accounted for between 2 and 10% of the mass eroded and showed no significant seasonal differences (Fig. 4.5).

To determine which variables might explain the greater erosion seen during the summer at the Island and Shoal sites, the site characteristics were reclassified to represent time periods of high and low erodibility (Table 4.4, 2 groups for the Shoal site, and 3 groups for the Island site based on the results of the ANOVA). The Creek site was excluded from this analysis because erodibility showed no significant variation with time. At the Shoal site, preceding wind speed, temperature and organic content were all significantly higher in time periods with high erodibility than in time periods with low erodibility. At the Island site, wind speed and organic content were both significantly higher in July than in other sampled time periods. No variables were significantly different in June from the rest of the sampling period based on post-hoc comparisons after ANOVA.

To examine possible causal relationships, the significant variables were then compared to the mass of sediment eroded using a simple linear regression (Fig. 4.6). Temperature was related to erodibilty at the Shoal site (p=0.003, R^2=0.96, one outlier excluded). Neither wind speed nor organic content were significantly related to the amount of sediment eroded in the Island site.

Discussion

Site characterization and sediment erodibility

The 6 predictive variables used in this study were chosen because of their widespread availability from monitoring programs and their possible relation to sediment erodibility. However, no variable clearly explained the temporal and spatial variability in sediment erodibility. The depth resolution used for sampling and the complex relationships between many of the variables and erodiblity explain the lack of explanatory power.

The depth resolution used in this study was based on previous monitoring research in Hog Island Bay, with all sediment characteristics measured in the top 2 cm of the sediment, except benthic chlorophyll, which was measured in the top 1 cm of the sediment. While many of the measured parameters vary on sub-mm depth scales (e.g. benthic chlorophyll (Tolhurst et al 2008)), many biological studies measure these variables on cm, or at most mm, depth scales (e.g. Sfriso and Marcomini 1997, Eyre and Ferguson 2002, Murray et al 2006). Benthic chlorophyll, frequently used as a measure of benthic microalgae, has been used as a proxy for biofilms with varying degrees of success (Friend et al 2003, Defew et al 2002, Andersen 2001). Sediment erodibility is also dependent on vertical distribution of the biofilm, with increased sediment erodibility at night due to vertical diatom migration (de Brouwer and Stahl 2001, Friend et al 2005). This vertical migration of benthic microalgae will not be captured with cm-scale depth resolution. Additionally, bulk measurements of benthic chlorophyll do not reflect the state of the microalgal mat (e.g. stable or disturbed) or any recent deposition on top of the mat. Similarly, sediment bulk density will likely decrease and organic content increase in the association with the development of a highly erodible, organic fluff layer at the sediment surface (Amos et al 1997). However, this fluff layer may be very thin (Orvain et al 2004), making changes in organic content and bulk density that are large at the submillimeter scale, but insignificant at the cm scale. Depth resolution of measurement must be carefully considered when attributing causal relationships between bed characteristics and sediment erodibility (Paterson et al 2000).

The lack of simple relationships between the predictive variables and erodiblity may also occur because many of these variables can have both stabilizing and destabilizing effects. Higher temperatures are related to greater sediment reworking by bioturbators, possibly due to anoxia in the sediment bed leading to greater bioirrigation (Ouellette et al 2004, Duport et al 2007) as well as increased growth and production of EPS by benthic diatoms (Lam et al 2005). The net effect of temperature on sediment erodibility will depend on the balance of these stabilizing and destabilizing processes. Similarly, forcing conditions (e.g. winds and tides) below threshold values increase sediment stability, while frequent resuspension, caused by forcing conditions above threshold values, decreases bed stability (Panagiotopoulos et al 1997, Paphitis and Collins 2005, Lundkvist et al 2007).

No variable showed a clearly dominant control on variations of sediment erodibility in space and time. In addition to the above issues of depth resolution and stabilizing and destabilizing effects of some variables, the interrelationships between variables may have further complicated efforts to find simple, readily available measurements to predict variation in sediment erodibility. Some of the variables chosen, such as bulk density, have a direct effect on erodibility, but they are also affected by other variables, such as preceding wind speed. While no variable explained the overall spatial and temporal variability, examination of the differences in erodibility across the lagoon and the growing season provides insight into the controls on erodibility in shallow systems.

Site differences

Many of the differences between sites may be explained by the differences in grain sizes and cohesive or non-cohesive behavior of the sediment bed. Both the Shoal and Island site were predominantly sand, but even a small quantity of fine material can result in cohesive properties of the bed. While early work on mixed beds focused on the mud content (% <63 μm) as a control on cohesive behavior, recent research has determined that clay content (% <4 μm) may be a more important metric (van Ledden et al 2004). Cohesive behavior and increases in critical shear stress can be seen in beds with clay contents as low as 5-10% (Dyer 1986, van Ledden et al 2004). However, the effects of these clays at such small quantities may be different than at larger concentrations. Very small quantities of clay material (<11 to 14%) can increase critical shear stress by affecting the bed roughness or internal friction angles (Panagiotopoulos et al 1997, Dong 2007). As the percent of fine material increases (>11-14% clay), fine sediment separates all the sand particles, greatly increasing the critical shear stress due to cohesion of the fine particles (Panagiotopoulos et al 1997).

The presence or absence of fine material creates most of the spatial variability in sediment erosion. Sediment at the Shoal site contains 6% clay which is roughly the minimum clay content for cohesive behavior (van Ledden et al 2004). Based on the Shields curve (Soulsby 1997), the cohesionless critical shear stress for particle motion of the mean grain size is 0.09 N m^{-2} at the Shoal site and 0.12 N m^{-2} at the Island site. However, the erosion tests showed little to no increase in erosion at the 0.16 N m^{-2} shear stress at the Shoal site, indicating that the critical shear stress is greater than that predicted by the Shields curve, likely due to the presence of fine material. At the Creek site, most sediment (74%) is in the mud size range (<63 μm), so the bed should behave cohesively. Some of the erodibility at low shear stresses at this site may reflect an easily erodible, highly organic fluff layer noted in field observations at the time of sampling. The lack of temporal variation at this site may indicate that erodibility is strongly controlled by cohesive properties of the sediment bed, with little biotic/seasonal influence. Though the Island site had minimal mud content (4% clay), erosion at this site was still depth-limited. This pattern may be caused by increasing critical shear stress with depth or winnowing of fine material. Within a mixed bed, the stress required for initial motion for all size classes is similar (Wiberg and Smith 1987), but a greater proportion of the fine sediment is suspended. Little effort was made in this study to characterize a definitive critical shear stress as all sites showed an apparent variation in critical shear stress with depth. Similarly, sediment erosion is characterized as the total mass eroded during each stress step (Fig. 4.4) or over each full experiment (Figs. 4.5 and 4.6) rather than attempting to determine time varying erosion rates. Since the experimental conditions were controlled and replicated for each sample, this approach allowed easy comparison across sites and seasons.

Temporal differences

Though the predictive ability of all of the measured sites variables is low, the greater erosion measured at the Shoal and Island sites during the summer months suggests a biotic influence on sediment erodibility as seen in numerous other studies (e.g. Andersen et al 2002, Orvain et al 2004). Because each month's sampling occurred on a single day at each site, care must be taken to insure that episodic variability is not mistaken for seasonal variability. The lack of any relationship between erosion and wind speed or tidal amplitude indicates that the variability is not due to differences in preceding forcing conditions. In the absence of clear relationships with the site variables, further information on the seasonality of benthic primary producer biomass and benthic faunal density in Hog Island Bay is needed to investigate biotic influences on sediment erodibility.

Seasonal variability of sediment erodibility in Hog Island Bay is likely related to seasonal variation in macroalgal biomass. Microalgal control of sediment erodibility was discounted because of a lack of relationship with benthic chlorophyll a and because erodiblity decreases significantly during the summer months in most sites in where erodibility is controlled by microalgae (e.g. de Brouwer et al 2000, Andersen 2001). Hog Island Bay is characterized by large accumulations of bloom-forming macroalgae, mostly *Gracilaria vermiculophylla*. Decay of this mat, either from underlying layers as the mat grows or following the macroalgal "crash" may form a fluff layer, leading to increased erodibility. However, in this study, increased erodibility coincided with peak macroalgal biomass, indicating the increased eroded material was not decaying macroalgae. Additionally, the inorganic matter flux was 1-2 orders of magnitude greater than the organic matter flux and showed a greater seasonality (Fig. 4.5), which is not consistent with the decaying mat as the source of the additional material.

The increased erodibility during the summer may be related to the trapping of fine material by the macroalgal mat. Numerous studies have shown that seagrass beds and salt marshes can trap fine material by slowing currents and decreasing wave energy (e.g. Peterson et al 2004, Fonseca and Cahalan 1992). Though macroalgae have received less attention, studies, including Chapter 2 of this dissertation, have shown that high densities of macroalgae can decrease hydrodynamic activity near the sediment surface. Macroalgal mats can both significantly decrease shear flow (Escartín and Aubrey 1995) and sediment suspension (Romano et al 2003). Stamski and Fields (2006) measured the mass and grain size of sediment trapped by macroalgae on a Hawaiian reef and found that macroalgae trapped more than 1 g of sediment per g DW biomass of macroalgae, with most of the trapped sediment finer than 63 μm. Just as sediment trapped by seagrass beds during the summer may be resuspended when the seagrass canopy is less full (Hasegawa et al 2008), in this study, fine sediment trapped by the macroalgal mat at the Shoal site was available for resuspension during the experiments because the experiments were conducted on "bare" sediment cores.

While trapping by the macroalgal mat may explain the summer increase in erodibility at the Shoal site, the Island site has low macroalgal biomass (peak annual biomass 15-20 g DW m^{-2}). The difference in erodibility at the Island site may instead be due to bioturbation. Invertebrate density is highest at the Island site and peaks during the summer months, with increased numbers of amphipods, snails and shrimp (Rosinski 2004). Snail activity has been shown repeatedly to increase sediment erosion (e.g. Andersen et al 2002, Orvain et al 2003, Orvain et al 2004). Snails may lead to development of a poorly consolidated, easily erodible fluff layer (Orvain et al 2003). The presence of this layer may explain the sediment erosion seen at low shear stresses (0.08 N m^{-2}) and the increased erosion during June and July at the Island site. While bioturbators generally decrease bulk density (Rowden et al 1998), no significant difference in bulk density was seen in this study, possibly due to the depth resolution of measurement and the relatively small changes in bulk density likely in sandy sediment. Though invertebrate density is lower at the Shoal site, the summer time increase in invertebrate density may also have some effect on erodibility at this site (Rosinski 2004). However, the effects of invertebrates at this site are likely to be overwhelmed by the effects of macroalgae. Further manipulative experiments will be needed to clearly define the effects of bioturbators on sediment erodibility in the study area.

Ecological significance

Increased erodibility during summer months has important implications for ecosystem light and nutrient availability. In shallow coastal lagoons, such as Hog Island Bay, light availability is controlled by internal sediment suspension (Lawson et al 2007). Assuming a water depth of 1 m, the increased sediment suspension would decrease light availability from 15% to 0.03% at the Shoal site and 35% to 2% at the Island site (based on equations from Lawson et al 2007, assuming a water column chlorophyll concentration of 9 $\mu g\ l^{-1}$). This difference in light availability is enough to make the area unsuitable for seagrass growth (based on light requirements from Duarte 1991). Changes in sediment suspension also have implications for nutrient flux, as explored in Chapter 5. The current results on erodibility must be viewed in the context of seasonal forcing conditions, with calmer wind conditions in the summer resulting in shear stresses that rarely exceed 0.16 Nm^{-2} in the shallow areas of Hog Island Bay (Lawson 2004). The increased erodibility is also dependent on exposure of bare sediment at the Shoal site.

Links between sediment erodibility and biotic factors are becoming more recognized, but are still understudied. The indirect effect of sediment trapping by macroalgae has received little attention but may have important effects for the ecosystem. This effect, particularly when combined with the increased bed scouring by low biomass accumulation of macroalgae described in Chapter 2, may result in seasonal pulses of nutrient release and seasonal light limitation. If macroalgal mats trap fine, highly erodible material, the increase in sediment suspension caused by scouring of the bed as macroalgal density declines will be intensified. The interactions and feedbacks between primary producer growth and sediment erodibility require further research and may provide significant insight into the functioning of coastal ecosystems. In this study, erodibility at sites within a single shallow coastal lagoonal system was controlled by different mechanisms, suggesting that careful consideration of sediment properties and biotic influences are necessary to describe sediment erodiblity.

References

Amos, CL, TF Sutherland and JL Luternauer. 1997. The stability of fine-grained sediments from the Fraser River delta. *Estuarine coastal and shelf science*. 45(4):507-524.

Andersen, TJ. 2001. Seasonal variation in erodibility of two temperate, microtidal mudflats. *Estuarine, coastal and shelf science*. 53(1):1-12.

Andersen, TJ, KT Jensen and L Lund-Hansen. 2002. Enhanced erodibility of fine-grained marine sediments by Hydrobia ulvae. *Journal of sea research*. 48(1):51-58.

Bale, AJ, JA Stephens and CB Harris. 2007. Critical erosion profiles in macro-tidal estuary sediments: Implications for the stability of intertidal mud and the slope of mud banks. *Continental shelf research*. 27:2303-2312.

Chen, XJ, and YP Sheng. 2005. Three-dimensional modeling of sediment and phosphorus dynamics in Lake Okeechobee, Florida: Spring 1989 simulation. *Journal of environmental engineering- ASCE*. 131(3):359-374.

de Brouwer, JFC, S Bjelic, EMGT de Deckere and LJ Stahl. 2000. Interplay between biology and sedimentology in a mudflat (Biezelingse Ham, Westerschelde, The Netherlands). *Continental shelf research*. 20(10-11):1159-1177.

de Brouwer, JFC and LJ Stahl. 2001. Short-term dynamics in microphytobenthos distribution and associated extracellualr carbohydrates in surface sediments of an intertidal mudflat. *Marine ecology progress series*. 218:33-44.

Defew, EC, TJ Tolhurst and DM Paterson. 2002. Site-specific features influences sediment stability of intertidal flats. *Hydrology and earth system sciences.* 6(6):971-981.

Dong, P. 2007. Two-fraction formulation of critical shear stresses for sand and silt mixtures. *Journal of waterway port coastal and ocean engineering – ASCE*. 133(3)238:241.

Duarte, CM. 1991. Seagrass depth limits. *Aquatic botany*. 40(4):363-377.

Duport, E, F Gilbert, JC Poggiale, K Dedieu, C Rabouille and G Stora. 2007. Benthic macrofauna and sediment reworking quantification in contrasted environments in the Thau Lagoon. *Estuarine, coastal and shelf science*. 72(3):522-533.

Dyer, KR. 1986. *Coastal and estuarine sediment dynamics*. Wiley, Chicehester.

Escartín, J and DG Aubrey. 1995. Flow structure and dispersion within algal mats. *Estuarine coastal and shelf science*. 40:451-472.

Eyre, BD and AJP Ferguson. 2002. Comparison of carbon production and decomposition, benthic nutrient fluxes and denitrification in seagrass, phytoplankton, benthic microalgae- and macroalgae-dominated warm-temperate Australian lagoons. *Marine ecology progress series*. 229:43-59.

Fonseca, MS and JA Cahalan. 1992. A preliminary evaluation of wave attenuation by 4 species of seagrass. *Estuarine coastal and shelf science*. 35(6):565-576.

Friend, PL, P Ciavola, S Cappucci and R Santos. 2003.Bio-dependent bed parameters as a proxy tool for sediment stability in mixed habitat intertidal areas. *Continental shelf research*. 23(17-19):1899-1917.

Friend, PL, CH Lucas and SK Rossington. 2005. Day-night variation of cohesive sediment stability. *Estuarine, coastal and shelf science*. 64(2-3):407-418.

Gust, G. and V. Müller. 1997. Interfacial hydrodynamics and entrainment functions of currently used erosion devices. In *Cohesive sediments*. Burt N., R. Parker, and J. Watts (eds). John Wiley and Sons. 149-174.

Hasegawa, N, M Hori and H Mukai. 2008. Seasonal changes in eelgrass functions: current velocity reduction, prevention of sediment resuspension, and control of sediment-water column nutrient flux in relation to eelgrass dynamics. *Hydrobiologia*. 596:387-399.

Haynes, H and G Pender. 2007. Stress history effects on graded bed stability. *Journal of hydraulic engineering-ASCE*. 133(4):343-349.

Lam, C, T Harder and PY Qian. 2005. Growth conditions of benthic diatoms affect quality and quantity of extracellular polymeric larval settlement cues. *Marine ecology progress series*. 294:109-116.

Lawson, SE. 2004. Sediment suspension controls light availability in a shallow coastal lagoon. MS Thesis. University of Virginia, Charlottesville, VA.

Lawson, SE, PL Wiberg, KJ McGlathery and DC Fugate. 2007. Wind-driven sediment suspension controls light availability in a shallow coastal lagoon. *Estuaries and coasts*. 30(1):102-112.

Lorenzen C (1967) Determination of chlorophyll and phaeopigments: spectrophotometric equations. *Limnology and oceanography*.12:343–346

Lundkvist, M, M Grue, PL Friend and MR Flindt. 2007. The relative contributions of physical and microbiological factors to cohesive sediment stability. *Continental shelf research*. 27(8):1143-1152.

Maa, J P-Y, LP Sanford and JP Halka. 1998. Sediment resuspension characteristics in Baltimore Harbor, Maryland. *Marine geology*. 146:137-145.

Maa, J P-Y, LD Wright, C-H Lee and TW Shannon. 1993. VIMS Sea Carousel:a field instrument for studying sediment transport. *Marine geology*.115(3/4):271-287.

Miller, DC, RJ, Geider and HL MacIntyre. 1996. Microphytobenthos: The ecological role of the "secret garden" of unvegetated, shallow-water marine habitats .2. Role in sediment stability and shallow-water food webs. *Estuaries*. 19(2A):202-212.

Murray, LG, SM Mudge, A Newton and JD Icely. 2006. The effect of benthic sediments on dissolved nutrient concentrations and fluxes. *Biogeochemistry*. 81:159-178.

Neumeier, U, CH Lucas and M Collins. 2006. Erodibility and erosion patterns of mudflat sediments investigated using an annular flume. *Aquatic ecology*. 40(4):543-554.

Orvain, F, PG Sauriau, A Sygut, L Joassard and P Le Hir. 2004. Interacting effects of Hydrobia ulvae bioturbation and microphytobenthos on the erodibility of mudflat sediments. *Marine ecology progress series*. 278:205-223.

Orvain, F, P Le Hir and PG Sauriau. 2003. A model of fluff layer erosion and subsequent bed erosion in the presence of the bioturbator, Hydrobia ulvae. *Journal of marine research*. 61(6):823-851.

Orvain, F, PG Sauriau, P Le Hir, G Guillou, P Cann, and M Paillard. 2007. Spatio-temporal variations in intertidal mudflat erodability: Marennes-Oleron Bay, western France. Continental shelf research. 27(8):1153-1173.

Ouellette, D, G Desrosiers, JP Gagne, F Gilbert, JC Poggiale, PU Blier and G Stora. 2004. Effects of temperature on in vitro sediment reworking processes by a gallery biodiffusor, the polychaete Neanthes virens. *Marine ecology progress series*. 266: 185-193.

Paarlberg, AJ, MAF Knaapen, MB de Vries, SJMH Hulscher, and ZB Wang. 2005. Biological influences on morphology and bed composition of an intertidal flat. *Estuarine coastal and shelf science*. 64(4):577-590.

Panagiotopoulos, I, G Voulgaris and MB Collins. 1997. The influence of clay on the threshold of movement of fine sandy beds. *Coastal engineering*. 32(1):19-43.

Paphitis, D and MB Collins.2005.Sand grain threshold, in relation to bed 'stress history': an experimental study. *Sedimentology*. 52(4):827-838

Paterson, DM, TJ Tolhurst, JA Kelly, C Honeywill, EMGT de Deckere, V Huet, SA Shayler, KS Black, J de Brouwer and I Davidson. 2000. Variations in sediment properties, Skeffling mudflat, Humber Estuary, UK. *Continental shelf research*. 20(10-11):1373-1396.

Peterson C.H., R.A. Luettich, F. Micheli and G.A. Skilleter. 2004. Attenuation of water flow inside seagrass canopies of differing structure. *Marine ecology progress series*. 268:81-92.

Quaresma, VD, CL Amos and M Flindt. 2004. The influences of biological activity and consolidation time on laboratory cohesive beds. *Journal of sedimentary research*. 74(2):184-190.

Romano, C, J. Widdows, MD Brinsley and FJ Staff. 2003. Impact of Enteromorpha intestinalis mats on near-bed currents and sediment dynamics: flume studies. *Marine ecology progress series*. 256:63-74.

Rosinski, JL. 2004. Controls on benthic biodiversity and trophic interactions in a temperate coastal lagoon. PhD Dissertation. University of Virginia. Charlottesville, VA.

Rowden, AA, CF Jago and SE Jones. 1998. Influence of benthic macrofauna on the geotechnical and geophysical properties of surficial sediment, North Sea. *Continental shelf research*. 18(11):1347-1363.

Sanford, LP and J P-Y Maa. 2001. A unified erosion formulation for fine sediments. *Marine geology*. 179:9-23.

Sfriso, A and A Marcomini. 1997. Macrophyte production in a shallow coastal lagoon. Part 1: Coupling with chemico-physical parameters and nutrient concentrations in waters. *Marine environmental research*. 44(4):351-375.

Soulsby, R.L. 1997. *Dynamics of marine sands*. Thomas Telford, London.

Stamski, RE and ME Field. 2006. Characterization of sediment trapped by macroalgae on a Hawaiian reef flat. *Estuarine coastal and shelf science*. 66(1-2):211-216.

Tengberg, A., H. Stahl, G. Gut, V. Muller, U. Arning, H. Andersson and P.O.J. Hall. 2004. Intercalibration of benthic flux chambers I. Accuracy of flux measurements and influence of chamber hydrodynamics. *Progress in oceanography*. 60:1-28.

Tolhurst, TJ, KS Black, DM Paterson, HJ Michener, GR Termaat and SA Shayler. 2000a. A comparison and measurement standardization of four in-situ devices for determining the erosion shear stress of intertidal sediments. *Continental shelf research*. 20(10-11):1397-1418.

Tolhurst, TJ, M Consalvey and DM Paterson. 2008. Changes in cohesive sediment properties associated with the growth of a diatom biofilm. *Hydrobiologia*. 596:225-239.

Tolhurst, TJ, R Riethmuller and DM Paterson. 2000b. In-situ versus laboratory analysis of sediment stability from intertidal mudflats. *Continental shelf research*. 20(10-11):1317-1334.

Tyler, AC, KJ McGlathery and IC Anderson. 2001. Macroalgae mediation of dissolved organic nitrogen fluxes in a temperate coastal lagoon. *Estuarine, coastal and shelf science*. 53:155-168 van Ledden, M, WGM van Kesteren and JC Winterwerp. 2004. A conceptual framework for the erosion behaviour of sand-mud mixtures. *Continental shelf research*. 24:1-11.

Wiberg, PL and JD Smith. 1987. Calculations of the critical shear stress for the motion of uniform and heterogeneous sediments. *Water resources research*. 23(8):1471-1480.

Zheng, LY, CS Chen and FY Zhang. 2004. Development of water quality model in the Satilla River Estuary, Georgia. *Ecological modeling*. 178(3-4):457-482.

Figures and Tables

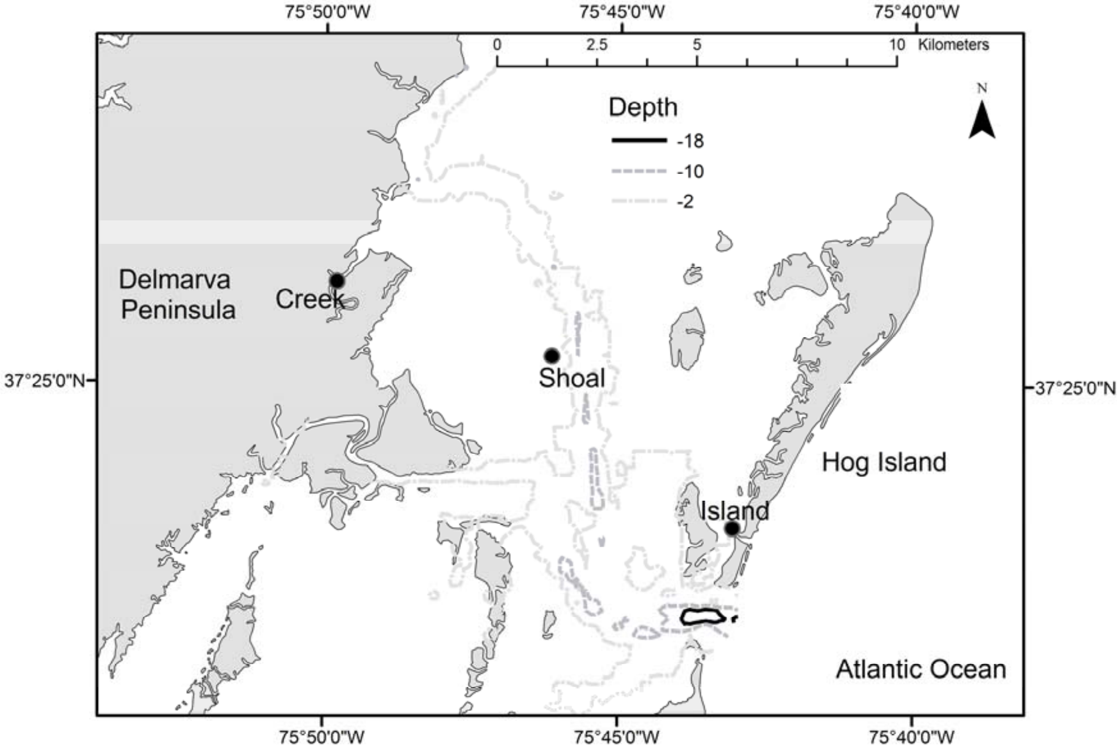

Figure 4.1. Site locations in Hog Island Bay. The 3 chosen sites represent a gradient of grain size, exposure and nutrient availability from the mainland to the ocean.

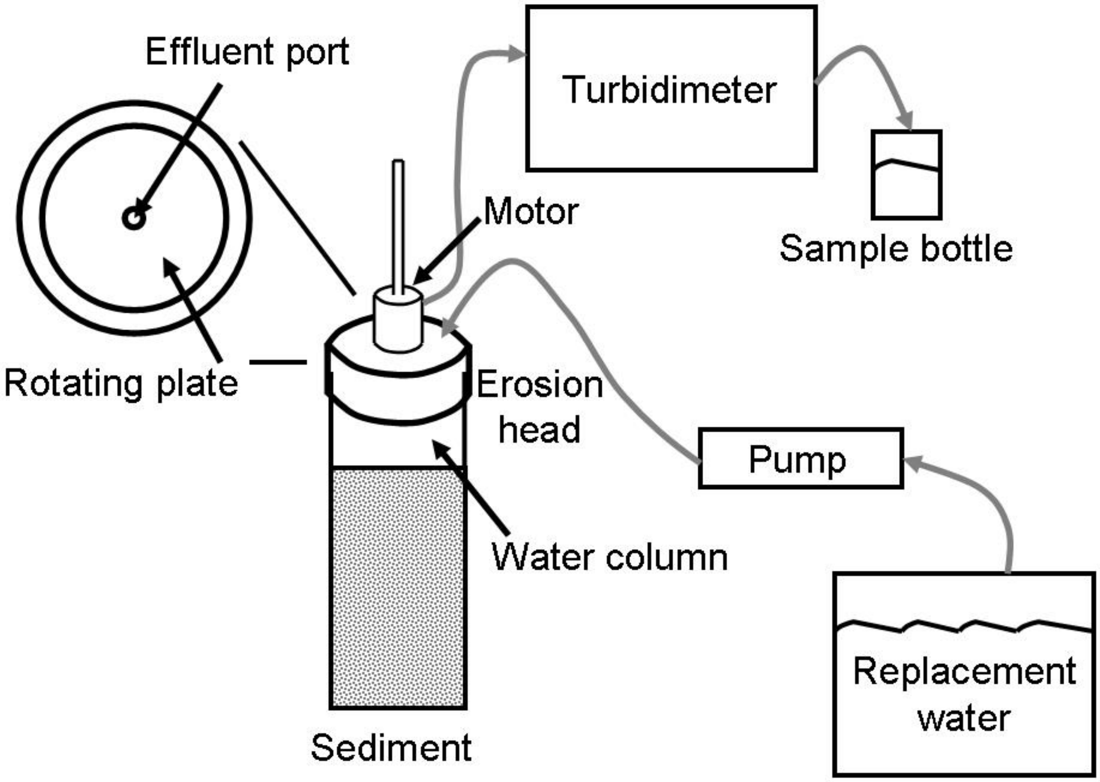

Figure 4.2. Schematic of the Gust microcosm. The microcosm uses a combination of a rotating plate and a push-through water system to create a calibrated shear stress on the sediment surface.

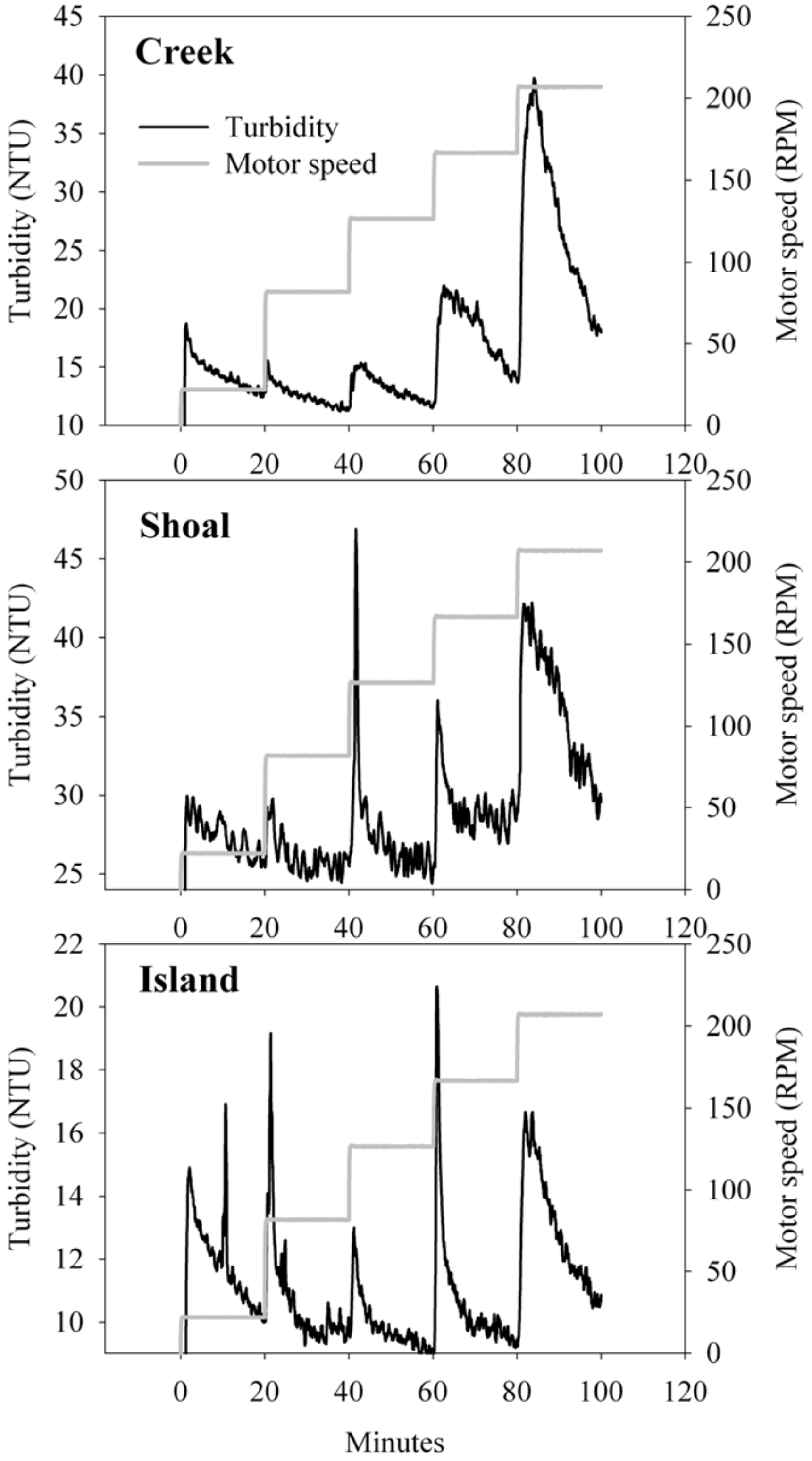

Figure 4.3. Sample time series from erosion experiments at all sites. Turbidity (used to measure sediment suspension) shows a pronounced, but short-lived peak with each shear stress increase (shown by motor speed).

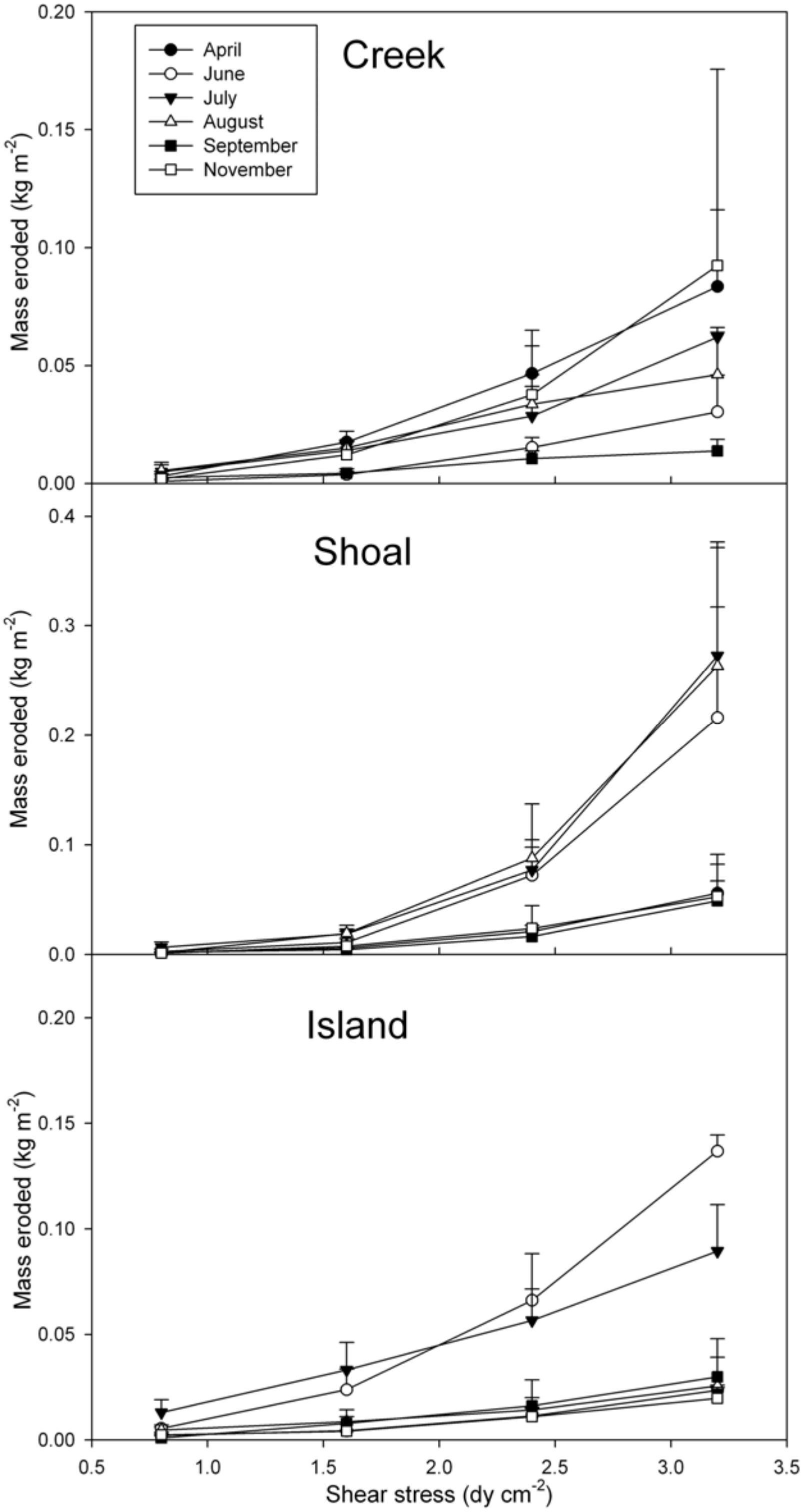

Figure 4.4. Cumulative mass eroded during the erosion experiments. The summer months clearly show greater erodibility at both the Island and Shoal site. Error bars are standard error.

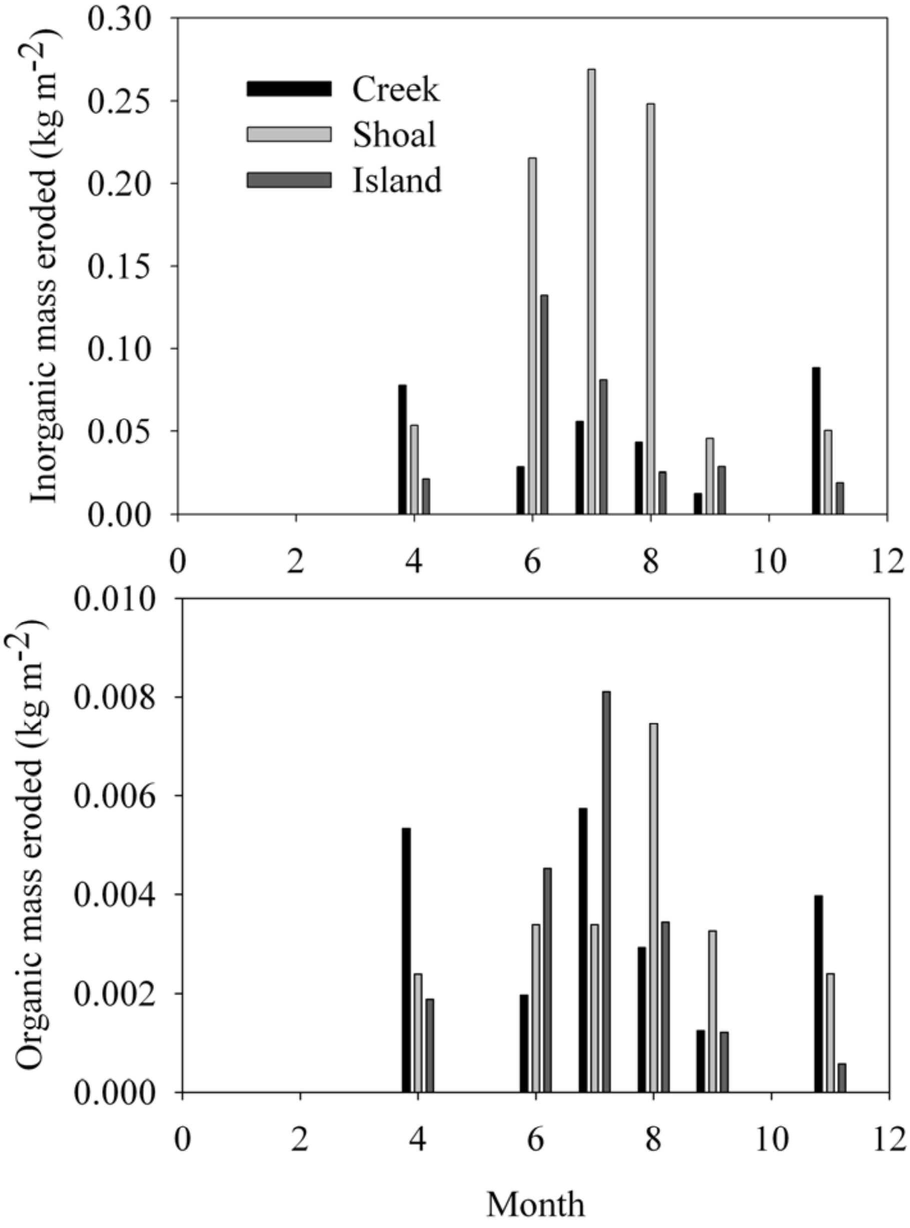

Figure 4.5. Total mass of organic and inorganic material eroded during the erosion experiments scaled to a m^2. Inorganic material is much greater and shows a similar seasonal pattern to the bulk erosion.

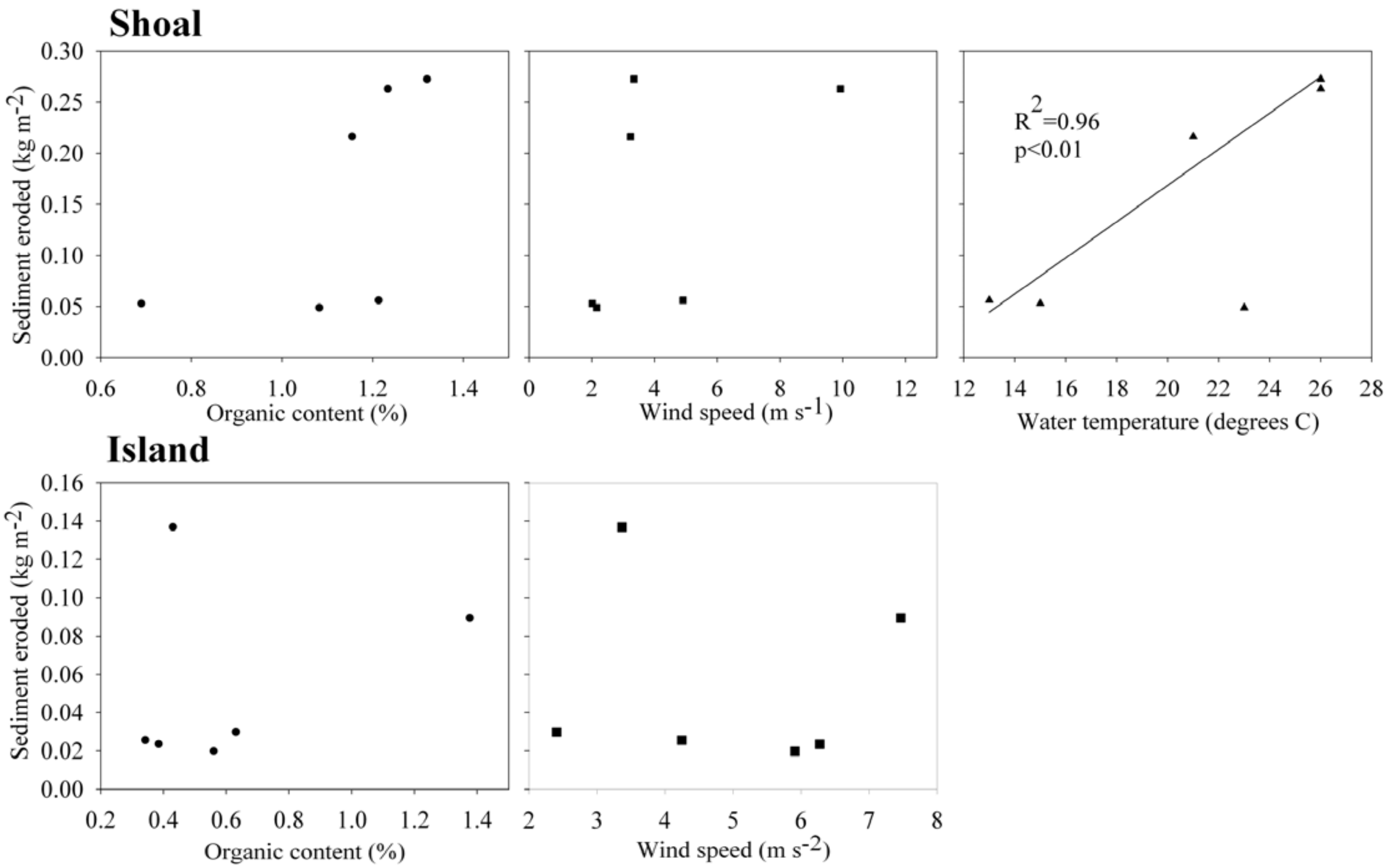

Figure 4.6. Regressions of predictive variables and sediment eroded. Sediment eroded was related to water temperature at the Shoal site. No characteristic had a significant relationship with sediment eroded at the Island site.

Table 4.1. Summary of site characteristics. Data with * are from McGlathery et al 2001, data with ** are from Thomsen et al 2006, and data with *** are from this study. Numbers in parentheses are standard error.

	Creek	**Shoal**	**Island**
Dissolved inorganic nitrogen (μM) *	4.4 (0.9)	2.3 (2.5)	1.2 (0.4)
Dissolved organic nitrogen (μM) *	15.4 (1.9)	12.1 (3.7)	11.8 (1.6)
Dissolved inorganic phosphorus (μM) *	1.4 (0.2)	0.8 (0.1)	0.5 (0.1)
Macroalgal biomass (g DW m^{-2}) **	19.4 (3.66)	128.44 (20.63)	4.58 (0.89)
Average grain size (microns) ***	28(9)	74(4)	120(2)
% clay (<4 microns) ***	41(3)	6(2)	4(0.7)

Table 4.2. Summary of measured sediment conditions. All characteristics showed spatial and temporal variability. Numbers in parentheses are standard error.

		April	**June**	**July**	**August**	**September**	**November**
	Bulk density (g cm^{-3})	0.6(0.03)	0.9(0.06)	0.6(0.02)	0.8(0.03)	0.7(0.03)	0.8(0.03)
Creek	*Organic content (%)*	3.5(0.2)	3.3(0.1)	4.1(0.1)	3.8(0.09)	3.9(0.1)	3.8(0.05)
	Benthic chlorophyll a (µg m^{-2})	3.7(0.4)	4.9(0.7)	5.8(0.8)	4.1(0.7)	14.3(1.7)	6.1(1.4)
	Bulk density (g cm^{-3})	1.1(0.02)	1.3(0.02)	1.2(0.01)	1.3(0.06)	1.3(0.04)	1.3(0.02)
Shoal	*Organic content (%)*	1.2(0.06)	1.2(0.1)	1.3(0.06)	1.2(0.1)	1.1(0.06)	0.7(0.04)
	Benthic chlorophyll a (µg m^{-2})	5.0(0.5)	6.2(0.6)	4.3(0.5)	---	---	3.1(0.2)
	Bulk density (g cm^{-3})	1.4(0.07)	1.4(0.02)	1.2(0.08)	1.4(0.04)	1.3(0.02)	1.3(0.02)
Island	*Organic content (%)*	0.4(0.03)	0.4(0.02)	1.4(0.1)	0.3(0.1)	0.6(0.06)	0.6(0.08)
	Benthic chlorophyll a (µg m^{-2})	10.9(1.2)	11.3(1.2)	14.5(1.8)	7.8(1.2)	11.4(1.3)	13.4(1.4)

Table 4.3. Summary of meteorological site characteristics. Water temperature was the only characteristic that showed a clear seasonal trend. Numbers in parentheses are standard error. No standard error is reported for water temperature.

		April	**June**	**July**	**August**	**September**	**November**
	Preceding wind speed (m s^{-1})	3.7(0.2)	7.9(0.3)	3.0(0.2)	6.2(0.3)	3.8(0.6)	12.0(0.8)
Creek	*Tide level change (m h^{-1})*	0.3(0.1)	0.1(0.020	0.2(0.02)	0.3(0.02)	0.2(0.01)	0.1(0.02)
	Water temperature (degrees C)	14	21	24	25	22	15
	Date of experiment	4/17/2006	6/7/2006	7/8/2006	8/14/2006	9/26/2006	11/16/2006
	Preceding wind speed (m s^{-1})	4.9(0.5)	3.2(0.3)	3.3(0.2)	9.9(0.2)	2.2(0.04)	2.0(0.2)
Shoal	*Tide level change (m h^{-1})*	0.2(0.03)	0.1(0.02)	0.1(0.03)	0.2(0.03)	0.2(0.04)	0.2(0.03)
	Water temperature (degrees C)	14	23	24	25	22	15
	Date of experiment	4/18/2006	6/8/2006	7/7/2006	8/15/2006	9/27/2006	11/15/2006
	Preceding wind speed (m s^{-1})	6.3(0.4)	3.4(0.6)	7.5(0.5)	4.2(1.0)	2.4(0.4)	5.9(0.1)
Island	*Tide level change (m h^{-1})*	0.2(0.03)	0.1(0.03)	0.1(0.03)	0.2(0.03)	0.2(0.02)	0.2(0.03)
	Water temperature (degrees C)	13	21	26	26	23	15
	Date of experiment	4/19/06	6/6/06	7/6/06	8/16/06	9/25/06	11/14/06

Table 4.4. Summary of p values from ANOVA's comparing all predictive variables grouped by time periods with significant differences in sediment erodibility. A significant p value (<0.05) indicates that the predictive variable is different in time periods with low erosion than in time periods with high erosion. For the Island site, post-hoc comparisons showed that both organic content and wind speed were unique in July and June showed no differences from the rest of the year.

Variable	**Shoal**	**Island**
Bulk density	0.38	0.14
Organic content	0.0083	<0.0001
Benthic chlorophyll a	0.99	0.1
Wind speed	0.0064	0.0017
Tidal amplitude	0.65	0.16
Water temperature	0.0003	0.08

Chapter 5: Spatial and temporal variability in hydrodynamic effects on ammonium uptake and efflux

Abstract

Hydrodynamic activity can affect nutrient fluxes across the sediment-water interface by altering both transport and biological processing of nutrients. This study examined hydrodynamically-forced ammonium (NH_4^+) flux at 3 sites within a shallow coastal lagoon from early spring to late fall. These sites represent a gradient from a mainland creek across the lagoon to a back-barrier island. Sediments at the sites range from organic rich (3.6±0.07(SE) %), fine-grained (28±9(SE) μm) sediment at the Creek site to low organic content (0.69±0.07(SE) %), sandy (120±2(SE) μm) sediment at the Island site. In the laboratory, sediment cores were exposed to increasing bed shear stresses using a Gust erosion microcosm. NH_4^+ fluxes ranged from -815±329(SE) μmols m^{-2} h^{-1} (Creek-September) to 617±434(SE) μmols m^{-2} h^{-1} (Island-June). NH_4^+ fluxes were almost an order of magnitude greater, both in terms of efflux and uptake, than those measured in previous low-flow incubations of cores taken at the same site. Our results suggest that NH_4^+ transport was controlled in part by desorption from suspended particles at the fine-grained site (Creek) and porewater advection at the coarse-grained site (Island). Both processes were important at the intermediate Shoal site. Nutrient flux at the Creek and Island sites was also affected by the preceding wind conditions, which may have caused breakdown of the benthic microalgal biofilm at the fine-grained site and a flushing of available porewater nutrients at the coarse-grained site.

Introduction

Nutrient flux across the sediment-water interface is a dynamic balance between physical transport mechanisms and biological cycling. Nutrient concentrations in the sediment are typically an order of magnitude higher than in the water column, largely as a result of mineralization of accumulated organic matter in the sediment. In some shallow coastal systems, these nutrient fluxes are greater than external loading (Sarker 2005) and can support from 30-100% of benthic and pelagic algal production (Gibbs et al 2005 and references within). The majority of studies quantifying the nutrient flux across the sediment-water interface have been conducted under low-flow incubations (e.g. Dollar et al 1991, Berelson et al 1998, Cabrita and Brotas 2000, Tyler 2002). However, recent studies have shown that hydrodynamic activity affects both the physical transport of nutrients (Huettel and Webster 2001, Lawrence et al 2004) and the biological cycling (Stahlberg et al 2006). Accurate portrayal of nutrient dynamics in coastal systems requires consideration of these hydrodynamic effects.

Three dominant mechanisms are responsible for physical transport of nutrients from the sediment bed to the water column: diffusion, desorption from suspended particles and porewater advection. Molecular diffusion is the dominant transport mechanism in low-flow cores and stagnant water. There has been relatively little work on the effects of hydrodynamics on this process, but Kelley-Gerreyn (2005) used modeling to show that although that the effects are small, increased hydrodynamic activity can cause thinning of the diffusive boundary layer leading to increased transport across the sediment-water interface. Thinning of the boundary layer caused only minor changes in nutrient flux, which were secondary to changes in oxygen penetration depth and its effect on nutrient transformation (Kelly-Gerreyn 2005). Desorption stems from the reversible exchange of ions attached to sediment (organic and inorganic) particles. The dissolved and sorbed nutrients reach an equilibrium/steady state concentration between the sediment and porewater. However, when sediment is suspended, it is moved in to an area of lower surrounding concentration, often resulting in desorption of the nutrients until a new equilibrium is reached. For ammonium (NH_4^+), the quantity desorbed is also dependent on the oxic/anoxic conditions of the surrounding water, with decreased desorption in oxic waters (Morse and Morin 2005). Nutrient efflux from the sediment may also be increased by porewater advection. In permeable sediments, irregularities in the bed caused by features such as sediment ripples create pressure gradients on the sediment surface that force overlying water into the sediment on the up-current, high pressure side of the ripples and an efflux of porewater on the down-current side (Huettel and Gust 1992, Huettel et al 2003). This advective porewater flux can increase nutrient flux 6-7 times in permeable sediments (Huettel and Gust 1992). Porewater advection can also be created by wave passage and pressure gradients created by isolated surface features such as animal burrows and tubes (e.g. Huettel and Gust 1992, Huettel et al 1996). A small quantity of porewater will also enter the water column from the thin layer of sediment that is eroded, but this flux will likely be negligible in relation to porewater pumping and desorption.

Hydrodynamic activity also affects the biological cycling of nutrients, largely because of changes in the physical transport of constituents. Bacterial processes, such as mineralization and nitrification, can be stimulated by increased availability of organic matter and oxygen through porewater advection or suspension of sediment (Forster et al 1996, Huettel et al 1998, Stahlberg 2006). Porewater advection brings oxygen rich surface water into the sediment creating zones of enhanced nitrification and also brings deeper anoxic porewater, with high NH_4^+ concentrations, to the surface (Huettel et al 1998) which can enhance bacterial uptake or nitrification. The amplification of bacterial processing from porewater advection is reflected in increased oxygen uptake with increased flow velocity in permeable sediments, particularly in the presence of detrital matter available for bacterial metabolism (Forster et al 1996). In addition, sediment suspension can more than double sediment re-mineralization rates, possibly due to increased surface area exposed to bacterial processing and decreased boundary layer thickness around bacterial cells (Stahlberg 2006).

This study examined NH_4^+ fluxes between the sediment and water column at 3 sites in a shallow coastal lagoon from the beginning to the end of the growing season (April to November). All sites were in the shallow subtidal and vary in sediment characteristics (grain size and organic content), primary producer dominance, exposure and nutrient standing stocks. This spatial variability combined with seasonal variability allows examination of some of the controls on hydrodynamic nutrient fluxes such as nutrient availability, sediment size, and biological activity. Shear stress was controlled experimentally in laboratory microcosms with consistent incremental increases on sediment cores taken from the field. The effects of increasing shear stress on sediment suspension from these experiments are presented in Chapter 4.

Methods

Site description

This study was conducted in Hog Island Bay, VA on the Delmarva Peninsula (Fig. 5.1). Hog Island Bay was historically dominated by seagrass, *Zostera marina*, until a hurricane wiped out populations already decimated by a wasting disease. Though restoration efforts have begun in the bay, primary productivity is still dominated by benthic algae. The dominance of primary producers varies seasonally in this lagoon with benthic primary producers (benthic macroalgae and microalgae) dominant early and late in the growing season and a temporary increase in phytoplankton following decline of the seasonal macroalgal bloom in mid-summer (McGlathery et al 2001). High gross mineralization in the sediments results in low turnover times for NH_4^+

but uptake processes, likely uptake by benthic microalgae or bacterial immobilization, result in negligible or negative efflux of NH_4^+ from the sediment (Anderson et al 2003). When macroalgae is present, it further prevents efflux of nitrogen from the sediment to the water column by intercepting remineralized nutrients (Tyler et al 2001, 2003).

Three shallow subtidal sites were chosen within Hog Island Bay to represent a gradient of sediment grain size, nutrient availability and primary productivity. The Creek site is characterized by organic rich, fine-grained sediment (mostly silt and clay). The site is next to a *Spartina alterniflora* marsh in a tidal creek with very little freshwater input. Primary productivity is dominated by benthic primary production, including benthic microalgae. The Shoal site is next to relic oyster reefs and has seasonally high accumulations of macroalgae. Seasonal accumulations of macroalgae that can exceed over 700 g DW m^{-2} (McGlathery, unpublished data). Previous research has shown that when this mat "crashes", the added organic matter is quickly transferred to the water column as dissolved organic and dissolved inorganic compounds (Tyler et al 2001). The Island site is located on the mainland side of a barrier island, between the island and a smaller marsh island. This site is characterized by the coarsest sediment of the 3 sites and relatively low organic content. Macroalgal biomass is lowest at this site with typical peak annual biomasses of only 10 – 20 g m^{-2} (McGlathery, unpublished data). Current velocities in this area are higher than at the Creek or Shoal site, but the large grain size results in little suspension and high light availability (Lawson et al 2007).

Site characterization

Site characterization was conducted to determine spatial and temporal variability in sediment characteristics and nutrient availability. The methods and results for grain size, organic content, bulk density and benthic chlorophyll a are presented in Chapter 4.

Additional site characterization was also conducted to determine nutrient availability and sediment conditions. Five replicate samples for extractable NH_4^+ were taken to 2 cm depth with a 3.5 cm diameter core. Three replicate polycarbonate cores with an internal diameter of 8 cm and a height of 23 cm were collected for laboratory sampling of porewater. All samples were kept at 4 °C during transport to the lab. Porewater samples were extracted from the sediment cores at 2 cm depth intervals to 10 cm depth using a stainless steel probe (Berg and McGlathery 2001) for the Island and Shoal sites and by centrifugation of 2 cm thick sections for the Creek site. The fine sediments at the Creek site clogged the porewater probe so it could not be used at this site. The samples were immediately filtered (0.45 μm) and frozen for later analyis. Exchangeable NH_4^+ was extracted for 1 h with an equal volume of 1N KCl solution. Porewater samples (for NH_4^+, phosphate (PO_4^{3-}), and nitrate (NO_3^-)) and NH_4^+ extractions were analyzed on a Lachat QuickChem 8500 using standard methods (Hach Company, Loveland, Colorado).

Shear stress experiments

<u>Sample collection, storage and preparation</u>

Sediment samples for the erosion experiments were taken by hand on a falling tide, within 1 h of predicted low tide, using polycarbonate core tubes with an internal diameter of 10.8 cm and a height of 22.5 cm, with a 10 cm water column preserved. Core tubes were sealed using rubber plumbing end caps and kept in the dark at 4 °C for transport back to the lab. Ambient water was collected in 20 l carboys for use as the replacement water during the experiments and for core storage until analysis. Upon arrival at the lab, within 1 h of core collection, the cores were submerged in a cooler of ambient water oxygenated by an aquarium bubbler and maintained in low light at ambient temperatures.

Shear stress manipulation

A Gust erosion microcosm (Gust & Müller 1997, microcosm, hereafter, Fig. 5.2) which consists of an erosion head with a rotating plate and a push through water system fitted over a polycarbonate core tube, was used in this study. The combination of the rotation of the plate and the suction from the water system in the center of the core generates a near-uniform bed shear stress and diffusive boundary layer thickness, though not a uniform pressure distribution (Tengberg et al 2004). Shear stress is controlled through a calibrated datalogger system that also records turbidity and motor RPM every second. Immediately prior to the experiment, a water sample was pumped from the replacement water to provide reference/background concentration values. The cores were then exposed to a low shear stress of 0.01 Nm^{-2} for 20 min as a flushing step, then incremental shear stress increases every 20 min to 0.08, 0.16, 0.24 and 0.32 Nm^{-2}, similar to the range of average shear stress in this shallow coastal lagoon (Lawson et al 2007). Shear stress increases were generated by calibrated increases in pumping rate and plate rotation rate.

Effluent water was collected in 1 l Nalgene bottles exchanged every 5-10 min, dependent on the pumping rate. Effluent samples and the reference water sample pumped before the experiment were sub-sampled for NH_4^+, NO_3^- and PO_4^{3-} then filtered (0.45 μm). Samples were frozen until analysis on a Lachat QuickChem 8500 following standard methods (Hach Company, Loveland, CO). NO_3^- and nitrite (NO_2^-) were not separated because NO_2^- values were frequently below the detection level. To correct for the mass of measured components carried in the replacement water, all fluxes were corrected with a background concentration. For all nutrient measurements, the background concentration was defined as the daily average of sub-samples pumped from the carboy of replacement water immediately before the experiments. Nutrient background values were treated differently than sediment because of the possibility of uptake or transformation of nutrients. Data from the flushing step were discarded and only data from the higher shear stress steps were analyzed. Data for PO_4^{3-} and NO_3^- are presented in the appendix.

Results

Site characteristics

Sediment characteristics such as bulk density and organic content were presented in Chapter 3. Nutrient availability, measured as exchangeable NH_4^+ and porewater concentrations of NH_4 decreased with distance from the mainland (Fig. 5.3). Measured NH_4^+ stocks were similar to those seen in previous studies in Hog Island Bay (McGlathery et al 2001, Tyler et al 2001, Tyler 2002, Anderson et al 2003).

Erosion experiments

The fluxes of NH_4^- varied with time and location in the lagoon (Fig. 5.4). Uptake of NH_4^+ was greatest at the Creek site, with a maximum uptake rate of 815 μmols m^{-2} h^{-1} (overall range -815 μmols m^{-2} h^{-1} to 572 μmols m^{-2} h^{-1}), while the Island site showed an efflux of NH_4^+, reaching a maximum of 617 μmols m^{-2} h^{-1} (overall range 39 μmols m^{-2} h^{-1} to 617 μmols m^{-2} h^{-1}). The range of values at the Shoal site (-659 μmols m^{-2} h^{-1} to 476 μmols m^{-2} h^{-1}) was similar to the range at the Creek site.

If desorption controlled the enhanced NH_4^+ flux under hydrodynamic forcing, the measured NH_4^+ flux should be related to the mass of sediment suspended and the concentration of adsorbed nutrients. The pressure differences created in the Gust microcosm and sediment permeability were consistent between sampling events within a site, so if porewater advection is the controlling mechanism, differences between the sampling events should be related to the NH_4^+ concentration in the porewater. A predicted flux was calculated as the mass concentration of exchangeable NH_4^+ multiplied by an availability coefficient determined from the ratio of measured flux and exchangeable NH_4^+ in the autoclaved desorption study (Chapter 3) multiplied by the mass of sediment eroded during the experiment (Chapter 4). At the Creek site, the measured flux was closely related to this predicted nutrient flux from desorption (Fig. 5.5, R^2= 0.95, p= 0.005, one outlier removed). All points falling below the 1:1 line indicate that the measured flux was lower than predicted flux. At the Creek site, the measured flux was lower than the predicted flux for all months except August (327 µmols m^{-2} h^{-1}) and November (572 µmols m^{-2} h^{-1}). At the Shoal site, there was no clear relationship between measured and predicted flux, with measured flux below predicted flux for all months except July (219 µmols m^{-2} h^{-1}) and August (476 µmols m^{-2} h^{-1}). At the Island site, all measured fluxes exceeded predicted fluxes, indicating an NH_4^+ source beyond desorption from suspended sediment. The data indicate that desorption was a more important control on NH_4^+ flux at the Creek site than the Shoal and Island sites.

The additional source of NH_4^+ at the Island site likely comes from porewater advection. An estimated depth of porewater advected can be calculated from the difference between the measured flux and the predicted desorption flux. Based on the measured porewater concentrations and porosity, the amount of porewater advection needed to create the measured flux can be calculated. For the Island site, the calculated depth of porewater advected ranged from 0.009 (June) to 0.04 cm (July). At the Shoal site, the two time periods that corresponded to NH_4^+ fluxes greater than the predicted desorption flux, July and August, required porewater advection to depths of 0.005 and 0.02 cm respectively. For the Creek site, calculated depths were 0.002 (August) and 0.005 (November). The differences in calculated depths may not indicate that the volume of porewater advected varied with the season, but may be the result of different biological processing. However, the calculated depths are a useful tool for examining the importance of porewater advection.

Factors controlling the hydrodynamically-forced NH_4^+ flux were also examined by comparing the residual from the predicted desorption flux with site variables. Because of the large number of possible predictive variables (see Chapter 3), the residuals were compared visually with all predictive variables and regressions were only calculated for those comparisons that were visually identified as the best fit. For both the Island and Creek site, the preceding wind speed explained greater than 70% of the variability in the residuals (Fig. 5.6, R^2=0.75, p=0.02, Creek; R^2=0.33, p=0.22, Shoal; R^2= 0.71, p=0.04, Island). However, wind speed was positively correlated with the residual flux at the Creek site and negatively correlated at the Island site. A positive correlation indicates that increased preceding wind speed either decreased uptake or increased efflux of NH_4^+. The relationships were fit with non-linear equations because the effect of wind speed can be expected to reach a threshold at higher speeds.

Discussion

Importance of hydrodynamic forcing

Our results from the laboratory erosion chambers indicate that hydrodynamic forcing is an important factor increasing the transport of nutrients between the sediment and water column. The magnitude of NH_4^+ fluxes measured in this study was almost an order of magnitude greater than sediment-water column fluxes measured in low-flow incubations of sediment cores taken at the same sites (Tyler 2002, Tyler et al 2003, Table 5.1). While low-flow incubations have long been the standard for quantifying nutrient flux across the sediment-water interface (e.g. Dollar et al 1991, Berelson et al 1998, Cabrita and Brotas 2000), recent research, including this study, has shown that this may not accurately represent nutrient flux. Huettel and Gust (1992) showed clearly that hydrodynamic activity directly affects nutrient transport, with measured solute fluxes 6-7 times higher as a result of porewater advection in permeable sediments. Hydrodynamic activity also influences nutrient cycling through increased delivery of organic matter and oxygen to the sediment bed (Forster et al 1996, Huettel et al 1998). Both of these processes and any nutrient flux from desorption will be missed by low-flow incubations. These hydrodynamic conditions should also be considered in studies of nitrification and mineralization rates, as still water conditions may give unrealistic results. These effects on nutrient cycling may be sustained longer than the instantaneous flux. Both porewater advection and desorption affect a limited depth into the bed, and therefore a limited quantity of nutrients, unless these nutrient stores are replenished either by diffusion or biological processing. Because the fluxes measured in this study were measured for only 100 minutes, they likely represent a peak rate that would not be sustained through time, even if forcing continued.

Mechanisms of nutrient flux

Desorption

Differences in sediment characteristics, particularly grain size, caused differences in the dominant mechanism of nutrient transport. Fine-grained sediments, such as those at the Creek site, have a greater surface area to volume ratio, meaning more area for adsorption of nutrients (Mackin and Aller 1984). Clays are also more likely to have charged surfaces and high organic content, additionally providing sites for nutrient adsorption. In these organic rich sediments, the matrix of organic matter and clay minerals may control adsorption behavior (Boatman and Murray 1982). These factors will all make desorption more important at fine-grained sites. Erodibility, controlled partially by grain size, will also affect the importance of desorption, as sediment suspension is required to bring the sorbed particles into a lower concentration environment, leading to desorption. At the Shoal site, high sediment erodibility likely led to the efflux of NH_4^+ in July and August despite average porewater and extractable NH_4^+ concentrations.

Porewater advection

Porewater advection is also dependent on grain size because fine sediments have lower permeability than coarser-grained sediments, leading to slow porewater velocities. Based on the measured grain size and porosity (calculated from bulk density), the calculated permeability at all sites in Hog Island Bay is roughly similar (2.5×10^{-11} m^2 Creek, 2.4×10^{-11} m^2 Shoal, 3.0×10^{-11} m^2 Island calculated by the Kozeny-Carman equation as presented in Huettel and Webster 2001) despite differences in grain size because of increasing porosity with decreasing grain size. Huettel and Gust (1992) proposed that porewater advection is only important in sediments with permeability greater than 10^{-12} m^2, and only affects sediment to depths approaching 10 cm with permeability greater than 10^{-11} m^2. Based on this classification, all sites in Hog Island Bay should have significant porewater fluxes if pressure gradients are generated. The sediment at the fine-grained Creek site would not likely form bedforms, but animal burrows or tubes could generate pressure gradients. Additionally in this study, the microcosm generates significant radial pressure gradients (Tengberg et al 2004). However, measured nutrient fluxes at the Creek site were closely related to sediment suspension and do not show an influence of porewater advection. This lack of porewater advection in the fine-grained sediments of the Creek site was similar to that seen when Forster et al (1996) compared total oxygen utilization in fine-grained (k= 5 x 10^{-12} m^2) and coarse-grained sediment (k= 5 x 10^{-11} m^2) exposed to increased current velocity. Oxygen utilization significantly increased in the coarse-grained sediment due to porewater advection, but in fine-grained sediment showed no relationship to current velocity (Forster et al 1996). The increased importance of porewater advection with increasing grain size is reflected in the higher calculated depths of porewater affected at the Island site and the greater efflux than predicted by desorption alone. Neither porewater advection or desorption was clearly dominant at the Shoal site because of the mix of sandy sediments and clay particles, making both processes important.

Controls on nutrient flux

Biological uptake

Biological uptake resulted in an uptake of NH_4^+ during some sampling events. While the Island site showed an efflux of NH_4^+ at all sampling times, both the Shoal and Creek site showed uptake of nutrients during some parts of the year. In a previous study in Hog Island Bay, Anderson et al (2003) attributed a lack of NH_4^+ efflux from the sediment, despite high mineralization rates, to uptake by benthic microalgae. At the Creek site, NH_4^+ uptake occurred during time periods of higher benthic microalgal biomass, except the November sampling. The Shoal site similarly had an uptake of NH_4^+ at all times except July and August, the two time periods with the highest sediment erodibility. Interestingly, the Island site showed an efflux of NH_4^+ during all sampling periods despite having the highest benthic microalgal biomass. The benthic microalgae may have been less able to use nutrients transported by porewater advection or the efflux from porewater advection may have been greater than the uptake by the benthic microalgae.

Wind speed

The opposite influence of wind speed on residual nutrient flux at the Creek and Island site is also explained by the characteristics at these sites. The inverse relationship of wind speed and nutrient flux at the Island site may be explained by flushing of available porewater. As explained in Chapter 3, porewater advection supplies a limited quantity of nutrients to the water column, limited by the nutrients available to the maximum depth of porewater affected (dependent on grain size and forcing conditions). Therefore, preceding high winds may result in flushing of the porewater, leaving low nutrient porewater, similar to the changes in oxygen profiles in permeable sediments exposed to increased flows (Forster et al 1996, Lohse et al 1996). The porewater profiles measured in this study cannot resolve this question as the samples were often taken on a different day than the cores for the erosion experiments. The Island site showed a positive NH_4^+ flux from the sediment to the water column for all time periods, indicating that the nutrient flux is controlled by a positive source, not an uptake mechanism. However, the results show significant uptake of NH_4^+ at the Creek site. If nutrient uptake at the Creek site is controlled by benthic microalgal uptake, the effect of wind speed may depend on the state of the microalgal mat. Calculated microalgal NH_4^+ demand at the site ranged from 310 to 453 µmols m^{-2} d^{-1} and exceeded mineralization rates throughout the year (Anderson et al 2003). However, biofilms can be damaged by significant sediment transport or be destroyed by bioturbating fauna (e.g. de Brouwer et al 2000, Miller 1989). The higher preceding wind speeds likely resulted in previous sediment suspension and therefore a breakdown of the biofilm, which would result in decreased NH_4^+ uptake. This breakdown may not be apparent in the measured chlorophyll a samples because the samples measured to 1 cm.

Conclusions

Numerous studies have shown that increased hydrodynamic activity can result in increased nutrient flux. However, this study showed that the controls on this flux can vary over a small distance and that increased hydrodynamic activity can result in increased uptake of nutrients as well as efflux. The effects of hydrodynamics on nutrient flux can not be ignored in creation of nutrient budgets and sediment characteristics must be considered in predicting the nutrient flux. Further research is needed to build an appropriate nutrient budget including explicit treatment of hydrodynamic effects not only transport of nutrients, but also on nutrient transformation rates.

References

Anderson, IC, KJ McGlathery and AC Tyler. 2003. Microbial mediation of 'reactive' nitrogen transformations in a temperate lagoon. *Marine ecology progress series.* 246:73-84.

Berelson, WM, D Heggie, A Longmore, T Kilgore, G Nicholson, and G Skyring. 1998. Benthic nutrient recycling in Port Phillip Bay, Australia. *Estuarine coastal and shelf science*. 46(6):917-934.

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

Boatman, CD and JW Murray. 1982. Modeling exchangeable NH_4^+ adsorption in marine sediments: Processes and controls of adsorption. *Limnology and oceanography*. 27(1):99-110.

Cabrita, MT and V Brotas. 2000. Seasonal variation in denitrification and dissolved nitrogen fluxes in intertidal sediments of the Tagus estuary, Portugal. *Marine ecology progress series*. 202:51-65.

de Brouwer, JFC, S Bjelic, EMGT de Deckere and LJ Stahl. 2000. Interplay between biology and sedimentology in a mudflat (Biezelingse Ham, Westerschelde, The Netherlands). *Continental shelf research*. 20(10-11):1159-1177.

Dollar, SJ, SV Smith, SM Vink, S Obrebski and JT Hollibaugh. 1991. Annual cycle of benthic nutrient fluxes in Tomales Bay, California, and contribution of the benthoc to total ecosystem metabolism. *Marine ecology progress series*. 79(1-2):115-125.

Dong, LF, DCO Thornton, DB Nedwell and GJC Underwood. 2000. Denitrification in sediments of the River Colne estuary, England. *Marine ecology progress series*. 203:109-122.

Forster, S, M Huettel and W Zeibis. 1996. Impact of boundary layer flow velocity on oxygen utilisation in coastal sediments. *Marine ecology progress series*.143:173-185.

Gibbs, M, G Funnell, S Pickmere, A Norkko and J Hewirr. 2005. Benthic nutrient fluxes along an estuarine gradient: influence of the pinnid bivalve Atrina zelandica in summer. *Marine ecology- progress series*. 288:151-164.

Gust, G and V Müller. 1997. Interfacial hydrodynamics and entrainment functions of currently used erosion devices. In *Cohesive sediments*. Burt N., R. Parker, and J. Watts (eds). John Wiley and Sons. 149-174.

Huettel, M and G Gust. 1992. Impact of bioroughness on interfacial solute exchange in permeable sands. *Marine ecology progress series*. 89(2-3):255-267.

Huettel, M, H Roy, E Precht and S Erhenhauss. 2003. Hydrodynamical impact of biogeochemical processes in aquatic sediments. *Hydrobiologia*. 494(1-3):231-236.

Huettel, M and IT Webster. 2001. Porewater flow in permeable sediments. In *The benthic boundary layer*. BP Boudreau and BB Jørgensen (eds). Oxford University Press. 144-179.

Huettel, M, W Ziebis and S Forster. 1996. Flow-induced uptake of particulate matter in permeable sediments. *Limnology and oceanography*. 41(2):309-322.

Huettel, M, W Ziebis, S Forster and GW Luther. 1998.Advection transport affecting metal and nutrient distributions and interfacial fluxes in permeable sediments. *Geochimica et cosmochimica acta*. 62(4):613-631.

Kelly-Gerreyn, BA, DJ Hydes and JJ Waniek. 2005. Control of the diffusive boundary layer on benthic fluxes: a model study. *Marine ecology progress series*. 292:61-74.

Lawrence, D, MJ Dagg, H Liu, SR Cummings, PB Ortner and C Kelble. 2004. Wind events and benthic-pelagic coupling in a shallow suptropical bay in Florida. Marine ecology-progress series. 266:1-13.

Lawson, SE, PL Wiberg, KJ McGlathery and DC Fugate. 2007. Wind-driven sediment suspension controls light availability in a shallow coastal lagoon. *Estuaries and coasts*. 30(1):102-112.

Lohse, L, EHG Epping, W Helder and W van Raaphorst. 1996. Oxygen pore water profiles in continental shelf sediments of the North Sea: Turbulent versus molecular diffusion. Marine ecology progress series. 145(1-3):63-75.

Mackin, JE and RC Aller. 1984. Ammonium adsorption in marine sediments. *Limnology and oceanography*. 29(2):250-257.

McGlathery, KJ, IC Anderson and AC Tyler. 2001. Magnitude and variability of benthic and pelagic metabolism in a temperate coastal lagoon. Marine ecology progress series. 216:1-15.

Miller, DC. 1989. Abrasion effects on microbes in sandy sediments. *Marine ecology progress series* 55:73-82.

Morse, JW and J Morin. 2005. Ammonium interaction with coastal marine sediments: influence of redox conditions on K*. *Marine chemistry*. 95(1-2):107-112.

Sarker, MJ, T Yamamoto, T Hashimoto and T Ohmura. 2005. Evaluation of benthic nutrient fluxes and their importance in the pelagic nutrient cycles in Suo Nada, Japan. *Fisheries science*. 71(3):593-604.

Stahlberg, C, D Bastvikeni, BH Svennson and L Rahm. 2006. Mineralization of organic matter in coastal sediments at different frequency and duration of resuspension. *Estuarine, coastal and shelf science.* 70:317-325.

Tengberg, A., H Stahl, G Gust, V Muller, U Arning, H Andersson and POJ Hall. 2004. Intercalibration of benthic flux chambers I. Accuracy of flux measurements and influence of chamber hydrodynamics. *Progress in oceanography*. 60:1-28.

Tyler, AC. 2002. Impact of benthic algae on dissolved organic nitrogen in a temperate coastal lagoon. PhD Dissertation. University of Virginia, Charlottesville, VA.

Tyler AC, KJ McGlathery and IC Anderson. 2001. Macroalgal mediation of dissolved organic nitrogen fluxes in a temperate coastal lagoon. *Estuarine coastal and shelf science*. 53:155-168.

Tyler, AC, KJ McGlathery and IC Anderson. 2003. Benthic algae control sediment-water column fluxes of organic and inorganic nitrogen compounds in a temperate lagoon. *Limnology and oceanography*. 48:2125-2137.

Figures and Tables

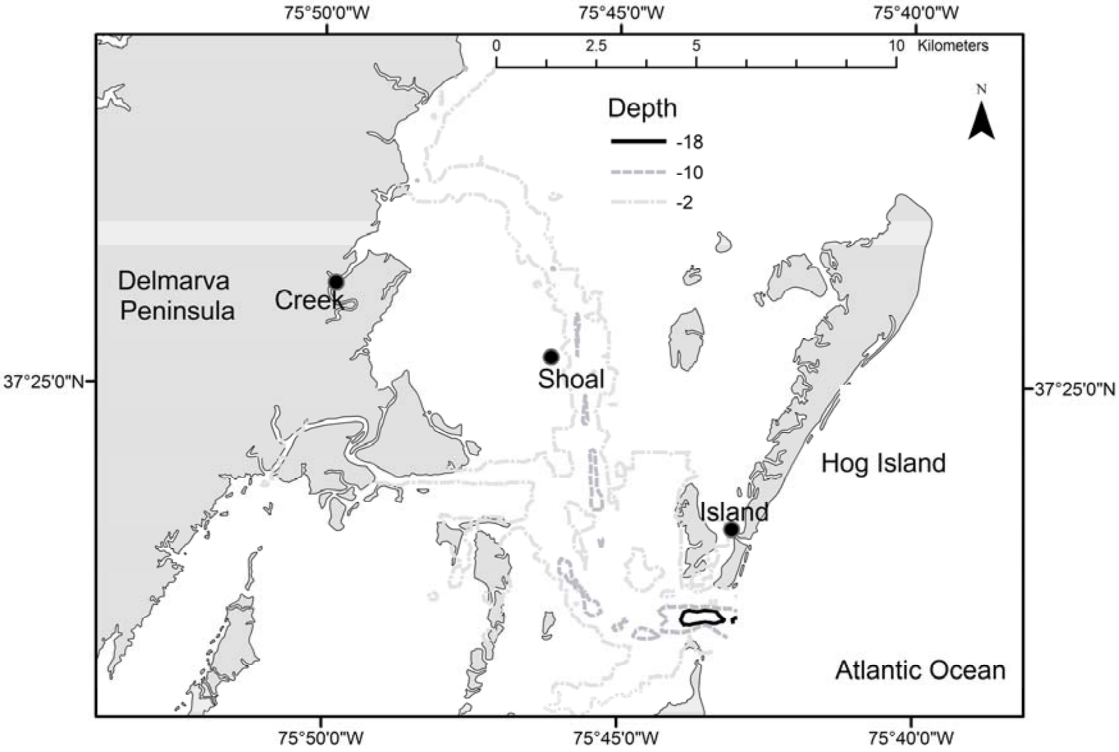

Figure 5.1. Site map. Three sites within a shallow coastal lagoon were used in this study. These sites represent a gradient from fine-grained, highly organic sediment at the Creek site to sandy, relatively low organic content sediment at the Island site.

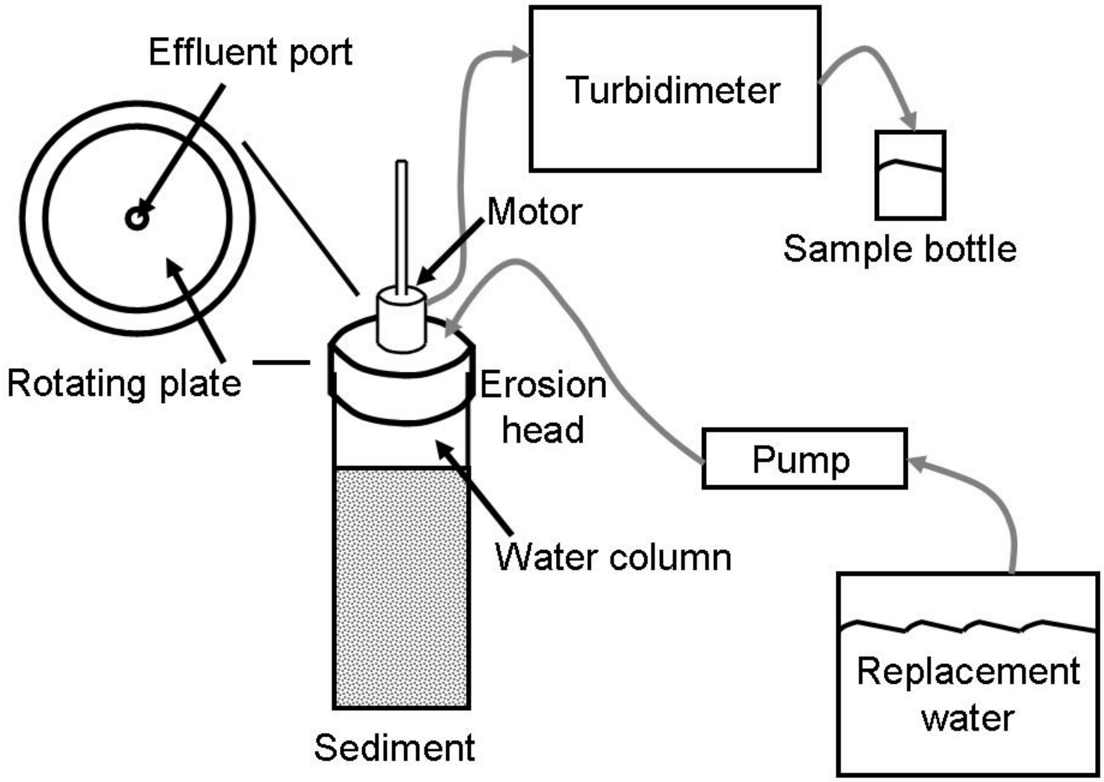

Figure 5.2. Gust erosion microcosm. The microcosm was used to expose the sediment cores to incremental increases in shear stress with the effluent water sampled for suspended sediment (Chapter 3) and nutrients.

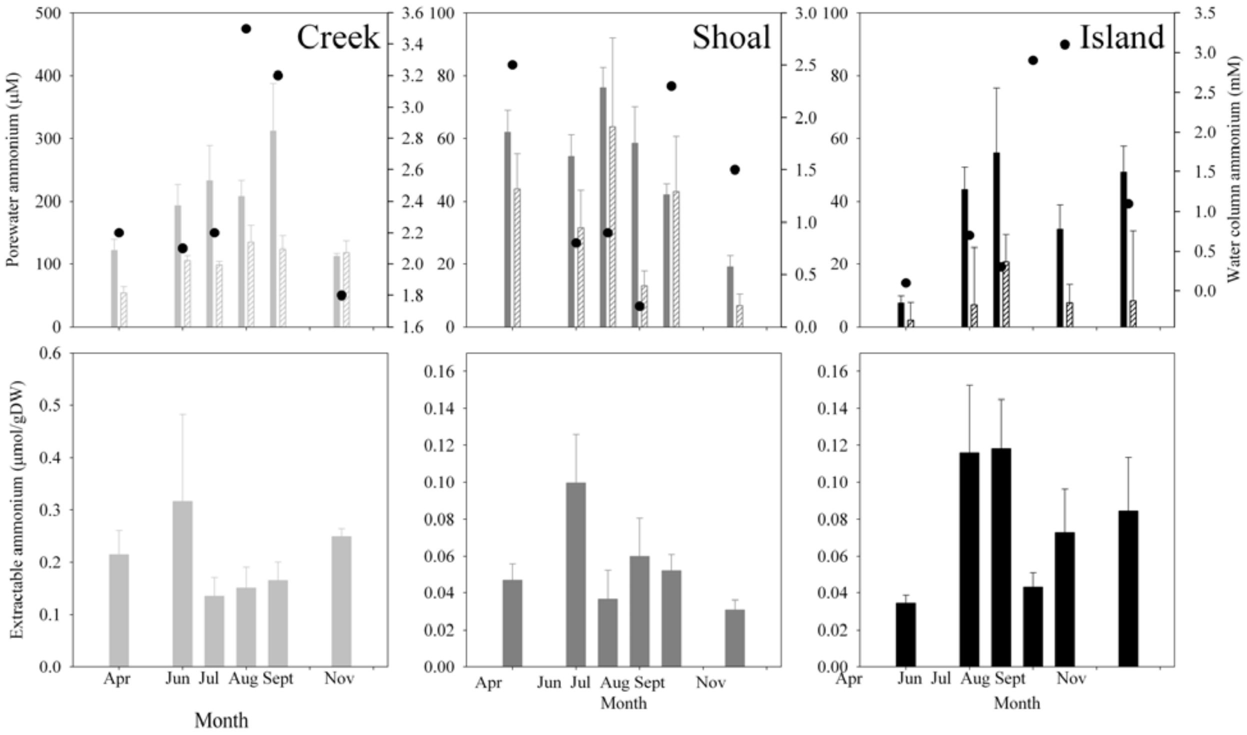

Figure 5.3. Summary of sediment NH_4^+ data. Other site characteristics are displayed in Chapter 3. For porewater data, hashed bars are the average nutrient concentration (0-10 cm depth), solid bars are the concentration in the uppermost 2 cm and black circles are the water column concentration. Error bars are standard error. No data is available for the Island site in August. Note different y-axes for the Creek site and the second y-axes for the water column concentrations.

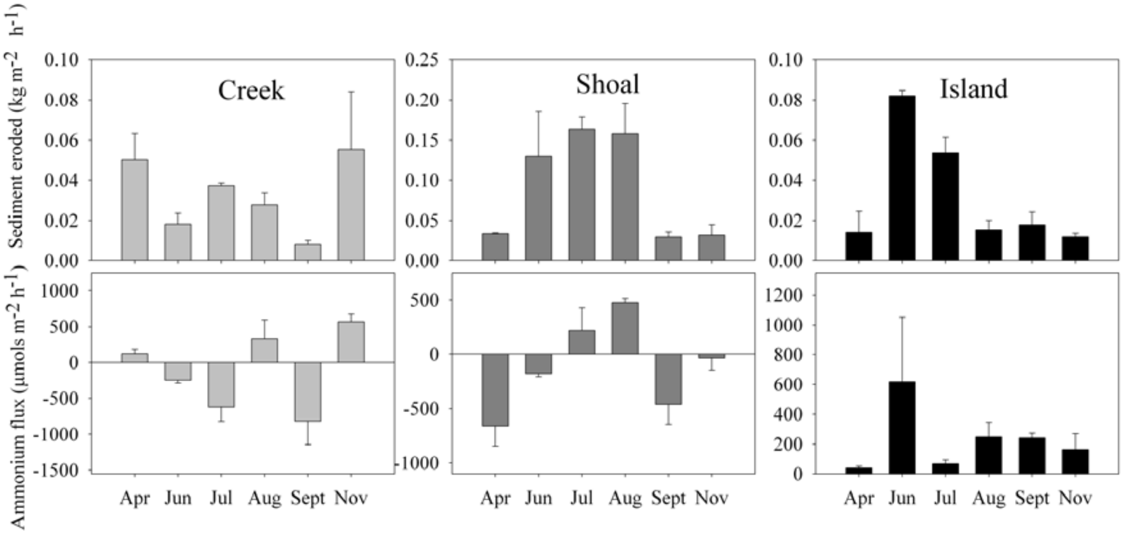

Figure 5.4. Measured sediment and NH_4^+ fluxes during the 100 minute experiments. All sites showed temporal variability and all both sediment and NH_4^+ varied with site.

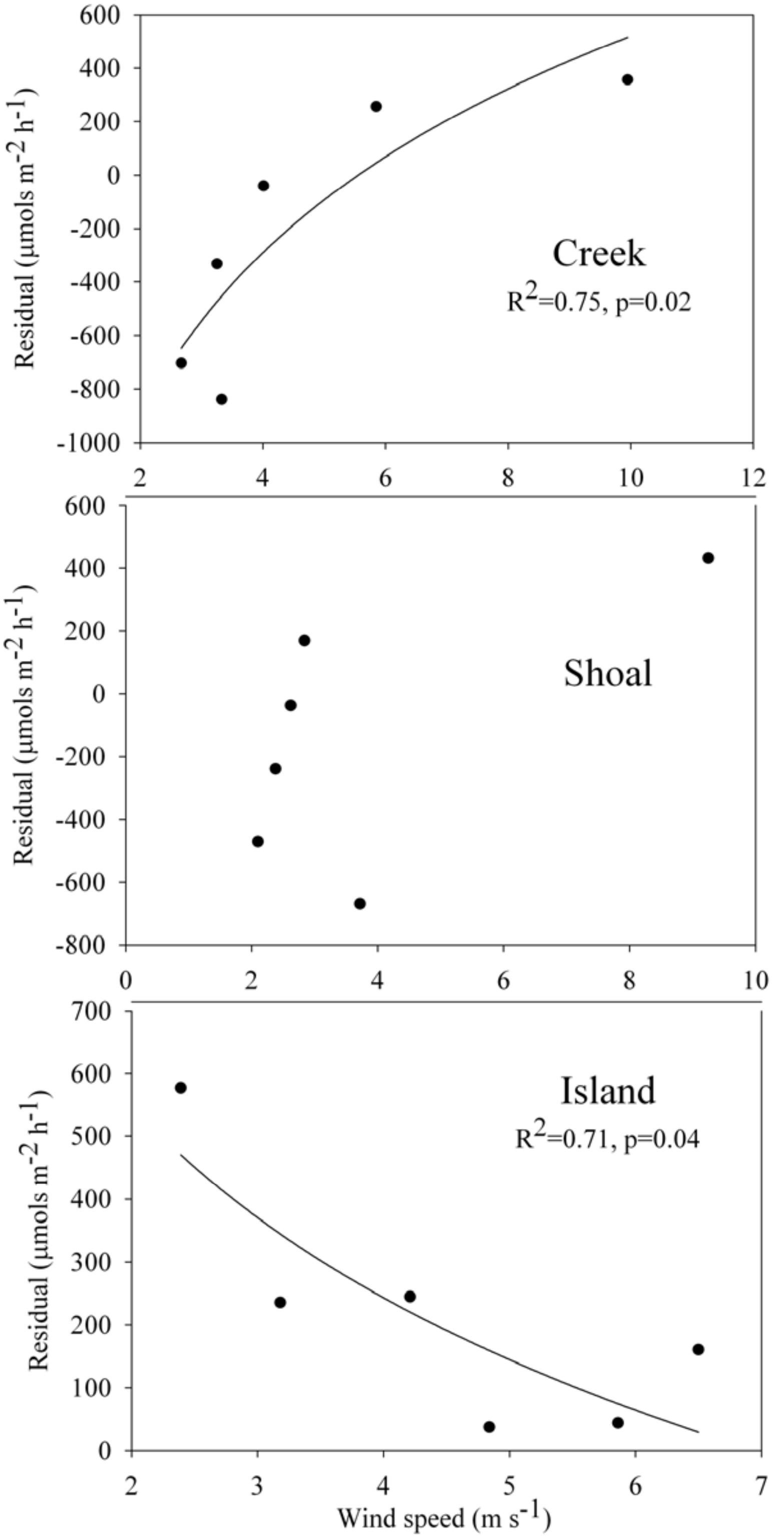

Figure 5.5. Relationship between measured and predicted fluxes of NH_4^+. The Creek site showed the closest relationship indicating that NH_4^+ flux is dependent on desorption. The dashed line is the predicted flux from desorption.

.

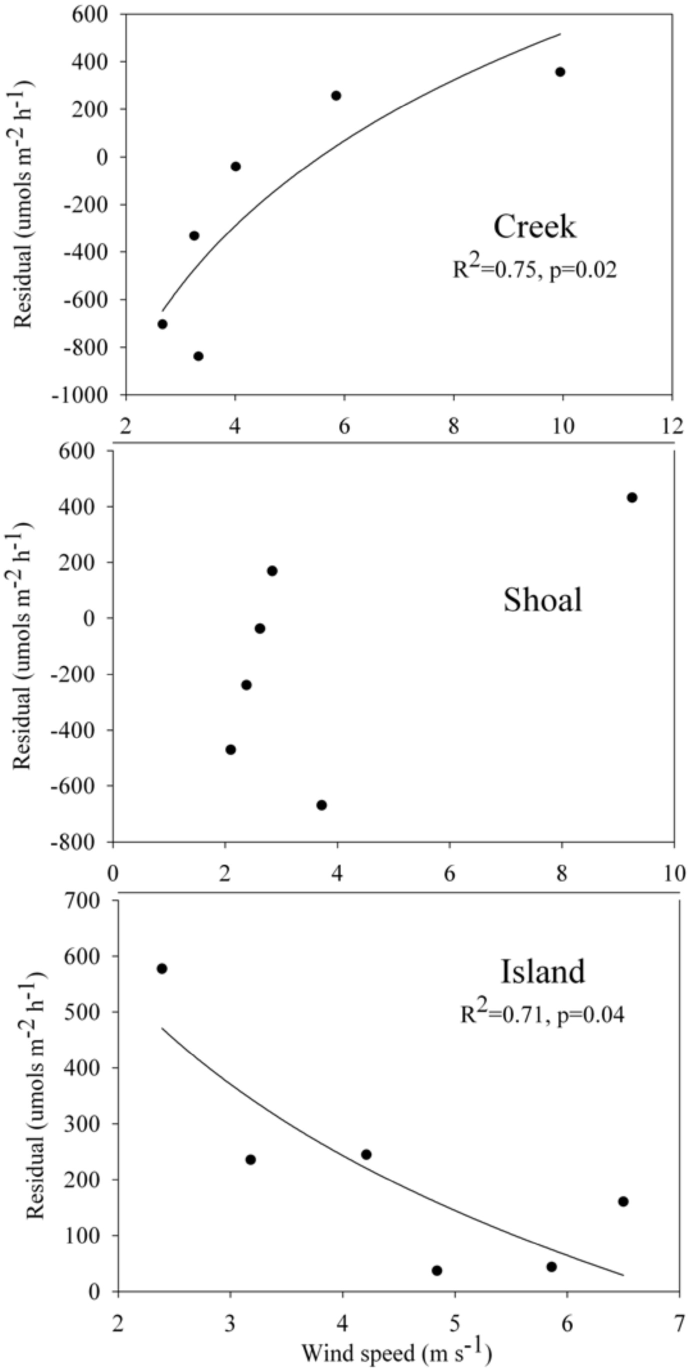

Figure 5.6. Relationship between wind speed and residual flux (measured flux – predicted flux). The relationship shows opposite trends at the Creek and Island site, indicating that different mechanisms control nutrient flux at these sites.

Table 5.1. Comparison of nutrient fluxes in sediment cores exposed to low-flow and high-flow. Data for the low-flow is from Tyler 2002 and shows much lower magnitude.

Though sample timing was not the same, the data can still be compared based on seasonal classifications.

	Creek		**Shoal**		**Island**	
	This study	*Low-flow*	*This study*	*Low-flow*	*This study*	*Low-flow*
Month						
January		-4.5		8.2		5.6
February						
March		35.5		9.2		-6.3
April	121.5		-659.4		38.8	
May		30.2		5.8		1.0
June	-245.6	18.8	-176.6	84.2	616.9	-5.8
July	-620.3		219.4		68.1	
August	327.2	74.5	475.9	33.3	247.4	6.2
September	-815.3		-461.8		240.8	
October		1.8		0.3		
November	571.6		-33.1		164.6	4.4
December						

Chapter 6: Conclusions

Fluxes of sediment and nutrients between the sediment bed and the water column are regulated by complex interactions of physical and biological controls (Fig. 6.1). These two processes have often been considered separately, with sediment suspension controlled by physical forcing and nutrient flux controlled by biological activity. Recent studies such as Huettel and Gust (1992), Lawrence et al (2004), and Morse and Morin (2005) have shown that hydrodynamic activity can greatly increase nutrient exchange between the sediment and water column. Other work, such as that by Fonseca and Fischer (1986), Gambi et al (1990), and Orvain et al (2004) has shown that primary producers, particularly seagrass, and benthic fauna can affect sediment erosion. However, relatively few studies have examined the connections between these processes. The results of this dissertation show that sediment suspension and nutrient flux are both controlled by the interaction of physical forcing and biological processes, particularly the density of benthic primary producers. The relative importance of these processes varies with site characteristics, particularly sediment grain size, and season, which can influence both primary producer biomass and standing stock of nutrients.

Hydrodynamic activity clearly affects nutrient flux.

While previous studies have shown that nutrient fluxes between the sediment and water column are important, most have been conducted in low-flow conditions which may underestimate the flux. Previous research has shown that nutrient efflux from the sediment can support 30 to 100% of the nutrient demand of benthic and pelagic algae

(Gibbs et al 2005 and references within). These fluxes can support primary producers particularly when water column nutrients are low (Kamer 2004), and in turn, uptake by benthic primary producers can reduce the flux of nutrients from the sediment (Qu et al 2003). However, the laboratory-incubated cores or field chambers used in these and other studies (e.g. Dollar et al 1991, Berelson et al 1998, Cabrita and Brotas 2000, Tyler et al 2001) represent only the diffusive flux of nutrients and ignore hydrodynamically-forced nutrient fluxes that are likely common in these systems.

In this study, increased flow resulted in both uptake and efflux of nutrients about an order of magnitude greater than seen in low-flow incubations on short time scales (100 min, Chapter 5). Using a Gust microcosm to increase hydrodynamic forcing (Gust and Muller 1997), the average magnitude of ammonium (NH_4^+) fluxes measured in this study from the spring to fall ranged from 229 μmols m^{-2} h^{-1} (Shoal site) to 450 μmols m^{-2} h^{-1} (Creek site, average magnitude at the Island site was 338 μmols m^{-2} h^{-1}). In comparison, the seasonal average magnitude of NH_4^+ fluxes in previous low-flow incubations at the same sites ranged from 5 μmols m^{-2} h^{-1} (Shoal site) to 28 μmols m^{-2} h^{-1} (Creek site, average magnitude at the Island site was 24 μmols m^{-2} h^{-1}) (Chapter 5, Tyler 2002, Tyler et al 2003). Increased hydrodynamic forcing enhanced both the transport of nutrients out of the sediment bed and the biological uptake of nutrients. Though this study is not the first to report increased nutrient fluxes with hydrodynamic forcing, the causes of variability in fluxes across multiple sites with varying grain size, primary producer dominance and exposure and between seasons has not been previously studied. Sediment grain size controlled the relative importance of desorption and porewater advection among the sites. The magnitude and direction of the flux was controlled by biological uptake and nutrient availability (Chapters 3 and 5).

While cumulative flux is important, the instantaneous flux rate, and its relation to uptake rates of primary producers, will control the use of enhanced nutrient flux by primary producers. Nutrient efflux from desorption is generally considered a short-term, fast process (Laima 1992), yet the time scale of porewater advection has rarely been considered. Most tracer studies show cumulative flux rather than instantaneous flux (e.g. Huettel and Gust 1992, Hutchinson and Webster 1998). These studies all show an asymptotic cumulative flux with hydrodynamic activity, indicating a decrease in the instantaneous flux rate. However, to the author's knowledge, no other study has specifically addressed the duration of the peak flux. Numerical simulations of porewater advection in a low permeability sediment (k= 5 x 10^{-12} m^2) and a high permeability sediment (k= 5 x 10^{-11} m^2) were used to examine this peak flux. Porewater advection in the high permeability sediment resulted in complete flushing of the porewater in about 3 h (Chapter 3). While the modeled peak flux in the high permeability sediment was an order of magnitude greater than the modeled peak flux in the low permeability sediment, the average fluxes were similar over 12 h. The significant temporal variability in fluxes from desorption and porewater advection makes comparison of these fluxes problematic. Both desorption and porewater advection have high initial rates but quickly taper off. Because of this, desorption and porewater advection must be measured on similar time scales. These fluxes may be best integrated over a forcing event (such as a storm) or viewed in the context of rates of biological uptake. For example, fast-growing species with high nutrient uptake rates may be better able to utilize the peak flux, potentially creating a competitive advantage for these species.

The mechanisms linking changes in hydrodynamic forcing to nutrient flux varied even within a relatively small geographic area. Based on the mechanistic experiments and numerical simulations in Chapter 3 and the seasonal experiments in Chapter 5, desorption was more important in fine-grained sediments; porewater advection was more important at the coarser-grained, higher permeability site. In both cases, the nutrient flux was dependent on the availability of nutrients in the sediment bed and in the case of desorption, the erodibility of the sediment.

Biological processes have significant effects on physical transport.

The initiation of transport of sediment and other materials from the sediment bed is a result of the resistance of the material to transport and the forcing conditions on the sediment bed, both of which are affected by biological activity. Sediment erodibility is affected by both benthic fauna and primary producers with both direct and indirect effects. Benthic macrophytes, such as seagrass and macroalgae, can modify hydrodynamic forcing (e.g. Fonseca and Fischer 1986, Gambi et al 1990) while benthic microalgae can increase the resistance of sediment to erosion (e.g. de Brouwer et al 2000, Quaresma et al 2004). Benthic fauna can similarly modify flow conditions by the construction of worm tubes and other emergent features (e.g. Friedrichs et al 2000) or by destabilization of the sediment through bioturbation (e.g. Orvain et al 2004). In the present study, trapping of fine sediment by macroalgae and bioturbation by benthic fauna increased sediment erodibility at 2 out of 3 sites during the summer months. The increased erosion of inorganic material indicated that the increased erosion was not just erosion of organic material (Chapter 4).

This study is also the first to show that low-density populations of benthic primary producers can increase hydrodynamic forcing, as reflected in sediment suspension and nutrient flux, at the sediment surface (Chapter 2). Extensive previous research (e.g. Gambi et al 1990, Fonseca and Cahalan 1992, Romano et al 2003) has shown that high density populations of benthic primary producers stabilize sediment and decrease near-bed hydrodynamic activity. Low-density populations affect hydrodynamics and nutrient flux very differently, resulting in an increase in sediment suspension. Using phosphate as a relatively conservative tracer, this study also showed that low-density populations of macroalgae can increase nutrient efflux from the sediment. This effect is analogous to results seen with other emergent features, such as polycheate tubes (e.g. Friedrichs et al 2000). These features can divert flow around rather than over the feature creating enhanced erosion. Macroalgae may also be transported as bedload material, acting as a tool to dislodge particles, thereby increasing erosion. The key feature leading to decreased sediment suspension and bed forcing is likely the development of skimming flow, in which water is directed away from the sediment bed. This effect of low-density populations of primary producers illustrates studies on fully-developed, high density populations of primary producers can not be used to explain developing or declining populations where densities are lower.

Feedback loops between benthic primary producers and hydrodynamic activity may help support alternate states.

Macroalgae and seagrass will respond differently to the effects of hydrodynamic forcing on sediment and nutrient fluxes. Increased near-bed hydrodynamic activity caused by low-density populations of seagrass and macroalgae will increase water column nutrient availability and reduce light availability through sediment suspension. While coastal systems are typically referred to as light or nutrient-limited, the relative importance of these limiting conditions may be more primary-producer specific than system specific. Seagrass typically has higher light requirements than macroalgae (Duarte 2002), which may make developing seagrass beds particularly vulnerable to forcing events. This is because developing beds are generally low-density and have short canopies which can increase sediment suspension and therefore light limitation. This increased sediment suspension, and any concurrent increased nutrient efflux, may favor macroalgae because of its greater demand for water column nutrients and lower light requirements. This mechanism may explain the failure of some seagrass restoration efforts and indicates that planting density must be carefully considered. The combination of increased water column nutrient availability and decreased light availability during forcing events in low-density populations may hinder the recovery of seagrass and support the growth of macroalgae, potentially leading to an alternate macroalgal-dominated steady state.

These effects on primary productivity may intensify coastal eutrophication by supporting continued growth of macroalgae and pelagic primary producers. Most of the effects of eutrophication (e.g. changes in primary producer biomass and dominance, changes in water quality) are attributed to increased nutrient loads. However, the availability of nutrients, both in time and space, to primary producers is also important.

In low nutrient systems, pelagic productivity is typically low because benthic primary producers effectively cap nutrient efflux from the sediment, resulting in minimal nutrient availability for pelagic productivity (Webster et al 2002, Tyler et al 2003). Desorption and porewater advection, however, may create fluxes high enough to either overwhelm the uptake of benthic primary producers or in the case of desorption, to simply bypass the benthic primary producers. In addition, the high magnitude, short duration peaks of these fluxes may favor growth of phytoplankton and macroalgae, both of which can take up nutrients at accelerated rates when exposed to high surrounding concentrations. Through these two processes, physical-biological coupling can enhance production of macroalgae and phytoplankton, similar to the changes expected with eutrophication (e.g. Nixon et al 2001, Taylor et al 1999, Herbert 1999, Boynton et al 1996). This increased production may amplify the effects of nutrient enrichment and intensify eutrophication.

References

Boynton WR, JD Hagy, L Murray, C Stokes, and WM Kemp. 1996. A comparative analysis of eutrophication patterns in a temperate coastal lagoon. *Estuaries*. 19(2B):408-421.

de Brouwer, JFC, S Bjelic, EMGT de Deckere and LJ Stahl. 2000. Interplay between biology and sedimentology in a mudflat (Biezelingse Ham, Westerschelde, The Netherlands). *Continental shelf research*. 20(10-11):1159-1177.

Duarte, CM. 2002. The future of seagrass meadows. *Environmental conservation*. 29(2)192-206.

Fonseca, MS and JS Cahalan. 1992. A preliminary evaluation of wave attenuation by 4 species of seagrass. *Estuarine coastal and shelf science*. 35(6):565-576

Friedrichs M, G Graf, and B Springer. 2000. Skimming flow induced over a simulated polycheate tube lawn at low population densities. *Marine ecology progress series*. 192:219-228.

Gambi, MC, ARM Nowell and PA Jumars. 1990. Flume observations on flow dynamics in *Zostera-marina* (eelgrass) bed. *Marine ecology progress series*. 61(1-2):159-169.

Herbert, RA. 1999. Nitrogen cycling in coastal marine ecosystems. *FEMS microbiology reviews*. 20(3):273-284.

Huettel, M and G Gust. 1992. Impact of bioroughness on interfacial solute exchange in permeable sands. *Marine ecology progress series*. 89(2-3):255-267.

Hutchinson, PA and IT Webster. 1998. Solute uptake in aquatic sediments due to current-obstacle interactions. *Journal of environmental engineering-ASCE*. 124(5):419-426.

Kamer, K, P Fong, RL Kennison, and K Schiff. 2004. The relative importance of sediment and water column supplies of nutrients to the growth and tissue nutrient content of the green macroalga Entermorpha intestinalis along the estuarine resource gradient. *Aquatic ecology*. 38(1):45-56.

Laima, MJC. 1992. Extraction and seasonal variation of NH_4^+ pools in different types of coastal marine sediments. *Marine ecology progress series*. 82(1):75-84.

Lawrence, D, MJ Dagg, H Liu, SR Cummings, PB Ortner and C Kelble. 2004. Wind events and benthic-pelagic coupling in a shallow suptropical bay in Florida. *Marine ecology-progress series*. 266:1-13.

Malecki, LM, JR White, and KR Reddy. 2004. Nitrogen and phosphorus flux rates from the sediment in the Lower St. Johns River estuary. *Journal of environmental quality*. 33(4):1545-1555.

Morse, JW and J Morin. 2005. Ammonium interaction with coastal marine sediments: influence of redox conditions on K*. *Marine chemistry*. 95(1-2):107-112.

Nixon, S, B Buckley, S Granger, and J Blintz. 2001. Responses of very shallow marine ecosystems to nutrient enrichment. *Human and ecological risk assessment*. 7(5):1457-1481.

Orvain, F, PG Sauriau, A Sygut, L Joassard, and P Le Hir. 2004. Interacting effects of Hydrobia ulvae bioturbation and microphytobenthos on the erodibility of mudflat sediments. *Marine ecology progress series*. 278:205-223.

Qu, WC, RJ Morrison, and RJ West. 2003. Inorganic nutrient and oxygen fluxes across the sediment-water interface in the inshore macrophyte areas of a shallow estuary (Lake Illawarra,Australia). *Hydrobiologia*. 492 (1-3):119-127.

Quaresma, VD, CL Amos and M Flindt. 2004. The influences of biological activity and consolidation time on laboratory cohesive beds. *Journal of sedimentary research*. 74(2):184-190.

Romano, C, J Widdows, MD Brinsley and FJ Staff. 2003. Impact of *Enteromorpha intestinalis* mats on near-bed currents and sediment dynamics: flume studies. *Marine ecology progress series*. 256:63-74.

Sarker, MJ, T Yamamoto, T Hashimoto, and T Ohmura. 2005. Evaluation of benthic nutrient fluxes and their importance in the pelagic nutrient cycles in Suo Nada, Japan. *Fisheries science*. 71(3):593-604.

Taylor, DI, SW Nixon, SL Granger, and BA Buckley. 1999. Responses of coastal lagoon plant communities to levels of nutrient enrichment: A mesocosm study. *Estuaries*. 22(4):1041-1056.

Tyler, AC. 2002. Impact of Benthic Algae on Dissolved Organic Nitrogen in a Temperate, Coastal Lagoon. PhD Dissertation. University of Virginia. Charlottesville, VA.

Tyler, AC, KJ McGlathery, and IC Anderson. 2003. Benthic algae control sediment-water column fluxes in a temperate coastal lagoon. Estuarine, coastal and shelf science. 53:155-168

Webster, IT, PW Ford, and B Hodgson. 2002. Microphytobenthos contribution to nutrient-phytoplankton dynamics in a shallow coastal lagoon. *Estuaries*. 25(4A):540-551.

Figure

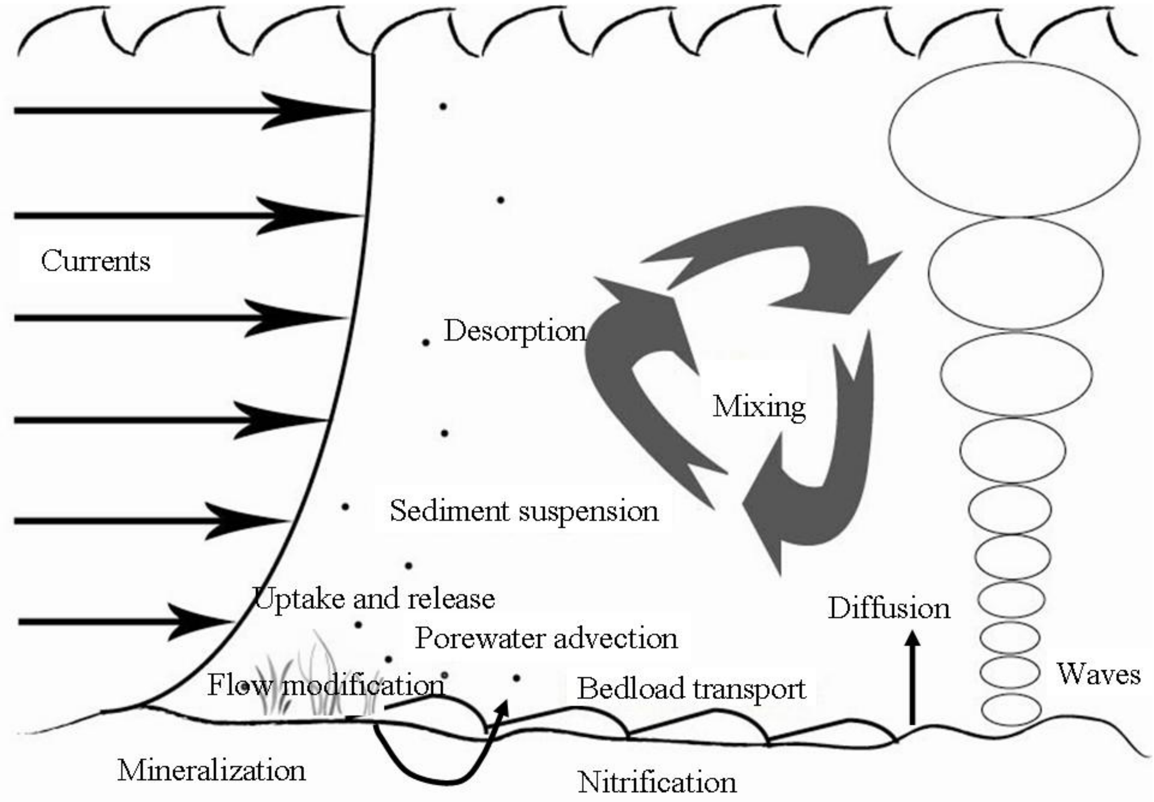

Figure 6.1. Combined physical and biological model of a shallow coastal system. Physical and biological processes are often considered separately; however, processes such as porewater advection and flow modification by primary producers integrate these processes.

Appendix I

Results of erosion experiments in South Bay, VA using macroalgae, seagrass and bare sediment cores (Chapter 2).

Day	**Treatment**	**Biomass (g DW m^{-2})**	**Sediment eroded (g m^{-2})**	**Shoots m^{-2}**	**NH_4^+ flux (µmols m^{-2} h^{-1})**	**PO_4^{3-} flux (µmols m^{-2} h^{-1})**	**NO_3^- flux (µmols m^{-2} h^{-1})**
1	*Control*	0	20		-75	-109	58
3	*Control*	0	32		35	-100	450
4	*Control*	0	12		-64	68	50
5	*Control*	0	23		-98	-154	81
1	*High algae*	53	25		-456	-104	55
3	*High algae*	60	11		-279	-262	-98
4	*High algae*	76	12		-103	68	-160
5	*High algae*	74	13		-471	-85	-103
1	*Low algae*	16	56		-208	-32	114
3	*Low algae*	17	41		720	383	124
4	*Low algae*	20	33		-386	108	-73
1	*Medium algae*	32	37		-42	2	196
3	*Medium algae*	40	50		-333	143	318
5	*Medium algae*	41	34		-254	-43	-85
5	*Medium algae*	33	11		-90	-143	131
1	*Seagrass*	66	20	127	-277	-107	15
3	*Seagrass*	142	39	159	1388	474	431
4	*Seagrass*	132	65	201	-71	34	-117
5	*Seagrass*	41	9	64			

Appendix II

Measured porewater profiles in South Bay. All nutrient concentrations are presented a μM and numbers in parentheses are standard error.

Ammonium

Depth(cm)	*Day 1*	*Day 2*	*Day 3*	*Day4*	*Day 5*
0	2.6(0.5)	0.3(0.3)	3.9(2.0)	0.1(0.1)	0
1	17(4.4)	9.5(5.0)	35(10)	8.7(6.7)	6(2.8)
3	67(21)	41(12)	76(10)	47(19)	33(8.9)
5	83(9.8)	66(0.6)	95(13)	38(11)	52(3.6)
7	77(8.2)	53(16)	99(27)	42(21)	60(6.1)
9	74(20)	44(12)	102(6.8)	32(17)	61(11)

Phosphate

Depth(cm)	*Day 1*	*Day 2*	*Day 3*	*Day4*	*Day 5*
0	1.3(0.6)	1.2(0.2)	1.2(0.0)	1.2(0.4)	1.5(0.3)
1	2.3(1.2)	1.6(0.6)	1.9(0.5)	1.1(0.3)	1.2(0.6)
3	3.1(1.1)	3.7(1.7)	4.3(1.0)	7.1(1.5)	2.1(0.6)
5	4.6(0.5)	4.1(0.3)	5.3(0.5)	5.7(1.0)	2.7(1.6)
7	4.7(0.6)	4.7(2.5)	6.1(1.1)	4.8(1.4)	4.7(1.1)
9	7.7(1.9)	3.3(1.9)	11(2.4)	5.1(0.9)	6.1(2.2)

Nitrate

Depth(cm)	*Day 1*	*Day 2*	*Day 3*	*Day4*	*Day 5*
0	2.5(1.0)	2.0(0.2)	2.4(0.6)	2.7(0.5)	3.3(0.9)
1	2.9(0.7)	1.5(0.1)	1.6(0.2)	2.5(0.5)	3.3(0.1)
3	3.1(1.5)	1.7(0.3)	2.3(0.1)	2.5(0.6)	2.6(1.1)
5	1.5(0.1)	1.9(0.1)	2.3(0.4)	2.8(0.8)	1.6(0.0)
7	1.7(0.1)	1.9(0.5)	2.1(0.4)	2.5(0.7)	1.8(0.2)
9	1.7(0.4)	1.3(0.1)	1.9(0.1)	2.8(0.6)	1.6(0.0)

Appendix III

Results of seasonal erosion experiments in Hog Island Bay using a Gust erosion microcosm. Values presented are the mass of sediment eroded during 20 minutes at the given shear stress (0.01,0.08,0.16,0.24, 0.32 N m^{-2}) scaled to a 1 m^2 area. Numbers in parentheses are standard error.

Site	**Date**	**0.01**	**0.08**	**0.16**	**0.24**	**0.32**	**Total**
Creek	*April*	0.8(0.0)	3.0(0.1)	14.5(0.6)	29.1(0.6)	36.9(1.3)	83.5(2.2)
Creek	*June*	2.3(0.1)	0.9(0.0)	2.8(0)	11.5(0.2)	15.1(0.7)	30.4(0.9)
Creek	*July*	4.2(0.1)	5.0(0.2)	9(0.2)	14.6(0.5)	33.4(0.5)	62(0.2)
Creek	*August*	1.0(0.1)	5.4(0.2)	9.7(0.2)	18.5(0.3)	12.6(0.5)	46.1(1)
Creek	*September*	2.8(0.1)	2.5(0.1)	1.9(0.1)	6.2(0.1)	3.2(0.1)	13.8(0.3)
Creek	*November*	1.3(0.0)	2.0(0.1)	10.1(0.4)	25.5(1.4)	54.7(3.2)	92.4(4.8)
Island	*April*	2.0(0.1)	2.2(0.0)	2.1(0.2)	7.1(0.3)	12.1(1.3)	23.5(1.7)
Island	*June*	1.4(0.1)	5.5(0.0)	18.4(0.5)	42.3(0.9)	70.7(0.9)	136.8(0.4)
Island	*July*	6.2(0.5)	13(0.3)	20.2(0.5)	23.3(0.7)	32.9(0.4)	89.4(1.3)
Island	*August*	3.8(0.1)	4.7(0.1)	3.9(0.1)	5.5(0.2)	11.4(0.5)	25.6(0.8)
Island	*September*	3.7(0.2)	0.9(0.1)	6.9(0.3)	8.4(0.5)	13.7(0.3)	29.9(1)
Island	*November*	1.2(0.0)	2.4(0.0)	1.8(0)	6.9(0.2)	8.7(0.3)	19.7(0.3)
Shoal	*April*	2.9(0.1)	1.8(0.1)	4.2(0.1)	15(0.2)	35(0.2)	56(0.1)
Shoal	*June*	0.2(0.0)	2.8(0.1)	8.2(0.5)	61.2(3.2)	143.9(5.5)	216.1(9.3)
Shoal	*July*	3.0(0.1)	6.7(0.3)	12.1(0.2)	58.1(0.8)	195.6(2.6)	272.6(2.6)
Shoal	*August*	4.6(0.1)	1.7(0.1)	17.6(0.3)	68.6(1.1)	175.4(5.4)	263.3(6.2)
Shoal	*September*	1.5(0.0)	2.2(0.0)	2.3(0.1)	11.9(0.3)	32.5(0.7)	48.9(1)
Shoal	*November*	1.0(0.0)	1.2(0.0)	6.5(0.4)	16.1(0.8)	29.1(1.1)	52.8(2.2)

Appendix IV

Results of seasonal erosion experiments in Hog Island Bay using a Gust erosion microcosm. Values presented are the mass of NH_4^+ transported during 20 minutes at the given shear stress (0.01,0.08,0.16,0.24, 0.32 N m^{-2}) scaled to a 1 m^2 area. Numbers in parentheses are standard error. Negative values represent uptake of nutrients; positive values represent efflux from the sediment.

Site	**Date**	**0.01**	**0.08**	**0.16**	**0.24**	**0.32**	**Total**
Creek	*April*	115(19)	110(44)	30(44)	93(14)	-30(25)	202(101)
Creek	*June*	85(39)	-57(39)	-91(29)	-62(64)	-200(44)	-409(71)
Creek	*July*	-2(34)	-240(92)	-126(168)	-362(110)	-307(208)	-1034(328)
Creek	*August*	194(45)	151(97)	161(103)	133(149)	100(102)	545(447)
Creek	*September*	-83(20)	-58(108)	-452(115)	-473(178)	-375(240)	-1359(548)
Creek	*November*	131(32)	100(23)	396(250)	87(27)	369(280)	953(176)
Island	*April*	16(3)	31(12)	-6(8)	19(21)	20(18)	65(21)
Island	*June*	247(78)	333(108)	184(167)	259(199)	252(252)	1028(724)
Island	*July*	198(8)	123(7)	0(9)	6(26)	-14(17)	113(42)
Island	*August*	17(13)	27(45)	123(59)	123(73)	140(24)	412(166)
Island	*September*	97(22)	54(3)	-136(47)	256(324)	227(222)	401(51)
Island	*November*	6(32)	-37(61)	515(189)	16(130)	-220(92)	274(175)
Shoal	*April*	-35(25)	-81(15)	-217(119)	-341(94)	-460(87)	-1099(309)
Shoal	*June*	27(22)	-64(50)	-32(27)	-103(30)	-95(35)	-294(49)
Shoal	*July*	-27(10)	-50(9)	-115(49)	-50(44)	581(379)	366(350)
Shoal	*August*	301(185)	245(69)	165(29)	226(24)	156(13)	793(64)
Shoal	*September*	22(47)	-84(124)	-179(160)	-401(62)	-105(145)	-770(302)
Shoal	*November*	59(61)	94(77)	122(94)	3(148)	-274(58)	-55(187)

Appendix V

Results of seasonal erosion experiments in Hog Island Bay using a Gust erosion microcosm. Values presented are the mass of PO_4^{3-} transported during 20 minutes at the given shear stress (0.01,0.08,0.16,0.24, 0.32 N m^{-2}) scaled to a 1 m^2 area. Numbers in parentheses are standard error. Negative values represent uptake of nutrients; positive values represent efflux from the sediment.

Site	**Date**	**0.01**	**0.08**	**0.16**	**0.24**	**0.32**	**Total**
Creek	*April*	0(2)	-2(3)	-3(7)	11(16)	-10(7)	-5(32)
Creek	*June*	47(11)	78(3)	68(4)	78(21)	70(16)	295(38)
Creek	*July*	14(6)	17(5)	-13(60)	10(32)	-71(15)	-56(82)
Creek	*August*	3(3)	-4(13)	3(22)	-3(27)	-15(33)	-18(93)
Creek	*September*	26(2)	-2(22)	96(34)	141(18)	60(17)	296(47)
Creek	*November*	1(2)	2(3)	-2(13)	-19(8)	-11(16)	-29(16)
Island	*April*	7(1)	11(2)	22(4)	26(4)	25(9)	84(18)
Island	*June*	80(15)	122(25)	93(46)	129(66)	90(38)	445(130)
Island	*July*	21(3)	25(9)	26(4)	10(4)	72(36)	133(45)
Island	*August*	-5(1)	-3(2)	20(4)	32(10)	17(8)	66(8)
Island	*September*	-4(3)	-10(8)	11(9)	-10(8)	-45(4)	-55(5)
Island	*November*	-6(3)	-20(4)	-12(8)	-24(13)	-42(19)	-99(25)
Shoal	*April*	-4(0)	9(7)	-7(1)	-1(3)	3(8)	5(11)
Shoal	*June*	7(7)	6(1)	9(9)	26(11)	26(12)	66(5)
Shoal	*July*	-5(6)	-3(7)	-15(17)	-32(8)	77(78)	28(54)
Shoal	*August*	37(34)	7(18)	17(24)	34(18)	28(33)	86(75)
Shoal	*September*	3(3)	21(17)	54(11)	51(13)	55(17)	180(30)
Shoal	*November*	6(0)	13(2)	1(0)	6(0)	35(8)	54(10)

Appendix VI

Results of seasonal erosion experiments in Hog Island Bay using a Gust erosion microcosm. Values presented are the mass of NO_3^- transported during 20 minutes at the given shear stress (0.01,0.08,0.16,0.24, 0.32 N m^{-2}) scaled to a 1 m^2 area. Numbers in parentheses are standard error. Negative values represent uptake of nutrients; positive values represent efflux from the sediment.

Site	**Date**	**0.01**	**0.08**	**0.16**	**0.24**	**0.32**	**Total**
Creek	*April*	13(2)	8(9)	-17(3)	93(34)	-16(11)	67(21)
Creek	*June*	-5(38)	1(64)	46(19)	52(6)	-40(60)	59(17)
Creek	*July*	0(19)	19(42)	-18(66)	-10(67)	-143(77)	-152(199)
Creek	*August*	65(11)	42(11)	1(19)	-10(24)	-11(20)	22(68)
Creek	*September*	-84(43)	-2(2)	-379(144)	-646(127)	-366(90)	-1392(99)
Creek	*November*	33(3)	16(2)	4(4)	-6(5)	16(15)	31(13)
Island	*April*	18(0)	58(3)	44(9)	31(12)	15(31)	149(31)
Island	*June*	27(7)	8(6)	-13(7)	-28(6)	-33(2)	-66(11)
Island	*July*	109(13)	52(10)	0(0)	0(0)	46(46)	99(56)
Island	*August*	5(5)	-67(42)	-35(6)	-44(8)	-39(9)	-186(25)
Island	*September*	-168(43)	-536(52)	-429(114)	-642(282)	-699(369)	-2306(336)
Island	*November*	-3(3)	-29(3)	-33(10)	-60(6)	-72(10)	-194(10)
Shoal	*April*	-33(21)	-128(27)	-160(30)	-218(12)	-268(24)	-775(26)
Shoal	*June*	24(4)	13(5)	-5(3)	-9(13)	-6(4)	-7(5)
Shoal	*July*	6(10)	27(36)	25(33)	69(14)	167(141)	288(75)
Shoal	*August*	24(6)	7(16)	-13(33)	-5(26)	-7(31)	-17(104)
Shoal	*September*	-276(10)	-713(100)	-1022(57)	-1180(249)	-1246(246)	-4162(375)
Shoal	*November*	9(0)	-26(0)	-33(6)	-75(10)	-92(2)	-226(19)

Appendix VII

Porewater profiles measured at the Creek site in Hog Island Bay. All concentrations are μM and numbers in parentheses are standard error.

Depth	April	June	July	August	September	November
0	8(1.5)	1.4(0.7)	3.6(0.6)	---	12(9.8)	0.5(0.3)
1	53.4(10.3)	105.2(8.2)	98.3(6.1)	134.5(27.8)	123.7(21.6)	118.5(18.2)
3	140.1(38.3)	143.5(31.9)	130.3(18.4)	170.6(31.6)	165.3(15.3)	99.1(5.8)
5	127.1(37.4)	179.2(15)	226.1(5.8)	207.3(35.8)	345(18.8)	111.3(20)
7	142.9(34.7)	263(9.9)	311.7(5.8)	237.4(32.8)	397.5(126.3)	108.6(6.8)
9	145.7(45.9)	275.3(12.9)	396.9(32.6)	285.1(32.4)	529.2(101)	125.1(26.1)

NH_4^+

Depth	April	June	July	August	September	November
0	0.5(0.2)	0.2(0.1)	1.6(0.1)	---	2.1(1.3)	0.4(0.1)
1	0.3(0.2)	0(0)	1.1(0.2)	0.6(0.4)	0(0)	0.6(0.5)
3	1.5(0.7)	0.6(0.5)	1.1(0.2)	2(0.2)	0(0)	0(0)
5	0.5(0.2)	2.7(2.1)	1.8(0.7)	4.2(3)	0(0)	1.1(1.1)
7	0.8(0.3)	0.4(0.4)	1.2(0.8)	3.3(2.8)	0(0)	0.2(0.2)
9	0.5(0.4)	0.4(0.4)	1(0.1)	3.7(1.4)	1.8(0.9)	0.2(0.2)

PO_4^{3-}

Depth	April	June	July	August	September	November
0	2.6(0.4)	0(0)	1(0.3)	---	0.3(0.3)	0(0)
1	2.6(1.2)	0(0)	0(0)	0(0)	0.7(0.3)	0.3(0.2)
3	1.7(1)	0(0)	0(0)	0(0)	0.8(0.2)	0(0)
5	1.5(0.3)	0(0)	0(0)	0(0)	0.6(0.2)	0(0)
7	2.5(1.2)	0(0)	0(0)	0(0)	0(0)	0(0)
9	2.5(0.7)	0(0)	0(0)	0(0)	0(0)	0(0)

NO_3^-

Appendix VIII

Porewater profiles measured at the Shoal site in Hog Island Bay. All concentrations are μM and numbers in parentheses are standard error.

Depth	**April**	**June**	**July**	**August**	**September**	**November**
0	8.7(2.6)	8.7(3.2)	9.5(1.1)	11.3(4.9)	3.9(0.3)	0.9(0.2)
1	43.8(11.4)	31.6(11.8)	63.8(28.2)	13(4.7)	43(17.7)	6.8(3.5)
3	63.1(8.7)	68.2(14.2)	75.3(15)	60.5(17.6)	33.5(10.7)	14.3(5.6)
5	83.2(--)	66.3(4.8)	98.3(18.7)	80.1(19.6)	34.3(11.6)	23.8(3.1)
7	69.8(15.4)	59.6(1.4)	78.9(17.2)	70.1(8.8)	49.9(12.3)	23.7(5.3)
9	50.3(--)	45.9(7.1)	64.7(14.9)	68.5(13.9)	49.2(2.8)	26.5(9.8)

NH_4^+

Depth	**April**	**June**	**July**	**August**	**September**	**November**
0	0.7(0.6)	1.8(0.7)	1(0.1)	3(0.7)	2(0.3)	0.5(0.1)
1	0.4(0.3)	8.1(2.8)	11(10)	12.4(3.5)	9.1(1.3)	1.3(0.6)
3	0.7(0.3)	6.9(4)	3.3(0.2)	19.2(3.6)	2.3(0.9)	0.9(0.5)
5	1.2(--)	4.1(1.2)	10.3(7.5)	5.6(1.8)	3.7(0.8)	0.7(0.2)
7	2(1.5)	2.1(0.2)	2.8(1.2)	5.9(0.8)	2.7(2)	1.2(0.9)
9	0.3(--)	2.3(1.2)	2.2(1.4)	8.8(5.8)	2.7(1.5)	0.8(0.5)

PO_4^{3-}

Depth	**April**	**June**	**July**	**August**	**September**	**November**
0	0.6(0.2)	0.5(0.2)	0.8(0.1)	1.5(0.9)	0(0)	0.2(0.2)
1	0.3(0.1)	0.2(0.1)	0.9(0.4)	0.7(0.5)	0.1(0)	0.8(0.4)
3	0.1(0)	0(0)	0.6(0.3)	0.2(0.1)	0(0)	0.6(0.5)
5	0.1(--)	0(0)	0.2(0.1)	0(0)	0(0)	0.2(0.1)
7	0.2(0.1)	0.6(0.6)	0.5(0.3)	0.2(0.2)	0(0)	0.5(0.4)
9	0(0)	0(0)	0.2(0.1)	0.2(0.2)	0(0)	1(0.5)

NO_3^-

Appendix IX

Porewater profiles measured at the Island site in Hog Island Bay. All concentrations are µM and numbers in parentheses are standard error.

Depth	**April**	**June**	**July**	**August**	**September**	**November**
0	4.9(1.3)	25.4(14.6)	7.9(1.1)		18.4(8.7)	1(0.5)
1	5.7(1.9)	18.2(8.6)	8.8(3)		5.7(3.9)	22.3(19.2)
3	5.7(0.2)	40.9(21.5)	124.7(52.7)		34.5(14)	38.9(38.5)
5	5.5(1.4)	46.8(12.4)	72.6(20.4)		42.3(8.8)	55.8(26.6)
7	5.2(2.6)	52.8(3.3)	20.5(-12)		50(3.7)	70.2(37.5)
9	16(3.8)	59.5(2)	50.7(10.9)		23.3(7.1)	58.5(23.5)

NH_4^+

Depth	**April**	**June**	**July**	**August**	**September**	**November**
0	0.2(1.3)	1(14.6)	1.4(1.1)		3.4(8.7)	0.5(0.5)
1	0.1(1.9)	0.6(8.6)	1(3)		2.4(3.9)	3.1(19.2)
3	1(0.2)	0.9(21.5)	21.6(52.7)		6(14)	8.7(38.5)
5	0.8(1.4)	1.3(12.4)	9.7(20.4)		2.9(8.8)	8.7(26.6)
7	0.6(2.6)	3.3(3.3)	11.6(-12)		3.9(3.7)	7.6(37.5)
9	0.9(3.8)	1.8(2)	6.2(10.9)		2.6(7.1)	5.4(23.5)

PO_4^{3-}

Depth	**April**	**June**	**July**	**August**	**September**	**November**
0	0.6(0.2)	4.3(0.5)	0.4(0.1)		0(1.1)	0(0.1)
1	0.9(0.1)	0.1(0.2)	0.5(0.2)		0(0.9)	0.4(2.4)
3	0.9(0.1)	0(0.8)	1(9.3)		0(2.4)	0.1(7.3)
5	1(0.4)	0.1(0.5)	0.5(3.2)		0.4(1)	0.1(2.2)
7	0.4(0.5)	0(2.5)	0.3(5.7)		0(0.5)	0.4(2.4)
9	0.3(0.7)	0.2(1)	0.2(2.3)		0(1)	0.4(1.4)

NO_3^-