ABSTRACT

Title of Document: INTERACTIONS BETWEEN AN ESTUARINE SUBMERSED PLANT BED AND ITS PHYSICAL AND BIOGEOCHEMICAL ENVIRONMENT: SEASONAL AND SPATIAL VARIATION

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Annual cycles of growth and morphology were analyzed in a bed of the canopy-forming submersed aquatic vegetation (SAV) species, *Stuckenia pectinata*, in relation to seasonal water quality conditions in a Chesapeake Bay tributary. A rapid accumulation of aboveground plant material occurred during the spring period of high water clarity, which aided plants in circumventing light limitation during the summer period of low water clarity. During summer, this SAV bed strongly attenuated wave energy, which contributed to growth-promoting feedback effects that improved light and nutrient availability for plants. Modification of hydrodynamic conditions also resulted in several negative feedback effects on SAV growth. Feedbacks were regulated by plant stand size and density and seasonal changes in plant canopy architecture. The findings of this study illustrate the significant impacts SAV beds

can have on their local environment, improving conditions and resulting in plant growth that could not otherwise occur in this degraded system.

INTERACTIONS BETWEEN AN ESTUARINE SUBMERSED PLANT BED AND ITS PHYSICAL AND BIOGEOCHEMICAL ENVIRONMENT: SEASONAL AND SPATIAL VARIABTILIY

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Background and Introduction

Importance of Submersed Aquatic Vegetation

Seagrasses and other submersed angiosperms are the foundation for some of the world's most diverse and vibrant ecosystems, which provide significant services relevant to human interests (Costanza et al., 1997). Beds of submersed aquatic vegetation (SAV) have been shown to stabilize shorelines (e.g., Tigny et al., 2007), even during extreme storm events such as tsunamis (Cochard et al., 2008). Additionally, they are known to be sites of enhanced nutrient cycling (e.g., McGlathery et al., 2007), where plants retain and facilitate removal of nutrients from coastal systems. Assimilation of solutes into plant biomass represents a temporary nutrient removal; however, SAV can also regulate nutrient retention (phosphorus sorption to sediments) and removal (coupled nitrification-denitrification) by controlling sediment characteristics (e.g., oxygenation) (McGlathery et al., 2007). Finally, SAV beds serve as critical refugia and feeding grounds for a wide variety of animals. Diverse and abundant communities of benthic invertebrates (e.g., Homziak et al., 1982) and fish (e.g., Lubbers et al., 1990) inhabit these meadows, including herbivorous grazers that feed on both the algal epiphytes of the seagrass (Prado et al., 2007) and the seagrass leaves themselves (Heck and Valentine, 2006).

Chesapeake Bay, the largest estuary in the United States, has historically benefitted from these ecosystem services in supporting large acreages of submersed plants (e.g., Stevenson and Confer, 1978). Several commercially important Bay species depend heavily on SAV meadows, including *Morone saxatilis* (Striped bass), which forages in and around beds (Lubbers et al. 1990) and *Callinectes sapidus* (Blue Crab), which utilizes beds as refugia during molting and feeding (Seitz et al., 2005). SAV is also a unique food source for waterfowl including diving and dabbling ducks, swans, and geese which graze on plant leaves, inflorescences, rhizomes, and tubers (Perry et al., 2007).

Declines in SAV Abundance

Unfortunately, a global-scale loss of submersed plants communities has occurred in recent years, predominantly due to anthropogenically-mediated eutrophication (Duarte, 1995; Short and Wyllie-Echeverria, 1996). This trend is evident in Chesapeake Bay, where SAV was estimated to cover 200,000 acres in the early 1900s. Over the last 50 years, large changes in plant densities and distributions have occurred (Stevenson et al., 1993), including declines in 15 species found in the upper Bay (Kemp et al., 2005). The primary mechanism responsible is the increased growth of phytoplankton and epiphytic algae, which decrease light to support SAV production and overwhelm plants when nutrient input rates are high (e.g., Twilley et al., 1985). Creation of impervious surfaces and subsequently higher sediment loads in runoff are other anthropogenic changes resulting in decreased light availability for plants (Kemp et al., 1983).

The importance of SAV for ecosystem services and as an indicator of overall Bay health has long been recognized (Dennison et al., 1993; Orth et al., 2002). The quantification of general minimum habitat criteria for sustaining plant growth (focused on light availability) represents an important step in identifying valuable habitat for SAV in the Bay (Dennison et al., 1993; Kemp et al., 2004). However, poor water quality conditions remain a major stumbling block in SAV recovery, resulting in slow and highly variable natural re-growth. Aerial photography mapping of Chesapeake Bay SAV beds over the last 20 years has shown slight improvements in acreage of some species, but declines in others (Moore et al., 2000). Although restoration efforts are underway, they have not promoted significant re-growth of SAV. A Bay-wide restoration goal of 185,000 acres by 2010 was set in 2003 (Chesapeake Executive Council, 2000), yet by 2008 plants covered just 76,861 acres or 42% of the total goal (http://www.chesapeakebay.net/).

Complex Interactions

One explanation for the lack of success in aquatic plant management and restoration is an incomplete understanding of the dynamic interactions between plants and their local environment. These interactions form a complex network and can be competitive (with other autotrophs) or physical (alteration of hydrodynamic regime) in nature. Examples of complex networks abound in the ecological literature, but researchers are still far from characterizing these systems or identifying their key properties in a cohesive way (e.g. Strogatz, 2001).

In freshwater systems, submersed plant competitive and physical interactions often have implications for the whole ecosystem. One of the most well-documented examples is the shift between macrophyte- and phytoplankton-dominated steady states in lakes, which is controlled by competitive (shading, nutrient uptake, allelopathy) and physical (water flow modification) interactions (Mulderij et al., 2007). When macrophyte dominance reaches a critical threshold or “tipping point”, the entire system can shift from a turbid to a clear-water state (Scheffer et al., 1993).

A thorough understanding of these regime shifts and the mechanisms that drive them can improve management decision-making capability (e.g. Qiu et al., 2001). It has recently been recognized that the incorporation of these complex interactions into management may vastly improve efforts to restore the structure and function of aquatic ecosystems (Byers et al., 2006; Halpern et al., 2007).

Water Flow Modification and Feedback Effects

Established aquatic plant communities can alter water flow within the plant stand, which is an example of "ecosystem engineering" (e.g. Jones et al., 1994), resulting in positive and negative feedback effects on plant growth (Koch, 2001; de Boer, 2007) (Fig. 0.1). Through the modification of biological, physical, geological, and chemical properties of the shallow coastal environment, feedbacks affecting light and nutrient availability and sediment suitability can work to the benefit or detriment of seagrasses. Key feedback effects resulting from competitive and physical interactions are reviewed below.

Feedbacks associated with plant bed friction

Increased frictional drag associated with plant canopies reduces water velocity (Gambi et al., 1990) and wave heights (Fonseca and Cahalan, 1992; Bradley and Houser, 2009) within the plant stand (Koch et al., 2006). This tends to increase deposition of suspended particles as velocities drop below a critical threshold (e.g. Sand-Jensen, 1998; Palmer et al., 2004; Huang et al., 2008), and can result in sediment accretion within the bed (Bos et al., 2007). Plant leaves also shelter the sediment surface, which reduces shear stress at the sediment-water interface, resulting in decreased sediment resuspension (Ward et al., 1984, Fonseca and Fisher, 1986;

Gacia and Duarte, 2001). Furthermore, SAV stands can deflect flow, both over the plants as “skimming flow” (Koch and Gust, 1999) and around the bed (Gambi et al., 1990), potentially leading to reduced input of particulates. Tall and dense canopy-forming seagrass beds have longer water residence times than unvegetated areas (Rybicki et al., 1997), which additionally contributes to particle trapping. Finally, particles are retained in seagrass beds due to direct adhesion to blades (Agawin and Duarte, 2002; Palmer et al., 2004; Hendriks et al., 2008).

The net effect of suspended particle trapping and reduced resuspension is to increase water clarity and light reaching seagrass leaves (e.g., Kemp et al., 1984; Moore, 2004), constituting a positive feedback. Light can also penetrate deeper, improving the habitat quality for benthic microalgae, that further stabilize the sediment surface via excretion of mucopolysaccharides (e.g., Paterson, 1989).

Reduced turbulent mixing and increased water clarity within the plant stand can also result in negative feedbacks. Lessening of turbulence and leaf movement can increase the diffusive boundary layer of seagrass leaves, reducing solute exchange at the leaf surface (Koch, 1994; Morris et al., 2008). Nutrient uptake rates have been shown to be positively correlated with turbulence and water velocity, so plants (Thomas and Cornelisen, 2003) and algal epiphytes (Cornelisen and Thomas, 2004) located within the bed may experience nutrient limitation, especially if ambient concentrations are low.

Reduced leaf movement may, however, increase the accumulation of epiphytic algae growing on leaf surfaces, as abrasive removal and adhesive failure of epiphytes decrease (e.g., Lavery et al. 2007). Increased light availability also benefits epiphytes, which are well-known to shade seagrasses, significantly reducing the host plant's ability to survive (Kemp et al., 1983; Stankelis et al., 2003). Although hydrodynamic modification by plants has the potential to reduce initial epiphyte propagule colonization, the light climate and quiescent conditions may increase competition between epiphytes and seagrasses for light and nutrients, constituting a negative feedback that may be most prominent early in the growing season when plant uptake is rapid (e.g. Lee and Dunton, 1999).

Secondary feedbacks associated with particle trapping

As a result of particle retention and organic inputs from the seagrass community, fine organic particles decompose within the plant stand and can serve as an important source of porewater dissolved nutrients (e.g., Kemp et al., 1984; Hemminga et al., 1991). However, the deposition of finer organics may also result in reduced oxygen penetration into the bottom sediments, resulting in an accumulation of phyto-toxic hydrogen sulfide (e.g., Holmer and Bondgaard, 2001). High respiration rates of the community coupled with high organic inputs can result in low oxygen conditions within submersed plant beds (e.g., D'Avanzo et al., 1996), exacerbated by reduced water mixing (Binzer et al., 2005).

The balance between organic particle deposition as a positive feedback (a source of nutrients, more available light) and a negative feedback (higher concentrations of porewater sulfide, low oxygen conditions) is key for plant survival. SAV are known to oxidize the rhizosphere through root-released dissolved oxygen from photosynthesis (e.g., Kemp and Murray, 1986; Pedersen et al., 2004), which potentially enhances coupled nitrification-denitrification processes in SAV beds (e.g., Caffrery and Kemp, 1990) and also may reduce porewater sulfide concentrations in microzones around roots (Lee and Dunton, 2000; Holmer et al., 2005).

Feedbacks Associated with Fauna

The presence of a submersed plant bed has numerous positive feedbacks as a habitat for diverse fauna. In attracting and supporting herbivorous fish species, SAV benefits from increased grazing on algal epiphytes (Heck and Valentine, 2006; Prado et al., 2007), which increases light availability at the leaf surface (Hays, 2005). Plant beds will also attract grazers that feed on SAV leaves, but some grazers appear to select blades with heavier epiphyte colonization and hence lower photosynthesis (e.g., Wressnig and Booth, 2007). Abundant macroinvertebrate benthic infauna living in the seagrass bed (e.g., Lee et al., 2001) tend to fertilize the sediment through direct excretion (Reynolds et al., 2007), while decreasing porewater sulfide concentrations through burrow formation (e.g., Zorn et al., 2006). The settlement of bivalve larvae (e.g. Bologna and Heck, 2000) and growth (Irlandi and Peterson, 1991) is also increased in plant beds, which could benefit plants through turbidity reduction and increased light availability associated with bivalve filtration (e.g. Newell and Koch, 2004).

Effects of Plant Canopy Structure

The impact of submersed plants on water flow has been shown to be regulated by shoot density (Peterson et al., 2004), canopy architecture (Fonseca and Cahalan, 1992), and bed size (e.g., Gambi et al., 1990; Fonseca and Koehl, 2006). Therefore, one might expect a tall, dense, and large stand of SAV to have strong associated feedbacks, unlike the low profile of meadow-forming seagrasses, where feedbacks can be more intermittent (e.g., Koch, 1999).

Canopy-forming vegetation with shoots that can grow to the water's surface in depths of one meter or more is common in many estuaries, including Chesapeake Bay (e.g., Stevenson and Confer, 1978). These species have two contrasting growth forms: a dense, tall, highly-branched, reproductive canopy during the summer months, and short, vegetative shoots during all other months of the year. One species, *Stuckenia pectinata* (L.) Boerner, formerly known as *Potamogeton pectinatus* L. and commonly called sago pondweed, forms monospecific stands during early summer in fresh to mesohaline regions of the Bay. Another common and morphologically similar species found throughout the Bay is *Ruppia maritima* (widgeon grass), which forms a reproductive canopy in late summer (e.g., Silberhorn et al., 1996). Little is known about positive and negative feedbacks (and the balance between them) in canopy-forming SAV beds, and many complex interactions are thought to occur (Fig. 0.2). An improved understanding of feedbacks may help elucidate patterns of plant survival, especially under degraded environmental conditions that characterize the Chesapeake Bay and many coastal areas worldwide.

Study Goals

The overall objective of this study is to develop an in-depth understanding of complex interactions in a monospecific SAV bed that may help to mitigate poor water quality conditions in an estuarine environment. This study involved intensive field measurements in a unique plant bed located in the mesohaline portion of the Choptank River estuary (a tributary of Chesapeake Bay) and was supplemented by more extensive comparative analyses of 19 other SAV beds of varying size and density over the period June 2007 – October 2008. The work was comprised of multi-scale physical, ecological, and biogeochemical measurements on fine time and space scales. This thesis is divided into three chapters, with separate yet inter-linked goals and themes.

In the first chapter, I provide basic information on the autecology of a successful canopy-forming bed of *S. pectinata* in the Choptank River Estuary. This includes the bed's physical structure, partitioning of biomass, and seasonal patterns. I then relate these observations to local water quality conditions and habitat requirements for SAV survival in Chesapeake Bay. In the second chapter, I investigate potential positive and negative feedbacks associated with competitive interactions and ecosystem engineering within this plant bed. I then explore the extent to which seasonally-varying plant canopy architecture influences feedback effects, and the interactions between plant canopy and physical variables such as wind and water level. Finally, I attempt to determine the extent to which feedbacks in this plant bed can modify light, nutrient, and sediment conditions and the overall impact of feedbacks on habitat quality (i.e. the balance between positive and negative feedbacks). In the last chapter, I explore fine-scale spatial patterns in water quality within this *S. pectinata* bed, helping to elucidate feedbacks identified in the previous chapter. I then compare spatial patterns in water clarity among a suite of canopy-forming SAV beds and assess the roles of canopy height, crown density, and cross-shore bed width in contributing to feedback development.

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Figures

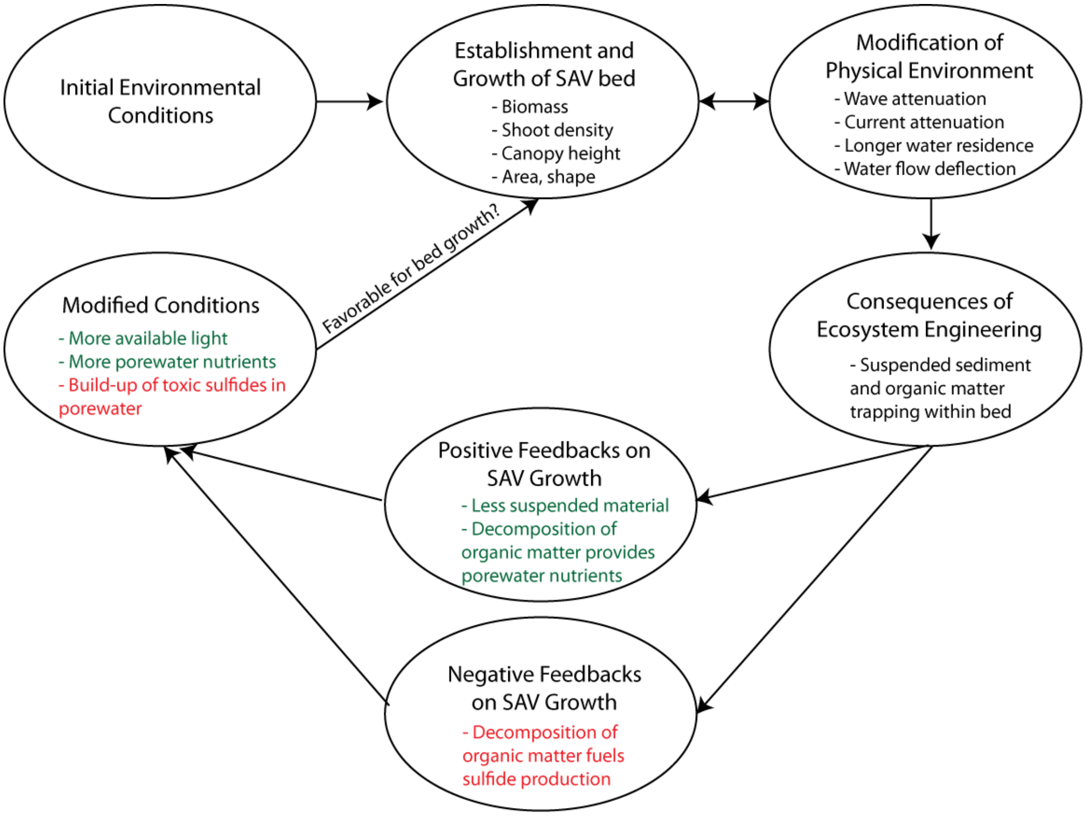

Figure 0.1: The development of positive and negative feedbacks due to ecosystem engineering by submersed plant beds. Particle trapping due to water flow modification by the plants is given as an illustration, but many other consequences exist.

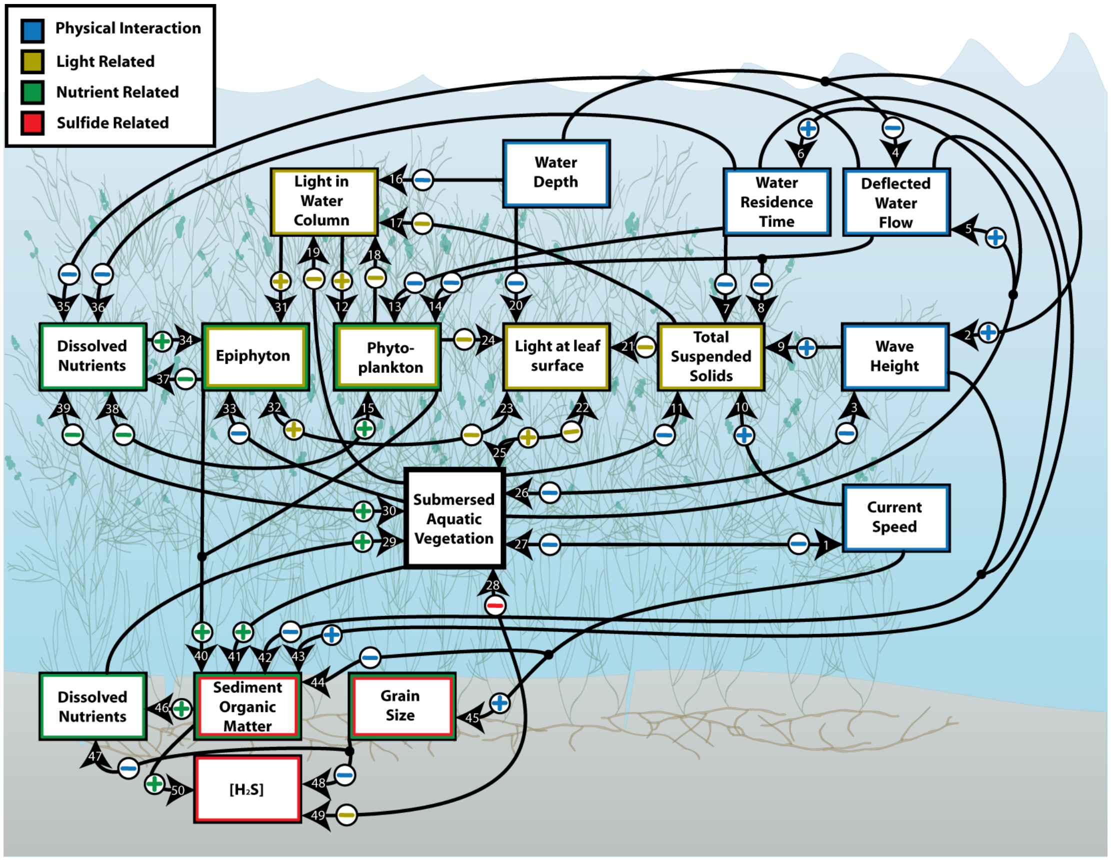

Figure 0.2: Conceptual diagram summarizing key feedback processes resulting from ecosystem engineering in a canopy-forming submersed plant bed. The growth of SAV is principally driven by factors associated with the availability of dissolved nutrients (green) and light (yellow) and by factors related to the accumulation of sediment organic matter and byproducts of decomposition (e.g., H_2S, red). Many of these factors are strongly influenced by feedbacks resulting from physical effects of plant bed friction on water flow (blue). Changes in a given variable tend to influence other variables (black arrows) in either positive (plus) or negative (minus) ways. The colors on the plus/minus symbols refer to which variables are involved in the feedback (i.e., nutrients, light, physical forces, H_2S levels). Supplement to Fig 0.2 summarizes all interactions.

Supplement to Fig. 0.2: Summary of key feedback processes resulting from ecosystem engineering in a canopy-forming submersed plant bed

Dense stands of SAV reduce current velocities (1) and wave heights (3) due to frictional drag from the plant canopy. Additionally, water flow is deflected around the plant stand (5) and water residence time within the stand increases (6). Deeper water (e.g., high tide) can work against wave attenuation (2) and water flow deflection (5) by decreasing the proportion of the water column occupied by SAV. Large waves (26) and fast currents (27) can directly constrain SAV growth.

As a result of flow modification TSS decreases within the plant stand due to decreased advection (8), particle settling (7), reduced resuspension (9, 10), and collisions with plant stems (11). Phytoplankton are also affected by flow modification directly (13, 14). A decrease in TSS and phytoplankton within the plant stand results in increased light penetration through the water column (17, 18), which increases light at the leaf surface (21, 24). Increased light penetration results in more available light for phytoplankton (12) and epiphyton (31, 32), varying with water depth (16, 20). Epiphyton also directly reduce light reaching leaf surfaces (23), which impacts SAV (25).

Dissolved water column nutrients, which improve growth of phytoplankton (15), epiphyton (34), and SAV (30), are affected by water flow modification. Less advection of dissolved nutrients into the bed (35) increases competition (36) between phytoplankton (13, 38), epiphyton (37), and SAV (39). SAV biomass increases competition for light in addition to nutrients, as leaves shade the water column (19) and other plants (22). However, denser SAV growth reduces epiphyte colonization through reduced advection of epiphyte propagules into the bed and mechanical removal through leaf rubbing (33).

Organic material accumulates within the plant bed due to algal and SAV biomass (40, 41) as well as allochthonous deposited material (42, 43, 44). This can reduce sediment grain size within the plant bed (45), which decreases sediment permeability (47, 48). Decomposing organic matter contributes to dissolved porewater nutrient pools (46), providing additional nutrients for SAV (29). However, phyto-toxic hydrogen sulfide can accumulate in sediment porewater (50), decreasing plant photosynthesis (28). Radial oxygen loss within the rhizosphere (49), which depends on photosynthetic rates, can balance sulfide intrusion into plant lacunae.

Chapter 1: Seasonal variations in the canopy-forming submersed vascular plant, *Stuckenia pectinata* in relation to water quality conditions

Abstract

The strong light-attenuation associated with poor water quality during summer months limits the growth of submersed aquatic vegetation (SAV) in many coastal systems, including Chesapeake Bay and its tributaries. Of the many SAV species historically occurring in Chesapeake Bay, canopy-forming plants of the mesohaline region (including *Stuckenia pectinata*) have been particularly affected by poor water quality. Despite adverse environmental conditions, however, some beds of SAV manage to survive and grow. Seasonality, phenology, and biomass allocation characteristics that induce plant bed success were identified by close monitoring of one large and persistent bed of *Stuckenia pectinata* located in the Choptank River estuary, MD in relation to monthly water quality. In general, *S. pectinata* has been shown to grow more vigorously in freshwater systems than in estuaries; however, this plant bed produced record levels of biomass and reproductive material in this brackish system despite ambient salinities that reached this species' reported tolerance threshold. Additionally, aboveground biomass was present throughout the year, which has never before been reported in Chesapeake Bay for this species. Biomass accumulation rates and daytime net oxygen production within the bed peaked during the late spring period of low light attenuation. The early development in this species, facilitated by overwintering aboveground biomass, seems to be critical

for bed development and assisted this submersed plant community in tolerating poor water quality conditions during summer months.

Introduction

Seagrasses and other submersed aquatic vegetation (SAV) form important communities in coastal regions worldwide and have been recognized as providing many significant ecosystem services (Costanza et al., 1997), including food and refugia for a variety of commercially important benthic and pelagic animals (e.g., Lubbers et al., 1990; Hemminga and Duarte, 2000; Seitz et al., 2008). Many coastal areas, including large ecosystems like Chesapeake Bay, have unfortunately experienced degraded water clarity due to increased anthropogenic loading of sediment and nutrients (Kemp et al., 2005), where the resulting decrease in light penetration as well as overgrowth of epiphytes on leaf surfaces have led to large-scale declines in submersed plants during recent decades (Kemp et al., 1983; Duarte, 1995). This decline in Chesapeake Bay SAV species, which began in the late 1960s (Orth and Moore, 1983), has reduced total plant coverage from ~200,000 hectares in the early 1900s to 76,000 hectares by 2008 (http://www.chesapeakebay.net/).

Stuckenia pectinata (L.) Boerner, formerly known as *Potamogeton pectinatus* L. and commonly called sago pondweed, is a canopy-forming submersed macrophyte that thrives worldwide under a wide range of conditions. Its cosmopolitan distribution in dense monotypic stands (St. John, 1916), importance as food for waterfowl (Perry et al., 2007), and its tendency to block navigation and interfere with water flow in ditches and streams have led to many studies, especially in the freshwater literature (review in Kantrud, 1990).

S. pectinata is a rhizophyte characterized by its parvopotamid growth form, where the entire plant remains submerged through the growing season, with the exception of its inflorescences (Hutchinson, 1975). Despite having thin cylindrical stems and narrow elongate leaves, *S. pectinata* beds manage to attain extremely thick and dense canopies that can result in nighttime hypoxia in shallow ditches (Madsen et al., 1988) or mechanical clogging of power plant water intakes (Peltier and Welch, 1969). *S. pectinata*'s canopy-forming growth form and its impacts on many human activities make it a highly visible macrophyte.

Commonly considered a ruderal, *S. pectinata* is highly competitive and stress-tolerant. It reproduces sexually through seed generation and asexually through formation of starchy over-wintering buds, which can form on rhizomes ("tubers") or aboveground axils. This species can also spread horizontally via stoloniferous growth (aboveground elongation and stem production from the stolon) (Yeo, 1965). *S. pectinata* is able to tolerate low-light conditions, being limited in depth to 4% of surface illumination (Bourne, 1932 cited in Howard-Williams and Liptrot, 1980) and is often the only macrophyte found in extremely turbid conditions (Kantrud, 1990). It is euryhaline in distribution, mainly found in freshwater lakes and streams, but also tolerates salinity up to ~15 (Verhoeven, 1975). In Chesapeake Bay, the current geographic distribution of *S. pectinata* is limited compared to this species' historic range (Moore et al., 2000; Orth et al., 2009), which included tidal fresh through mesohaline regions (Stevenson and Confer, 1978). The vast majority of research on

S. pectinata comes from freshwater lakes with a few notable descriptive studies in brackish systems (Verhoeven, 1975; Howard-Williams and Liptrot, 1980; den Hartog, 1981; van Wijk et al., 1988).

The recognition of SAV in general as an indicator of overall Chesapeake Bay health and as a critical source of food and shelter for many commercially important species of fish, invertebrates, and waterfowl has led to its inclusion in restoration plans (Chesapeake Executive Council, 2000). The challenges faced by SAV in overcoming poor water quality have been recognized with the exposition of generalized minimum habitat requirements for sustaining plant growth (Dennison et al., 1993; Kemp et al., 2004). These criteria are helpful both in predicting regions of the Bay that may experience re-growth of SAV and focusing restoration efforts in areas where habitat is most suitable. Despite public acknowledgement of poor Bay-wide habitat conditions for submersed plants and interest in restoration (Orth et al., 2002), restoration efforts have been met with mixed success and natural re-growth has been slow (Moore et al. 2000).

Although *Stuckenia pectinata* provides many important ecosystem functions, there is little information available on its life history in estuaries. In Chesapeake Bay, populations of mesohaline canopy-formers declined greatly along with other SAV groups. However, this trend continues up to the present, making studies on these species especially timely. Some successful submersed plant beds do persist in Chesapeake Bay, and identification of previously overlooked qualities that promote their success may help clarify strategies for management and restoration despite degraded environmental conditions. This study is focused on one such successful plant bed composed of *Stuckenia pectinata* located in the mesohaline region of the Choptank River estuary, a tributary to the Chesapeake Bay.

The overall objective of this chapter is to investigate the seasonal changes in structure of this plant bed in relation to variations in water quality to improve understanding of how this species survives degraded habitat conditions. Specific goals include: (1) to describe the basic autecology of this plant bed including seasonality, phenology, and biomass allocation; (2) to determine habitat quality within this particular bed by comparing seasonal light penetration and nutrient availability to published requirements; and (3) to compare bed productivity to expected performance given environmental conditions.

Methods

Study Site

This study represents an intensive field sampling effort over a full annual cycle (June 2007 – May 2008) from a single monotypic stand of *Stuckenia pectinata* located on the northern shore of the Choptank River estuary, MD (a tributary to Chesapeake Bay). The bed was situated at the mouth of Irish Creek, within the Choptank system (Fig 1.1). During the summer months, the bed covered an area exceeding 5 hectares, but the size and shape changed seasonally. The bed was bordered to the east and within the mouth of Irish Creek by beds of *Ruppia maritima.* This particular bed was selected due to its continued survival over time despite relatively poor water quality (e.g., Orth et al., 2008).

To support sampling equipment, three platforms were attached to pressure-treated wooden pilings that had been jetted into the sediment in May 2007. Platforms were placed along a cross-bed transect forming three station locations at: 1) the dense inner portion of the bed 210 m inside the bed's seaward perimeter ("Bed"), 2) the edge region 90 m inside the perimeter ("Edge"), and 3) an unvegetated site 160 m outside the bed's perimeter ("Bare"). Upon conclusion of sampling in 2007, the platforms were removed and were then reinstalled in April 2008 at slightly different locations as per U.S. Coast Guard specifications, with the Edge and Bare stations located 40 m inside and 110 m outside the bed's seaward perimeter, respectively (Fig. 1.2).

Water Quality

Water samples (800 ml) were collected using automated discrete samplers (Teledyne Isco, Inc., Model 6712) secured to each platform. Programmed collection occurred at 2 - 4 h intervals (depending on the month) for week-long deployments during June 2007 (period of peak plant biomass), August 2007 (plant bed decline), and May 2008 (peak plant growth). Sampler tubing was cable-tied to the platforms, with the intake located at mid-water column depth (about 60 - 80 cm from the sediment surface, varying slightly by deployment). Each sampler held an ice block in the center of an isolated cylinder to maintain a chilled environment for samples, which were retrieved daily, placed on ice, and transported back to the lab for immediate processing.

At the laboratory, water samples were shaken to homogenize and filtered onto pre-weighed and ashed (4 h at 550° C) filters (0.45 μm GF/Fs). Filters were rinsed with deionized water to remove salt and then dried (3 d at 60° C), and weighed to determine total suspended solid (TSS) concentrations. The filters were then ashed (4 h at 550° C), cooled in a desiccator, and re-weighed to provide an estimate of percent particulate organic matter (% POM). An additional, known volume of water sample (60 - 120 ml) was passed through filters, which were wrapped in aluminum foil and frozen for subsequent chlorophyll-*a* (chl-*a*) analysis. Within 6 mo of collection, the filters were thawed, extracted in the dark with 100% acetone, sonicated, filtered, and read on a fluorometer (10-AU, Turner Designs).

Filtrate was aliquoted into 5 ml vials, which were immediately frozen and stored for later nutrient analysis. Water column concentrations of ammonium (NH_4^+), nitrate (NO_3^-), and ortho-phosphate (PO_4^{3-}) were determined colorimetrically (Technicon Auto Analyzer II) within 1 yr of collection (US EPA, 1979).

Each day during water sample retrieval, a hand-held sensor system (Yellow Springs Instruments, Inc., Model 85) was used to record water temperature, salinity, and dissolved oxygen at each site. In addition, Secchi depth and a photosynthetically active radiation (PAR) vertical profile (LICOR, LI-1000 hand-held 2π sensor) were taken daily at approximately noon at each site to calculate diffuse downwelling PAR attenuation coefficients (K_d). Because light measurements taken within the bed included significant shading from plants, light attenuation was also measured in a patch (1 m^2) with aboveground plant tissue removed adjacent to the Bed station.

To detect high-frequency changes in selected water quality variables, one data sonde (YSI 6600) equipped with a sensor for dissolved oxygen (model 6562) was deployed at each station and programmed to record every 15 min. Calibrated prior to each deployment, data sondes were secured to the platforms with sensors placed adjacent to water sampler intakes. The sondes were deployed for 1 - 2 weeks coincident with deployment of automated samplers and during two additional weeks in October 2008.

For months when sampling equipment was not in place, Choptank water quality for 2007 and 2008 was obtained from the Maryland Department of Natural Resources (MD DNR) Water Quality Mapping program (http://mddnr.chesapeakebay.net/sim/index.cfm, Matthew Hall, personal communication). Weekly water samples were taken as part of quality checks for continuous monitoring equipment at the nearby station XFG5054 (Mulberry Point, 38.7494° N -76.2440° W) in the lower Choptank segment (CHOMH1) (Fig. 1.1). Dissolved inorganic nitrogen [(DIN), composed of NH_4^+, NO_3^-, and NO_2^-] and phosphorus [(DIP), composed of PO_4^{3-}] were measured along with TSS and chl-*a* concentrations.

Plant Bed Morphology

Aboveground and belowground plant materials were collected once per month (twice in May 2008) in triplicate samples from June 2007 through August 2008. PVC quadrat frames (0.25 m x 0.25 m) were placed in random locations within the bed and all aboveground biomass (stems, leaves, inflorescences) within the frame was clipped at the sediment surface and placed in plastic zip-lock bags. The belowground biomass (roots, rhizomes, tubers) was sampled within each clipped area using a 13.7 cm diameter acrylic corer, driven sufficiently deep (≥ 20 cm) into the sediment to collect all root material. Belowground material was sieved in nylon mesh bags (0.5 cm) to remove all sediment and placed in plastic zip-lock bags. Biomass samples were placed on ice in the field, and kept chilled until processing.

Within three days of collection, above- and below-ground plant biomass samples were washed in fresh water and scraped free of epiphytes. Number of total shoots, reproductive shoots, inflorescences, and belowground propagules (tubers) were counted for each sample. Reproductive (flowering) and vegetative (non-flowering) shoots were separated and 10 shoots from each were randomly selected for length measurement. All above- and below-ground biomass was then placed in aluminum foil packets, dried to constant weight (60° C), and weighed. Average shoot density, total biomass, and canopy height were determined for every month.

After weighing, a portion of each sample (~1 g) was finely ground with a mortar and pestle and analyzed for total carbon, hydrogen, and nitrogen (Exeter Analyical, Inc., CE-440). Ground plant material was also weighed, ashed in crucibles (4 h at 550° C), extracted in 1 N hydrochloric acid, and analyzed (Technicon Auto Analyzer II) for total phosphorus (Aspila et al., 1976).

Ecosystem Metabolism

Daily rates of daytime ecosystem production (P_a) and nighttime respiration (R_n) were computed for areas inside and outside the *S. pectinata* bed using time-series measurements of dissolved oxygen concentration (O_2) and percent saturation from data sondes, and recorded times of sunrise and sunset (e.g., Ziegler and Benner, 1998). P_a was calculated as the net apparent O_2 production during daylight hours using a program developed for SAS v9.1 (Jim Hagy, pers. comm.). R_n was calculated as the net apparent O_2 production (negative, indicating consumption) during the night.

Hourly rates of P_a and R_n were integrated for periods of day and night based on day length. Average water column depths varied between 1.5 and 1.8 m during sonde deployments and air-sea O_2 exchange corrections were based on percent saturation calculated for O_2 concentrations (plus temperature and salinity values and an exchange coefficient of 0.5 g O_2 m^{-2}) measured by sondes in surface waters (e.g., D'Avanzo et al., 1996).

Vertical integrals of P_a and R_n were estimated using O_2 values measured with sensors deployed in upper and lower portions of the water column and occasional measurements of vertical O_2 profiles. It was assumed that the Bare site water column was well-mixed for all deployments. Time-series data collected in May and October indicated that the Bed site could also be assumed to be well-mixed for these months (Fig 1.3). However, during June and August, the plant bed was vertically stratified, with substantially lower O_2 measured with the sonde deployed near the sediment surface. Based on analysis of vertical O_2 profiles relative to sensor deployment height it was assumed that the average O_2 for the whole water column could be closely approximated by the mean of concentrations measured in upper and lower sensor deployments. In August 2007, however, vertical profiles indicated that the water column was well-mixed above the upper sonde (deployed at mid-depth ~80 cm) and decreased linearly with depth to the lower sonde (e.g., Fig 1.4). In this case, O_2 metabolism rates were computed separately for upper and lower water volumes. A weighted average (F_T) of the O_2 rates was calculated for the whole water column depth (mean 1.6 m) based on the fraction of water column represented by rates calculated for each sonde, where the bottom layer rate was an average of the upper

(F_U) and lower (F_L) O_2 fluxes: $F_T = \frac{90}{160} \cdot F_U + \frac{70}{160} \cdot \left[\frac{F_U + F_L}{2} \right]$. The net ecosystem production (NEP) for each day was calculated as the sum of P_a and R_n.

Statistical Analysis

All statistical analyses were conducted using SAS software (v9.1) with significance levels of $\alpha = 0.05$. Time-series water quality data from automated samplers were tested for significant monthly differences using one-way mixed model ANOVA with time treated as a random effect. Natural log data transformation was sometimes necessary to meet ANOVA assumptions of homoscedasticity and normality; means and 95% confidence limits were then back-transformed. Tukey-Kramer adjusted least-squared means were calculated and all possible pair-wise comparisons computed. Ecosystem metabolism rates did not require transformation, and differences between sites were assessed using one-way Model I ANOVA for each month.

Results

Water Quality

The study site experienced a broad range of temperature (5.7 – 27.3 °C), which reached a maximum during the summer months, and salinity (9.1 – 16.2), which peaked during the winter (Fig. 1.5). DIN and DIP showed opposite patterns, where DIP increased through the summer while DIN decreased. In summer months (June and August), TSS and chl-*a* were highly variable and significantly elevated

($p<0.0001$) compared to spring (May) over the weeks sampled (Table 1.1). During May, TSS showed generally low concentrations and variability, except at the end of the sampling period when cownose rays (*Rhinoptera bonasus*) arrived at the site (Fig. 1.6). During fall, winter, and spring months (Nov – May), light penetration was high and Secchi discs were visible on the bottom (~1.3 m). During the summer months, however, light penetration was low, with K_d significantly ($p<0.0001$) elevated compared to May.

Plant Bed Morphometrics

Live plant material was present throughout the year, with an aboveground biomass minimum occurring in December (mean ± SE, 66 ± 36 g DW m^{-2}) and a maximum in June (641 ± 21 g DW m^{-2}), while belowground biomass varied little over the year (mean of 87 g DW m^{-2}) (Fig. 1.7A). Aboveground biomass measurements made during summer months of 2008 were similar to 2007, and thus data is presented out of chronological order as a complete annual cycle. Total live biomass (above and belowground) reached a peak in June (mean value 781.6 g DW m^{-2}), which also corresponded with the highest observed densities of tubers and inflorescences (1429 ± 483 m^{-2} and 987 ± 417 m^{-2}, respectively). Maximum canopy height followed trends in biomass, peaking in June and July at 106 ± 6 cm during the reproductive phase of growth. Short, vegetative shoots were present throughout the winter months (mean 17 ± 0.8 cm). Shoot density varied widely over the year, decreasing through the summer months, while flowering occurred during June and July (Fig 1.7B). Viable tubers were found year-round in the bed, with highest densities occurring in June.

Live plant tissue phosphorus (%P) and nitrogen (%N) contents varied over the year, while carbon (%C) content was more stable (34.4 ± 0.4%). %N and %P peaked during April (2.44 ± 0.14% and 0.32 ± 0.3%, respectively) and declined through the summer to relatively low levels in August (1.87 ± 0.07% and 0.15 ± 0.01%). Belowground biomass contained a higher %C, but lower %N and %P than aboveground biomass (Fig 1.8).

Ecosystem Metabolism

Seasonal patterns in ecosystem metabolism were much more pronounced at Bed compared with Bare stations. Daytime net production in the plant stand followed trends in plant growth, reaching a significant maximum (328.7 ± 28.9 mmol O_2 m^{-2} d^{-1}, $p<0.0001$) with rapid accumulation of biomass (May) and decreasing with each successive month (Table 1.2). Outside the plant stand, daytime production followed trends in chlorophyll-*a* concentration, increasing through the summer and surpassing the plant bed rates ($p<0.04$) in August when chl-*a* concentrations were significantly elevated (10.5 μg L^{-1}) and plants showed signs of senescence.

Nighttime values for ecosystem respiration were consistent at the Bare station, while the Bed station exhibited significantly elevated rates during spring and early summer months ($p<0.0001$), with the greatest rate (mean ± SE) occurring in June (-267.3 ± 12.2 mmol O_2 m^{-2} d^{-1}), which coincided with peak plant biomass. P_a:R_n ratios indicated net heterotrophy (<1.0) during October and June (Bed only). While both locations were net autotrophic (>1.0) the rest of the year, the Bare station had consistently greater P_a:R_n ratios.

Discussion and Conclusions

Autecology of *S. pectinata*

In terms of morphology and phenology, this *Stuckenia pectinata* bed was unique among previously studied estuarine populations. Although *S. pectinata* tolerates mesohaline water ≤15 (Verhoeven, 1975), its highest productivity has been reported to occur in sheltered freshwater systems. This species' biomass in lakes can approach 2 kg DW m^{-2} (Zaky, 1960, cited in Kantrud, 1990), but reports from estuarine sites with physical conditions similar to those at the present study site barely exceed 300 g DW m^{-2} (van Wijk, 1988). Research has shown that even in populations adapted to brackish conditions, biomass and tuber production decrease significantly with increasing salinity (van Wijk et al., 1988). Despite experiencing salinities up to 16 (above this species' upper tolerance level) during several months of the year, this plant bed produced a peak June biomass (>600 g DW m^{-2}) twice that found at other brackish sites.

The study site also had high reproductive potential given the salinity regime. Maximum tuber density observed in June (~1500 m^{-2}) exceeded values from other studies with similar conditions by three-fold (van Wijk, 1988). Additionally, inflorescence densities (>1000 m^{-2}) were nearly ten-fold greater than the maximum reported from populations in the brackish Baltic Sea (Kautsky, 1987). Of its multiple propagule types, tubers have been cited as the most important for long-term survival of a *S. pectinata* population, as seed germination is generally poor for this species and axillary buds rarely remain within a bed (van Wijk, 1989a).

Tuber production likely played a major role in this bed's interannual persistence despite poor water quality conditions observed over the period of this study. Based on annual aerial surveys of Chesapeake Bay SAV, the study site had been intermittently inhabited during the 1990s, and continuously inhabited by *Ruppia maritima* beginning in 2002, which then transitioned into *S. pectinata* (Orth et al., 2008). During 2007, there were some small, sparsely vegetated beds of *S. pectinata* elsewhere in the Choptank River, but no other dense monotypic stands (pers. obs.). In 2008, the study site represented the only *S. pectinata* and 15% of the total SAV bed area found in the Choptank River, as compared to 2004 (a relatively productive year for SAV), when the bed only occupied 2% of total bed area (Orth et al., 2005). The previous occupation of the study site by *R. maritima* and low seed germination in *S. pectinata* suggest that this bed did not initially colonize bare sediment, but developed (likely from tubers) under the protection or "nursery bed effect" of *R. maritima* (Hengst, 2007).

The seasonal cycle of this *S. pectinata* bed showed surprising differences from previous studies on canopy-forming populations in Chesapeake Bay. First, the mean peak biomass in a bed of this species was reported as $\leq$100 g DW m^{-2} in 1977 (Stevenson et al., 1993), which is less than a sixth of peak biomass measured during this study. Additionally, previous studies have reported the month of August as the period of peak aboveground biomass for Chesapeake Bay canopy-formering SAV species (Moore et al., 2000), while the study bed reached peak biomass in the month of June. Limited field observations and over ten years of SAV aerial mapping data suggest that the Potamogeton community (dominated by canopy-formers *S. pectinata* and *Potamogeton perfoliatus*) has an annual life cycle with a die-off of aboveground biomass December through April (Stevenson et al., 1993; Moore et al., 2000). Although it has been observed that *S. pectinata* occasionally maintains aboveground biomass during the winter months in some temperate water bodies (Kantrud, 1990), the perennial life cycle observed at the study site has never before been documented in Chesapeake Bay.

Water Quality

The performance of this *Stuckenia pectinata* bed was surprising given water quality conditions during the study period. Published habitat requirements for this and other SAV species in Chesapeake Bay indicate that for the mesohaline region, water quality must not exceed the following values during the growing season: TSS < 15 mg L^{-1}, chl-*a* < 15 μg L^{-1}, DIN < 10 μM, DIP < 0.33 μM, and $K_d < 1.5$ m^{-1} (Dennison et al., 1993). During the months of June and August, TSS concentrations were above this threshold, and were measured in exceedance roughly half the period of sampling. DIN and DIP tended to remain below habitat thresholds, but DIP occasionally surpassed 0.33 μM. Chl-*a* never exceeded 15 μg L^{-1}during any month sampled, but light attenuation exceeded these limits in both June and August.

In addition, unforeseen local disturbances had a large (though temporary) impact on water quality. In late May during the week automated samplers were deployed, intense cownose ray (*Rhinoptera bonasus*) activity was observed outside and at the edge of the bed. Digging in the sediment by groups of rays (presumably in search of prey) resulted in elevated TSS concentrations that persisted through the end of the sampling week. Although rays did not seem to penetrate into the center of the bed, the bed's edge experienced TSS concentrations up to four times the habitat threshold level. Anecdotal accounts of cownose ray destruction of SAV beds in Chesapeake Bay exist (e.g., Orth, 1975; Bartleson, 2004), but ray impact has not been well quantified. Ray feeding activity can decimate beds of other SAV species through excavation of plants (Orth, 1975); however, the dense canopy of *S. pectinata* at this study site seems to have hindered ray entrance into the bed.

Plant and Ecosystem Production During Spring

Tissue nutrient contents in plant biomass strongly indicated luxury uptake of nitrogen and phosphorus, especially during the spring period of rapid biomass accumulation. During this time, the aboveground growth rate based on three biomass samples (two from May, one from June) was 8.7 g DW m^{-2} d^{-1} (~3.0 g C m^{-2} d^{-1}). April values well exceeded critical contents (1.3% N and 0.13% P) that indicate thresholds for nutrient limitation in a group of freshwater *Potamogeton* species (Gerloff and Krombholz, 1966). In addition, another study has shown the critical P for *S. pectinata* to be 0.15%, which corresponded to a water column concentration of 3 – 4 μM PO_4^{3-} (with no belowground nutrient uptake occurring) (van Wijk, 1989b). The same study concluded that low water column NO_3^- concentrations (3.2 μM) could not support any plant growth, and even higher concentrations (57 μM) were still limiting to plants. Given the relatively low water column DIN concentrations measured during this study, it seems likely that the majority of N and P in plant biomass is either rapidly accumulated during the spring months or acquired continually from sediment porewater through root uptake.

The seasonality and magnitude of calculated ecosystem metabolism also indicate the spring period as extremely important. Previous work has shown that seagrass bed ecosystems often have a P_a:R_n ratio near 1.0 for most of the season (Ziegler and Benner, 1998; Gacia et al., 2005), but estimated P_a:R_n ratios showed high seasonal variability in the present study. Other studies have reported similar seasonal patterns in net production (Barron et al., 2006), but with maximum fluxes much less than those calculated in this study (Gazeau et al., 2005; Yarbro and Carlson, 2008). In temperate submersed plant systems, epiphytic algae have often been credited with these relatively high peak production values (Kemp et al., 1984; Moncreiff et al., 1992), but this explanation does not hold for the high spring production observed in the present study as epiphytic algal growth was minimal during this time.

Although data are limited, other beds of Chesapeake Bay submersed plants show similar seasonal trends, though much lower respiration during summer months (Murray and Wetzel, 1987); however, these studies focused on beds with much less aboveground biomass than the study site. This high nighttime respiration rate (267.3 ± 12.2 mmol O_2 m^{-2} d^{-1}) and net heterotrophy (P_a:R_n = 0.9, NEP = -39 mmol O_2 m^{-2} d^{-1}) at the study site during the period of peak plant biomass suggests large inputs of allochthonous organic material (Kemp et al. 1984; Kennedy et al., 2004), possibly due to trapping of organic particles by the plant canopy (e.g., Ward et al., 1984; Gacia et al., 2002).

A growth strategy featuring high productivity and biomass accumulation during the spring months resulted in extensive canopy development early in the season, which may have afforded the plant bed protection from mechanical disturbance. This strategy may have also resulted in modification of habitat conditions (e.g., Kemp et al., 1984; Koch, 2001; de Boer, 2007) during the periods of low water clarity characterizing summer months. This early spring period has been previously identified (Moore et al., 1996) as a critical time for meadow-forming SAV development, which can determine if beds will survive poor water quality conditions later in the season. If viable, persistent plant beds are the goal of SAV restoration, perhaps the focus should be shifted to species with life history patterns that are able to preempt the consistently degraded summer conditions of this region.

In summary, the record levels of spring biomass and densities of reproductive material measured for this *S. pectinata* stand indicate an apparently robust population. In addition, this plant bed has been able to tolerate osmotic stress associated with relatively high salinities. Many aspects of this bed appear to be unique for Chesapeake Bay as well as other estuaries. Overwintering of aboveground plant biomass (which has never before been documented in the Bay for this species) combined with high tuber production allowed this bed to grow rapidly early in the season while light penetration was still high. This intensely productive spring period primed this SAV bed for poor water quality during the summer months and provided some protection from physical disturbance (e.g., cownose rays), giving it an advantage over other species.

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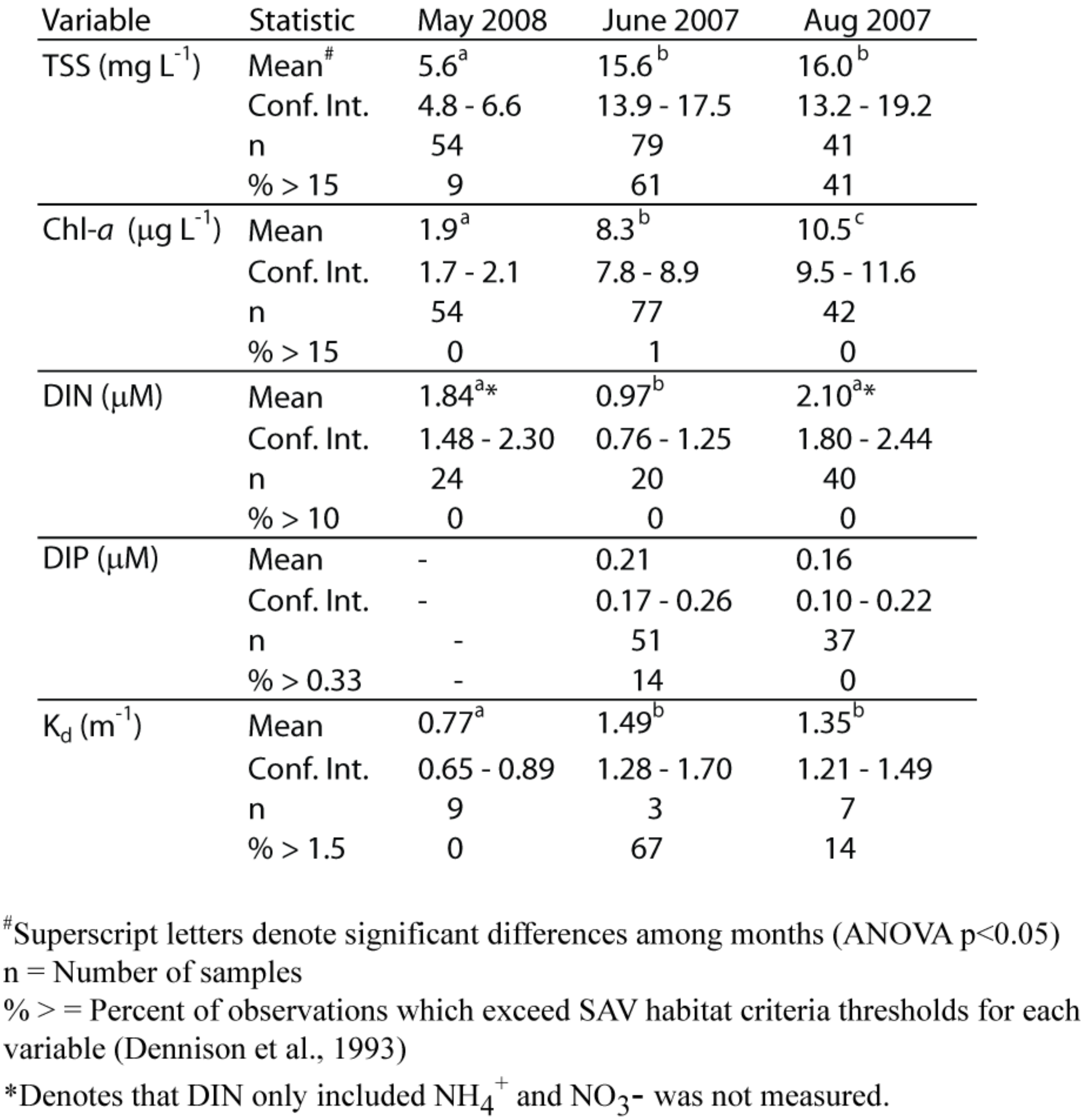
Tables

Table 1.1: Weekly least-squared means and 95% confidence intervals of TSS, chl-*a*, DIN, and DIP measured from water samples collected with an automated sampler outside the plant bed. K_d was calculated from vertical light profiles taken during the week.



Variable	Statistic	May 2008	June 2007	Aug 2007
TSS (mg L^{-1})	Mean$^{\#}$	5.6^{a}	15.6^{b}	16.0^{b}
	Conf. Int.	4.8 - 6.6	13.9 - 17.5	13.2 - 19.2
	n	54	79	41
	% > 15	9	61	41
Chl-*a* (μg L^{-1})	Mean	1.9^{a}	8.3^{b}	10.5^{c}
	Conf. Int.	1.7 - 2.1	7.8 - 8.9	9.5 - 11.6
	n	54	77	42
	% > 15	0	1	0
DIN (μM)	Mean	1.84^{a*}	0.97^{b}	2.10^{a*}
	Conf. Int.	1.48 - 2.30	0.76 - 1.25	1.80 - 2.44
	n	24	20	40
	% > 10	0	0	0
DIP (μM)	Mean	-	0.21	0.16
	Conf. Int.	-	0.17 - 0.26	0.10 - 0.22
	n	-	51	37
	% > 0.33	-	14	0
K_d (m^{-1})	Mean	0.77^{a}	1.49^{b}	1.35^{b}
	Conf. Int.	0.65 - 0.89	1.28 - 1.70	1.21 - 1.49
	n	9	3	7
	% > 1.5	0	67	14

$^{\#}$Superscript letters denote significant differences among months (ANOVA $p<0.05$)
n = Number of samples
% > = Percent of observations which exceed SAV habitat criteria thresholds for each variable (Dennison et al., 1993)
*Denotes that DIN only included NH_4^+ and NO_3- was not measured.

Table 1.2: Mean ± SE (units of μmol O_2 m^{-2} d^{-1}) daytime net production (P_a), nighttime respiration (Rn), net daily production (NEP), and daytime:nighttime ratio (P_a: R_n) calculated from time-series of dissolved oxygen measurements collected with data sondes at a vegetated (Bed) and unvegetated (Bare) station.

Month	P_a		R_n		NEP		$P_a : R_n$	
	Bare	Bed	Bare	Bed	Bare	Bed	Bare	Bed
May 08	106.7 ± 15.0	328.7* ± 28.9	-36.8 ± 7.6	-195.1* ± 25.6	69.9	133.6	2.9	1.7
June 07	127.7 ± 8.9	228.3* ± 30.2	-87.8 ± 8.9	-267.3* ± 12.2	39.9	-39.0	1.5	0.9
Aug 07	186.8 ± 24.4	92.1* ± 17.6	-88.6 ± 19.2	-65.4 ± 7.0	98.2	26.7	2.1	1.4
Oct 08	49.2 ± 8.8	59.2 ± 7.7	-63.0 ± 8.1	-61.9 ± 5.4	-13.8	-2.7	0.8	1.0

*Indicates significant differences in P_a and R_n between stations within months.

Figures

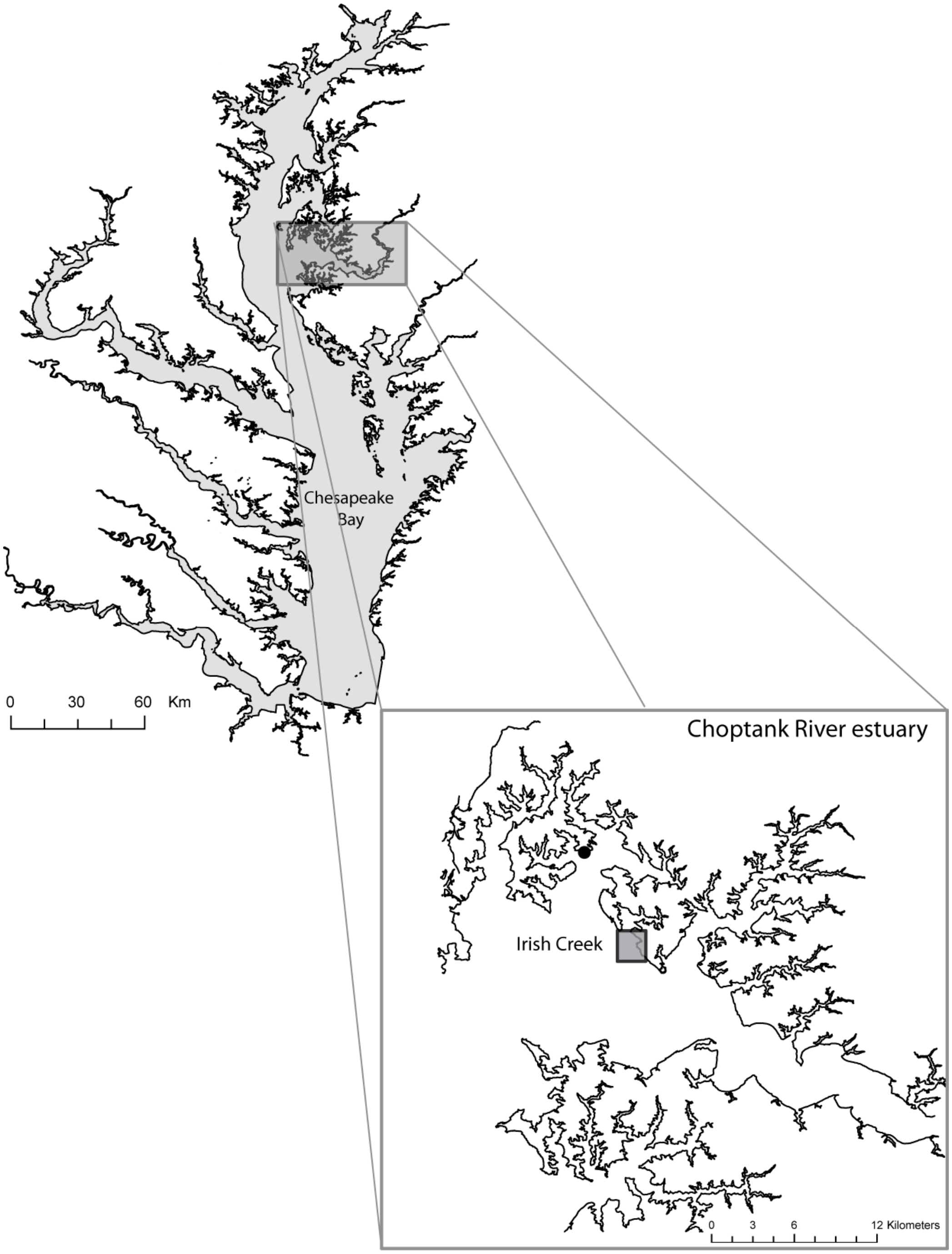


Figure 1.1: Location of the *Stuckenia pectinata* study site at the mouth of Irish Creek in the Choptank River estuary (gray box) and Maryland DNR continuous monitoring station at Mulberry Point (black circle).

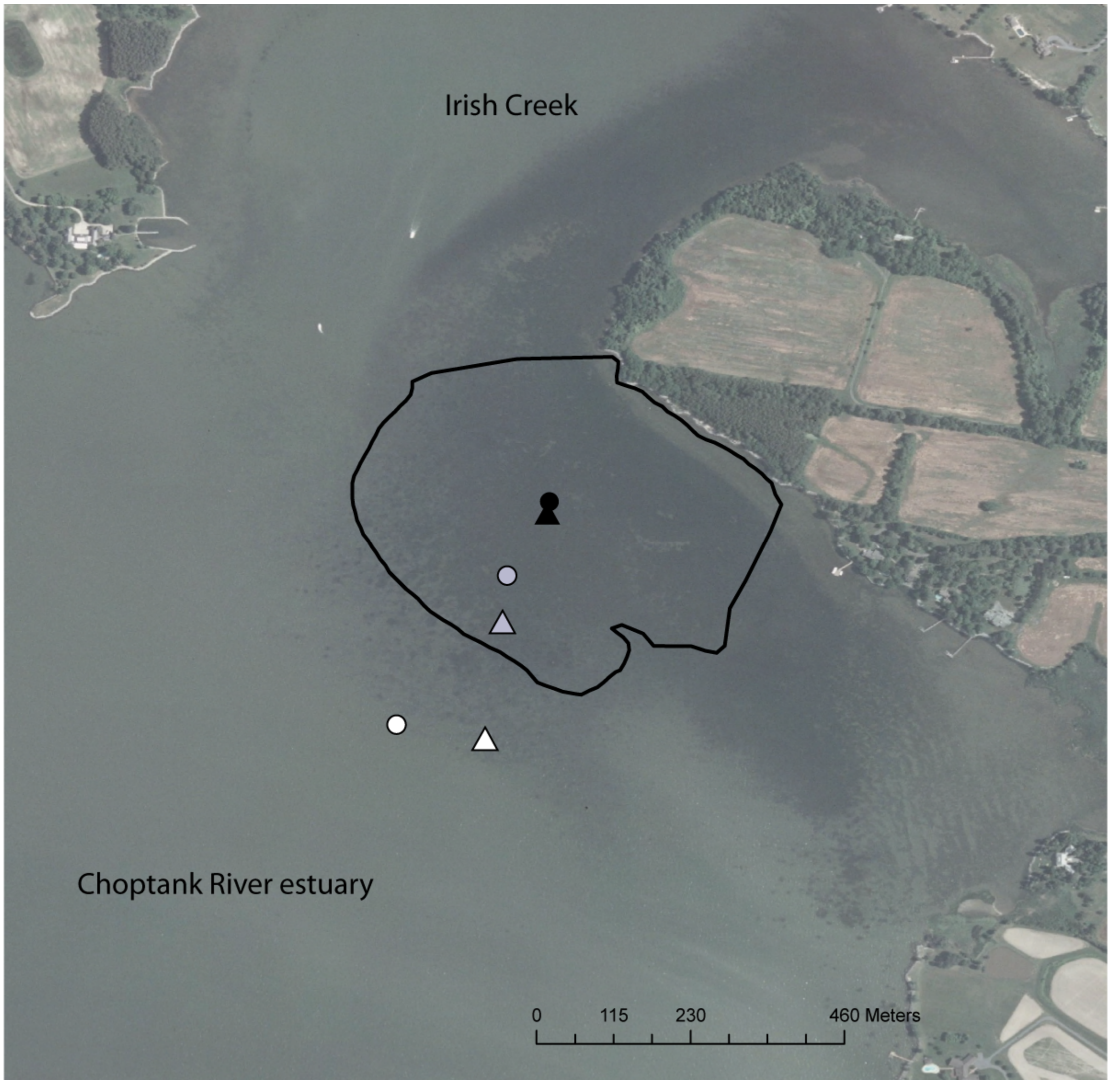


Figure 1.2: Sampling platform locations at the Irish Creek study site (plant bed perimeter in black). Bed (black), Edge (grey), and Bare (white) stations are shown for 2007 (circles) and 2008 (triangles). The background aerial photograph was taken prior to 2007.

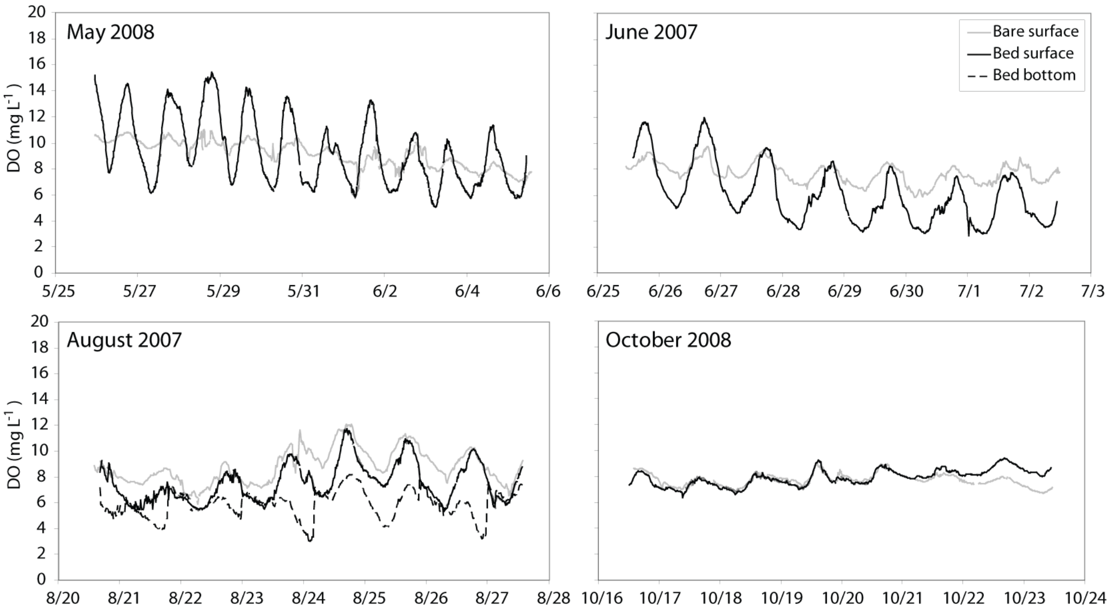


Figure 1.3: Time-series of dissolved oxygen measurements collected by data sondes during four deployments. In August 2007, stratification developed between surface and bottom water over the week sampled.

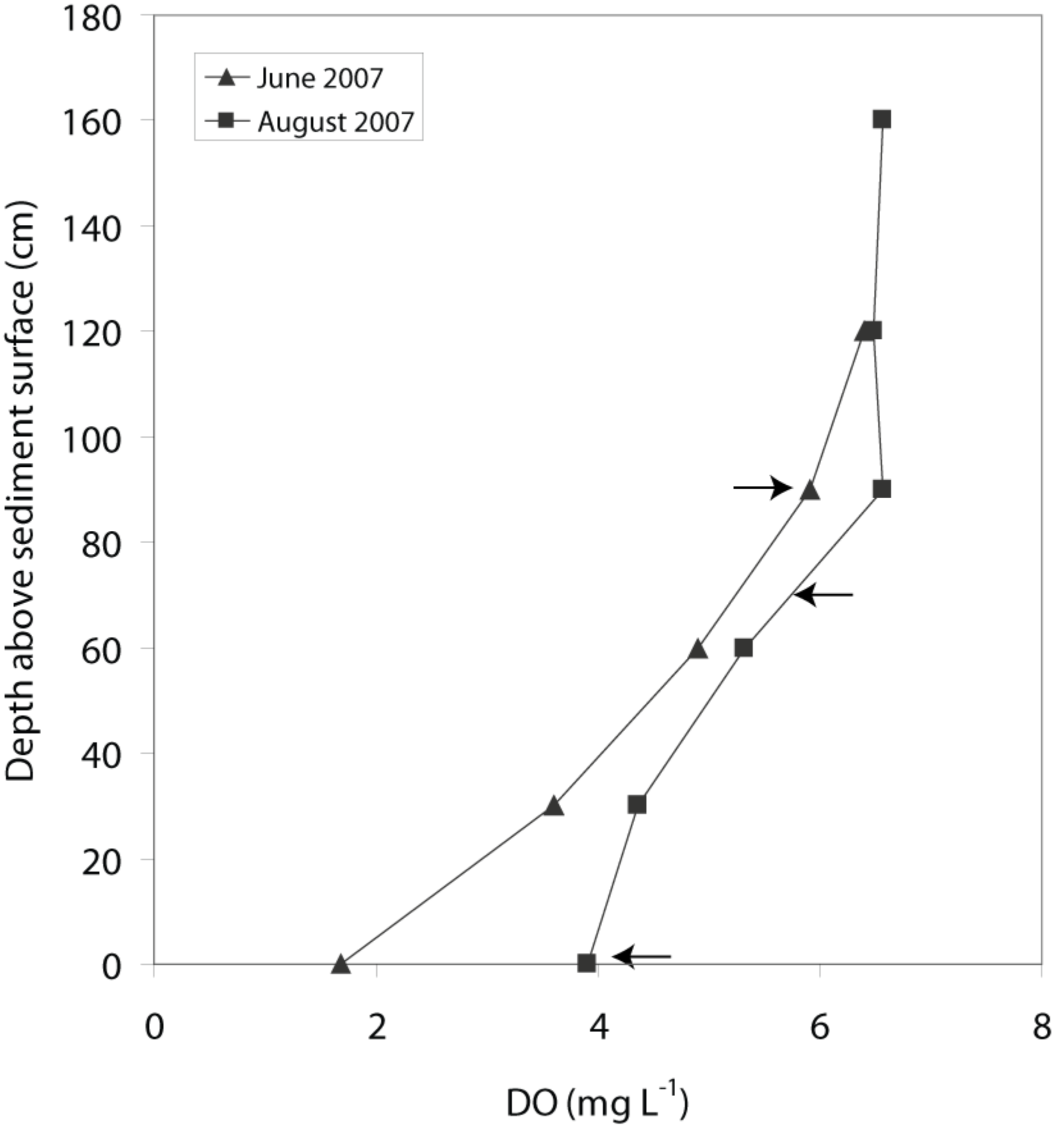


Figure 1.4: Vertical profiles of dissolved oxygen within the plant bed in June (triangles) and August (squares). Arrows indicate depth of data sondes above the sediment surface in June 2007 (90 cm) and August 2007 (5, 70 cm).

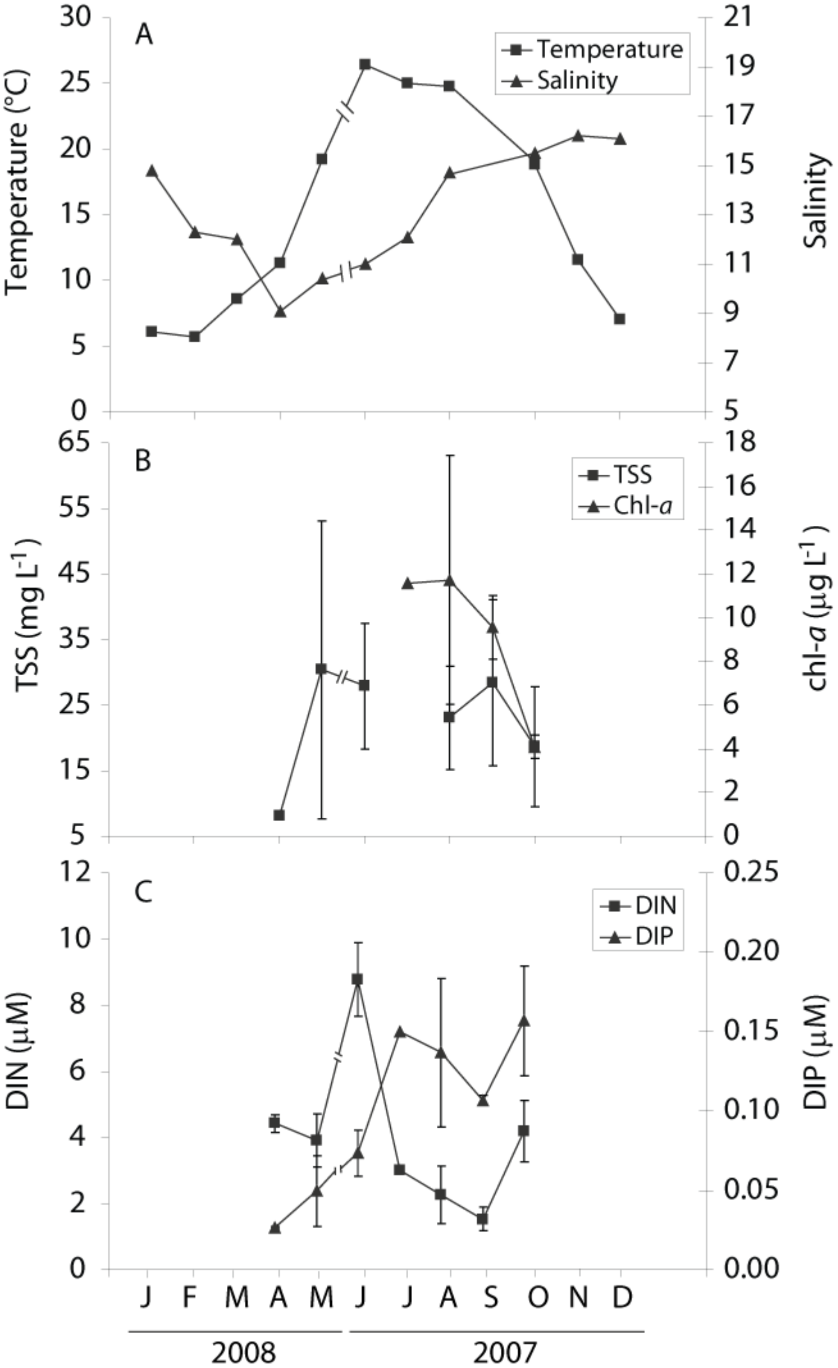


Figure 1.5: Monthly temperature and salinity (A) taken with a hand-held sensor at the study site (Bare) as well as TSS/chl-*a* (B), and DIN/DIP (C) from the nearby MD DNR Mulberry Point sampling station. Error bars indicate standard error.

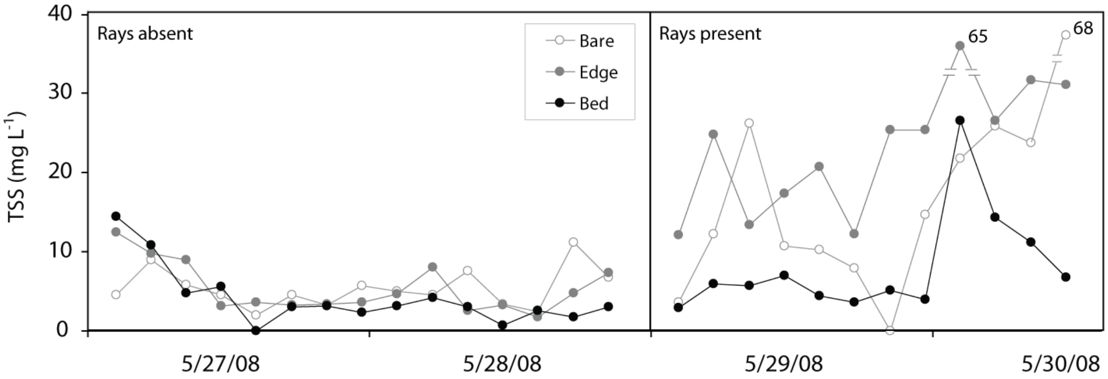


Figure 1.6: Time-series of TSS taken at three stations with automated samplers during May 2008 with cownose rays absent and present.

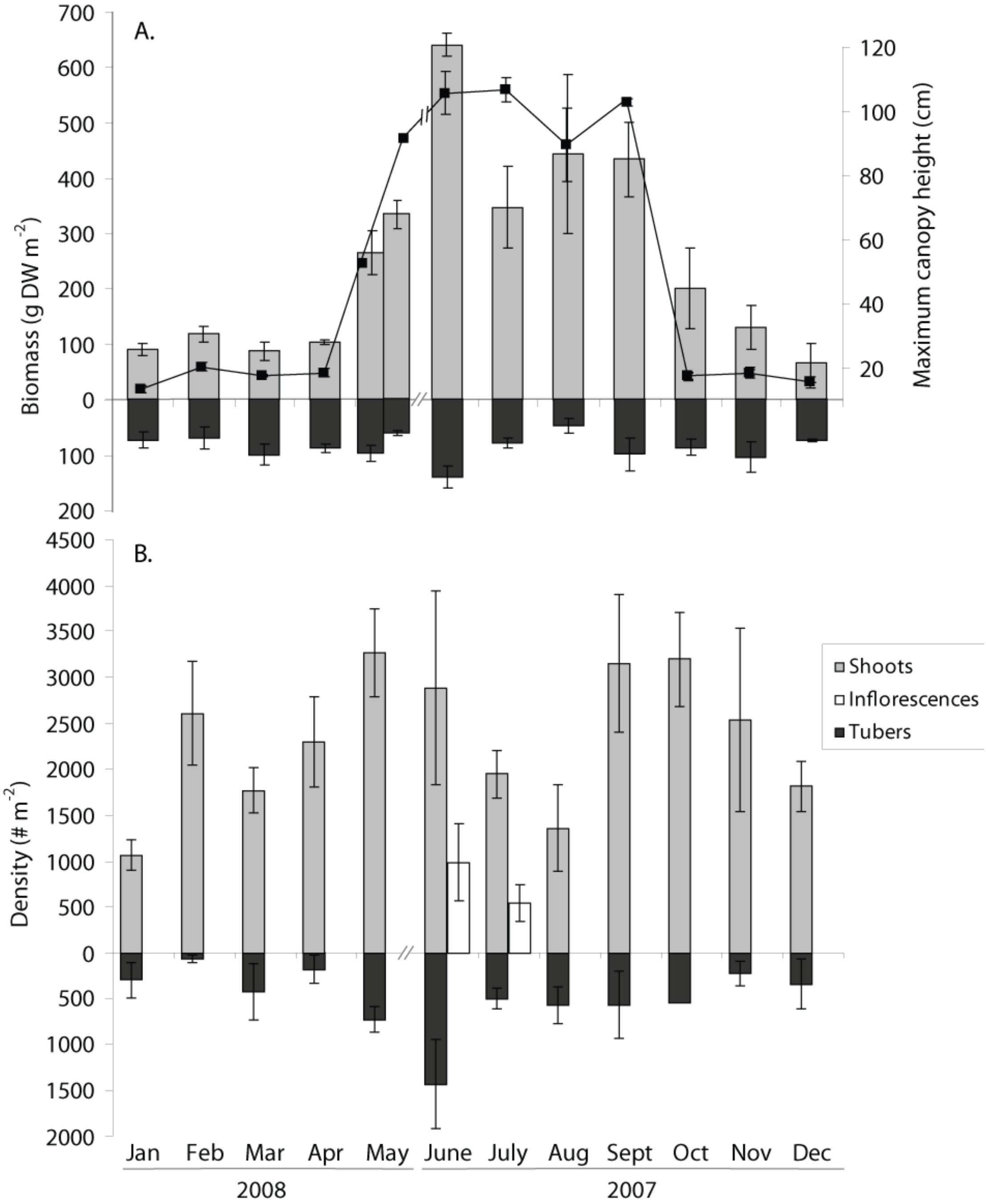


Figure 1.7: Monthly characteristics of the plant bed above- (light gray) and below-ground (dark gray). Values are mean ± SE. Top panel (A) shows biomass (bars) and plant canopy height (points). There were two biomass samples taken in May 2008. Bottom panel (B) shows density of shoots, inflorescences, and tubers.

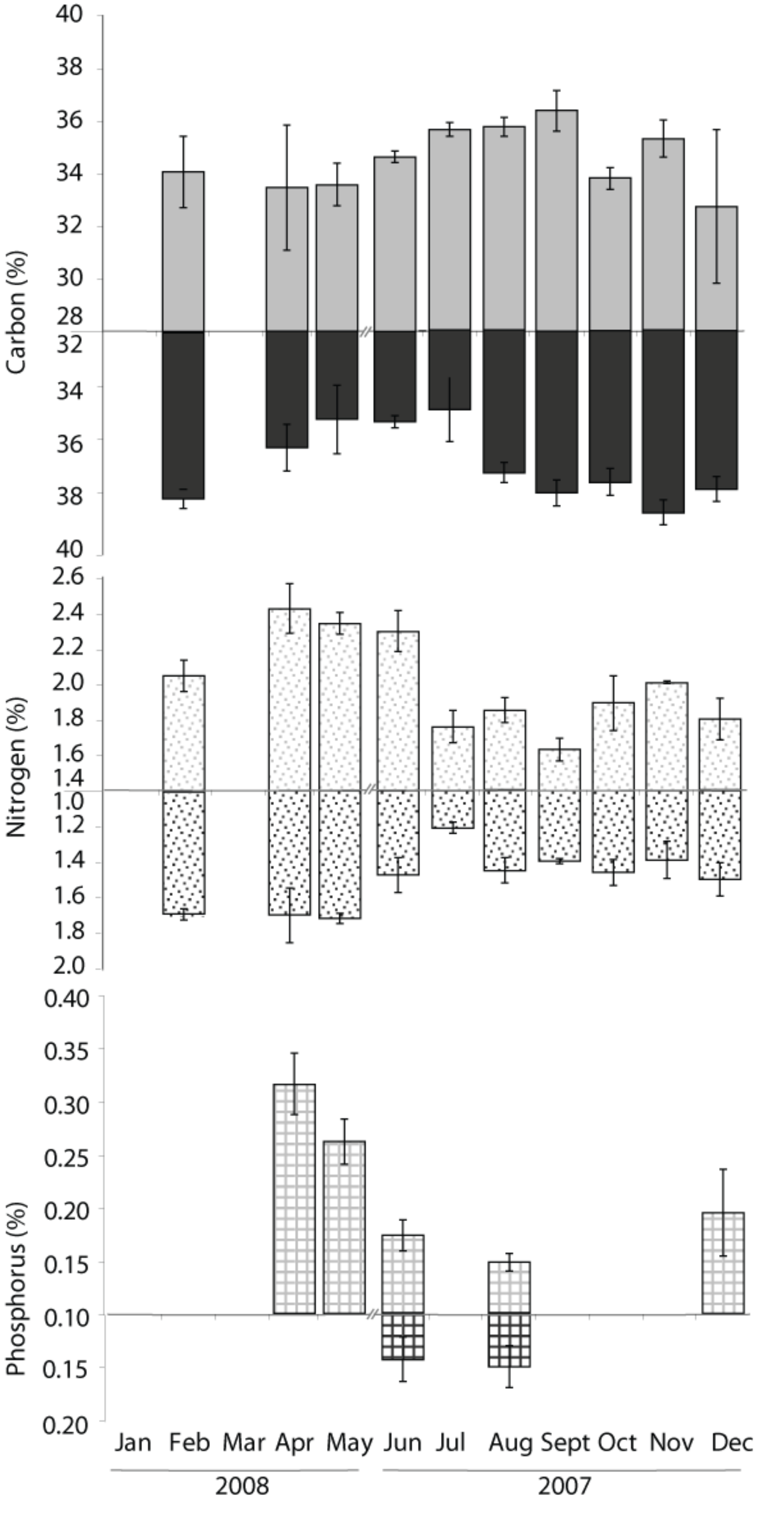


Figure 1.8: Monthly above (gray) and belowground (black) plant tissue nutrient (C, N, and P) content of *S. pectinata*. Values are mean ± SE. Bars missing on tissue P plot are missing samples.

Chapter 2: The effects of a submersed canopy-forming plant bed on local hydrodynamics: Feedbacks related to light, nutrients, and sediment

Abstract

This study quantifies effects of a bed of the canopy-forming submersed plant species, *Stuckenia pectinata*, in modifying local hydrodynamics, resulting in positive and negative feedbacks on plant growth. Measurements of waves and tidal currents along with water and sediment quality were taken outside, at the edge, and within the plant bed. Feedback effects on light/nutrient availability and sediment suitability were explored and related to plant bed character. During the June period of peak plant biomass, significant wave height was reduced by ~44% within the plant stand, resulting in attenuation of total suspended solids (TSS) by ~60% compared to levels outside. Canopy effects on TSS were most resilient to perturbation by high wind and water level during this period. Light reaching plant leaves was also greater within this SAV bed due to reduced epiphytic accumulation. Percent of incoming light at the leaf surface was estimated to be 50% within the bed as compared to 0.5% without the benefits of positive feedbacks. In addition, the decomposition of greater sediment organic matter content within the bed increased NH_4^+ and PO_4^{3-} pools in sediment porewater, providing an important source of nutrients for plants. Trends in suspended material concentrations along with elevated porewater nutrient and sulfide pools at the bed's edge suggest that particle trapping by the canopy may be focused at the edge. Negative feedback effects on plant growth were also observed, including

elevated porewater sulfide, dissolved inorganic carbon limitation, and low dissolved oxygen events, but these did not seem to impact plants substantially.

Introduction

Seagrasses and other submersed aquatic vegetation (SAV) form globally important communities which have been recognized as providing many significant ecosystem services (Costanza et al., 1997). Plant beds represent valuable coastal habitats that serve as food and refugia for a variety of commercially important benthic and pelagic animals (e.g., Lubbers et al., 1990; Hemminga and Duarte, 2000). Additionally, submersed plant beds are sites of enhanced nutrient cycling and facilitate the removal of nutrients from coastal systems (McGlathery et al., 2007). Unfortunately, many coastal waters worldwide, including large ecosystems such as Chesapeake Bay, have experienced degraded water clarity due to increased anthropogenic loading of sediment and nutrients (Kemp et al., 2005). The resulting decreased light penetration and overgrowth of algal epiphytes on leaf surfaces have led to large-scale declines in submersed plants (Kemp et al., 1983; Duarte, 1995).

In Chesapeake Bay, submersed vegetation has long been recognized as critical to overall ecosystem health, and attempts to protect these communities have been a priority for several decades. Large declines in many plant species occurred throughout the Bay in the late 1960s as a result of poor water quality (Kemp et al., 2005), and degraded habitat conditions continue to persist at present (e.g., Williams et al., 2009). Despite a plethora of restoration strategies (e.g., Fonseca et al., 1998) and management action (e.g., Orth et al., 2002), re-growth of submersed plant beds has been slow and highly variable (Moore et al., 2000).

Canopy-forming SAV species represent a highly visible and important group of plants common in many estuaries, including Chesapeake Bay. These apical meristem angiosperm species form tall, highly-branched canopies that can reach the water's surface in shallow near-shore habitats (0.5-2 m). Canopy-formers typically appear in two contrasting growth forms: a dense and highly-branched reproductive phase with tall flowering shoots during the summer months, and a lower vegetative phase during all other months of the year (e.g., Kantrud, 1990). This latter form results in plant beds with similar structure to that of meadow-forming seagrass species (e.g., Koch et al., 2006). One salt-tolerant canopy-forming species common to freshwater systems is *Stuckenia pectinata* L. (Boerner), which is know to be an important food source for waterfowl in Chesapeake Bay and other systems (e.g., Kantrud, 1990; Perry et al., 2007). Historically, this species was widely distributed throughout the Bay and its tributaries (e.g., Stevenson and Confer, 1978), but has a more limited geographic range at present (e.g., Orth et al., 2009).

Submersed plants are known to impact local hydrodynamics, resulting in many positive and negative feedbacks on plant growth (Koch, 2001; de Boer, 2007), which may help plants cope with poor water quality. The ability of submersed plant beds to attenuate waves and currents depends on frictional drag associated with the plant stand. Canopy-forming vegetation has been found to be particularly effective in attenuating wave energy, as these species tend to occupy a large fraction of the water column (Fonseca and Cahalan, 1992). In addition, shoot density provides a useful index of canopy structure and frictional effects on hydrodynamic modification (Peterson et al., 2004; Widdows et al. 2008). One important positive feedback associated with this water flow modification is increased light penetration (e.g., Moore, 2004) due to the sinking of suspended particulate material (e.g., Ward et al., 1984) and reduced resuspension within the plant bed (Gacia and Duarte, 2001). In addition, the decomposition of deposited allochthonous material and retained autochthonous material may augment sediment porewater nutrient pools (e.g., Hemminga et al., 1991), further improving conditions for plant growth. However, this decomposition also increases the concentration of phyto-toxic hydrogen sulfide in porewater, which can reduce plant photosynthesis (e.g., Holmer and Bondgaard, 2001), resulting in a negative feedback on plant growth. For canopy-forming species with seasonally-varying growth forms, plant control on waves and currents (and thus feedbacks) may experience large variation with canopy architecture and shoot density (Hasegawa et al., 2008).

Local physical conditions including wave height, tidal current patterns, and water depth (Koch and Gust, 1999) influence the effects of SAV beds in modifying hydrodynamics and associated feedbacks (e.g., Ward et al., 1984). Although data are scarce, the interactions between seasonal changes in the plant stand and ambient hydrodynamics are likely to modulate SAV bed effects on water quality and sediment conditions. In addition, feedback effects are likely unevenly distributed throughout a plant stand, as modification of hydrodynamics by plants has been shown to vary with the size of submersed plant beds (e.g., Fonseca and Koehl, 2006). Water quality conditions may therefore vary depending on location within the plant bed. Model results and some preliminary evidence indicate the presence of “edge effects” in seagrass beds, where the majority of flow attenuation (and possibly particle deposition) occurs at the bed’s edge (Chen et al., 2007; Bradley and Houser, 2009) and may depend on shoot density (Peterson et al., 2004). However, in many natural submersed plant beds the edge is not well-defined, consisting of a series of patches or lower density regions that experience variable hydrodynamic conditions (e.g. Maltese et al., 2007) and likely receive little benefit from feedbacks as a result.

Although substantial research has demonstrated the influence of submersed plants on hydrodynamics, the majority of these studies have taken place in flumes and have focused on unidirectional flow rather than oscillatory or *in situ* conditions. With a few exceptions (e.g., Rybicki et al., 1997; Hasegawa et al., 2008), most studies have ignored natural plant communities. The effects of meadow-forming seagrasses on water flow is predominant in the literature, with relatively little work focused on quantifying impacts of canopy-forming submersed plant species. Most previous work has also been conducted in relatively pristine environments rather than eutrophied, degraded systems where such research is most pertinent for management. Studies have typically centered around describing bed effects at peak biomass, rather than quantifying seasonal variability, which is large for canopy-forming species. Furthermore, very few studies have compared feedback effects on a full suite of ecological and biogeochemical processes.

To address these issues, the goals of this study were to: (1) explore positive and negative feedback effects on light, nutrients, and sediments in a canopy-forming bed of *Stuckenia pectinata*, (2) assess the seasonally-varying relationship between these processes and plant canopy architecture, and (3) determine if feedbacks can create suitable conditions for plant growth that are otherwise unattainable in a degraded estuarine system. The associated hypotheses were that: (1) a canopy-forming SAV bed can significantly modify wave height and current speed, resulting in positive (light and nutrients) and negative (porewater sulfide) feedbacks, (2) water flow modification and associated feedbacks are most prominent during periods of robust plant canopy, (3) feedbacks effects are weaker at the bed's edge with variable hydrodynamic conditions, and (4) perturbation of feedbacks involving water clarity by extreme physical events (i.e., storms) depends on plant canopy architecture.

Methods

Study Site

This study spanned over a full annual cycle (June 2007 – October 2008) and involved intensive field sampling of a monospecific stand of the canopy-forming SAV species *Stuckenia pectinata*. The submersed plant bed was located on the northern shore of the Choptank River estuary (a Chesapeake Bay tributary, ~85 km from the Bay mouth) adjacent to a small creek (Irish Creek) (Fig 2.1). The bed covered an area exceeding 5 ha, the size and shape of which did not change substantially between 2007 and 2008. The study bed was bordered to the east and within the mouth of Irish Creek by beds of *Ruppia maritima.* This particular submersed plant bed was selected because of its continued survival despite relatively poor water quality (e.g., Orth et al., 2008).

To support sampling equipment, three platforms were attached to pressure-treated wooden pilings that had been jetted into the sediment in May 2007. Platforms were placed along a cross-bed transect forming three station locations at: 1) the dense inner portion of the bed 210 m inside the bed’s seaward perimeter (“Bed”), 2) the edge region 90 m inside the seaward perimeter (“Edge”), and 3) an unvegetated site 160 m outside the bed’s seaward perimeter (“Bare”). Upon conclusion of sampling in 2007, the platforms were removed and were then reinstalled in April 2008 at slightly different locations as per U.S. Coast Guard specifications, with the Edge station located 40 m within and the Bare station 110 m outside the bed’s seaward perimeter (Fig 2.2). Despite the transect length, water depths were similar among stations with Bare, Edge, and Bed at 1.40, 1.14, and 1.13 m MLLW, respectively.

Water Quality

Water samples (800 ml) were collected using automated discrete samplers (Teledyne Isco, Inc., Model 6712) secured to each platform. Programmed collection occurred at 2 - 4 h intervals (depending on the month) for week-long deployments during June 2007 (period of peak plant biomass), August 2007 (plant bed decline), and May 2008 (peak plant growth). Sampler tubing was cable-tied to the platforms, with the intake positioned at mid-water column depth (about 60 - 80 cm from the sediment surface, varying slightly by deployment). Each sampler held an ice block in the center of an isolated cylinder to maintain a chilled environment for samples, which were retrieved daily, placed on ice, and transported back to the lab for immediate processing.

At the laboratory, water samples were shaken to homogenize and filtered onto pre-weighed and ashed (4 h at 550° C) filters (0.45 μm GF/Fs). Filters were rinsed with deionized water to remove salt and then dried (3 d at 60° C), and weighed to determine total suspended solid (TSS) concentrations. The filters were then ashed (4 h at 550° C), cooled in a desiccator, and re-weighed to provide an estimate of percent particulate organic material (% POM). An additional, known volume of water sample (60 - 120 ml) was passed through filters, which were wrapped in aluminum foil, and frozen for subsequent chlorophyll-*a* (chl-*a*) analysis. Within 6 mo of collection, the filters were thawed, extracted in the dark with 100% acetone, sonicated, filtered, and read on a fluorometer (10-AU, Turner Designs). For two samples in each daily series (noon and midnight), water was also passed through pre-ashed filter (0.45 μm GF/Fs), which were retained for particulate carbon and nitrogen (Exeter Analytical, Inc., CE-440) and phosphorus analysis within 6 mo of collection. Filters retained for particulate inorganic phosphorus were ashed (90 min at 550° C) and digested in 1 N HCl (2 d) (Aspila et al., 1976). Supernatant liquid was then aliquoted into plastic cuvettes and concentrations were determined colorimetrically (Technicon Auto Analyzer II).

Filtrate was aliquoted into 5 ml vials, which were immediately frozen and stored for later nutrient analysis. Water column concentrations of ammonium (NH_4^+), nitrate (NO_3^-), and ortho-phosphate (PO_4^{3-}) were determined colorimetrically (Technicon Auto Analyzer II) within 1 yr of collection (US EPA, 1979). Additional filtrate from noon and midnight samples was also aliquoted into 20 ml bottles and frozen for analysis of total dissolved phosphorus (TDP) and nitrogen (TDN) within 3 mo of collection (Valderrama, 1981).

To detect high-frequency changes in selected water quality variables, one data sonde (Yellow Springs Instruments, Inc., YSI 6600) equipped with a series of sensors for turbidity (model 6136), chlorophyll (model 6025), dissolved oxygen (6562), conductivity/temperature (6560), and pH (6516) was deployed at each station and programmed to record every 15 min. Calibrated prior to each deployment, data sondes were secured to the platforms with sensors placed adjacent to water sampler intakes. Sondes were deployed for 1 - 2 weeks coincident with water sampler deployments and additional two week deployments in both August 2008 and October 2008. Two additional data-logging sensors (YSI 600XLM) were added for the 2008 deployments and were placed 5 cm above the sediment surface at Bare and Bed stations to record near-bottom water quality.

Each day during water sample retrieval, a hand-held sensor system (YSI Inc., Model 85) was used to record surface and bottom water temperature, salinity, and dissolved oxygen (O_2) at each site. In addition, Secchi depth and a photosynthetically active radiation (PAR) vertical profile (LICOR, LI-1000 hand-held 2π sensor) were taken daily at each site to calculate diffuse downwelling PAR attenuation coefficients (K_d). Because light measurements taken within the bed included significant shading from plants, light attenuation was also measured in a patch (1 m^2) with aboveground plant tissue removed adjacent to the Bed station. To assess the choice of sensor and intake depth placement, detailed depth profiles were taken in August 2007 at each station. Plastic tubes were mounted on the platforms at 30 cm intervals above the sediment surface, and water was collected for TSS and chl-*a* analyses as described above. No significant differences were detected between height intervals by site.

Plant Canopy

Aboveground and belowground plant materials were collected once per month (twice in May 2008) in triplicate samples from June 2007 through August 2008. PVC quadrat frames (0.25 m x 0.25 m) were placed in random locations between Bed and Edge stations and all aboveground biomass (stems, leaves, inflorescences) within the frame was clipped at the sediment surface and placed in plastic zip-lock bags. The belowground biomass (roots, rhizomes, tubers) was sampled within each clipped area using a 13.7 cm diameter acrylic corer, driven sufficiently deep (≥ 20 cm) into the sediment to collect all root material. Belowground material was sieved in nylon mesh bags (0.5 cm) to remove all sediment and placed in plastic zip-lock bags. Biomass samples were placed on ice in the field, and kept chilled until processing. Within 3 d of collection, above- and below-ground plant biomass samples were washed in fresh water and scraped free of epiphytes. Number of total shoots, reproductive shoots, inflorescences, and belowground over-wintering buds (tubers) were counted for each sample. Reproductive (flowering) and vegetative (non-flowering) shoots were separated and 10 shoots from each were randomly selected for length measurement. All above- and below-ground biomass was then placed in foil packets, dried to constant weight (60° C), and weighed. After weighing, a portion of each sample (~1 g) was ground with a mortar and pestle and analyzed for elemental carbon, nitrogen, and phosphorus as described above. Average shoot density (vegetative and reproductive), above- and belowground biomass, average canopy height (reproductive and vegetative shoots), and maximum canopy height (reproductive shoots only) were determined for every month.

Physical Measurements

During the May 2008 deployment, a data-logging anemometer (Campbell Scientific, Inc., 05103-L R.M. Young) was deployed at the Bare station. The anemometer was secured to an aluminum pole 10 ft above the water surface and collected wind speed and direction at 5 min intervals for a week. Post-deployment, wind data were downloaded (PC200W software) and wind direction was converted from degrees magnetic to true. Measurements were comparable (Appendix 1, Fig. AI.1) to long-term land-based wind measurements on the south side the of the Choptank River Estuary, 13.5 km away (Horn Point Weather Station, http://www.cbos.org).

Datalogging wave gauges (Coastal Leasing, Inc., MacroWave Pressure Gauge) were deployed monthly (April-October 2008) inside and outside the *S. pectinata* bed and burst-sampled pressure at a frequency of 5 Hz. Raw data were downloaded post-deployment, and Fast-Fourier transformed (MATLAB) to determine significant wave height (Platt and Denman, 1975). Precision among wave gauges was assessed by a two-day deployment in a laboratory wave-generating flume (Engineering Laboratory Design, Inc.). Wave attenuation by the plant canopy was calculated as $\%WA = 100 - \frac{H_{bed}}{H_{bare}}\sqrt{\frac{c_{bed}}{c_{bare}}} \cdot 100$ where H is significant wave height and c is group velocity (Koch et al., 2006). Assuming shallow water waves at the site, group velocity = phase speed ($c = \sqrt{gh}$) where g is the acceleration due to gravity and h is the height of the water column. Assuming waves are linear, wave orbital velocity can be calculated as $u = \frac{A}{h} \cdot \sqrt{gh}$ where wave amplitude (A) is half the significant wave height.

In addition, tidal current speed and direction were burst-sampled (5 min every 15 min) at a frequency of 2 Hz at 10 cm vertical intervals using an acoustic doppler current profiler (Nortek AS, AquaDopp Current Profiler) at Bare and Bed (within the de-vegetated patch) stations over different stages of tide during May and June 2008.

Epiphytes

To provide an index of epiphyte effects on light availability to plants, epiphytes were sampled using artificial substrates during each week of automated sampler deployment (June, August, and May) at each station. Triplicate grids consisting of 0.25 m x 0.25 m mesh squares with attached 0.7 cm-wide ribbon (2007) or 2.5 cm-wide Mylar strips (2008) were placed at random near each platform (e.g., Stankelis et al., 2003). Grids were fastened to the sediment surface using 10 cm metal stakes. Artificial substrate strip lengths were 30-40 cm in 2007, and 120 cm in 2008. The ribbon was flexible and slightly buoyant, maintaining an upright position in the water column; small foam floats were attached to the upper ends of Mylar strips to attain the same orientation. Grids were checked periodically and collected after 8–10 d deployments.

Collection consisted of cutting a portion of each strip while still underwater, placing portions in individual WhirlPak bags, and processing them upon returning to the laboratory. Epiphyte strips were scraped, rinsed with de-ionized water, and scrapings were homogenized in a known volume of de-ionized water by vigorous shaking. This mixture was then passed through pre-ashed filters (0.45μm GF/Fs) for total and inorganic epiphyte mass and chl-*a* analysis, following the same procedures as above.

To test the assumption that epiphyte mass did not differ by depth sampled, strips in 2008 were each partitioned into four 30 cm sections, and cuttings were analyzed from each section. Neither total epiphyte dry mass nor chl-*a* concentration differed significantly between the second section from the bottom (30-60 cm, representative of the 2007 samplers) and any of the other three sections (at any of the sites), so this section was used to represent epiphyte growth in May.

The amounts of inorganic, algal, detrital organic, and total trapped material were estimated assuming a C:chl-*a* ratio of 50:1 for algal epiphytes (Cloern et al., 1995) with *TotalMass* = *Inorganic* + *Organic* where *Organic* = *Algal* + *Detrital* and *Trapped* = *Inorganic* + *Detrital*. Trapping rates were calculated based on duration of artificial substrate deployment (June=7, August=6, and May=10 d).

Sediment

To investigate sediment characteristics, triplicate sediment samples were taken with a cut-off 60 ml syringe (2.6 cm diameter) at each station. For sediment chl-*a* analysis, the surface 0.5 cm was removed and deposited into aluminum foil-wrapped 15 ml tubes, which were frozen until subsequent analysis. Within 2 - 4 weeks of collection, sediment chl-*a* samples were thawed and extracted in 90% acetone. After sonication in a water bath (Branson 1510) and centrifugation, the supernatant liquid was poured into glass vials and read on a fluorometer (Turner Designs, Model 10-AU).

Triplicate samples of surface sediment (top 1 cm) were also collected and placed in Whirlpak bags for analysis of sediment bulk density and elemental carbon, nitrogen, and phosphorus. Within 1 wk of collection, sediment bulk density samples were placed in pre-weighed aluminum boats, weighed wet, dried overnight, weighed dry, ashed (4 h at 550°C), and re-weighed when cool. Wet bulk density was calculated with $\rho_{bulk} = (1-\phi)\cdot\rho_{part} + \phi\cdot\rho_{pw}$ where porosity ($\phi = \frac{V_v}{V_T}$, with V_V = pore volume and V_T = total volume) was calculated using salt-corrected volumes (e.g. $V_v = \frac{W_{frac}}{\rho_{pw}\cdot(1-F_{salt})}$). Porewater density ($\rho_{pw}$) was 1.025 g cm^{-3}, particle density (ρ_{part}) was 2.65 g cm^{-3}, salt fraction (F_{salt}) was 0.011, and fraction of water (W_{frac}) was calculated with wet and dry sediment weights as $W_{frac} = \frac{Wet - Dry}{Wet}$. Sediment elemental carbon, nitrogen, and phosphorus samples were dried, ground, and run with the same procedures as filters from water column samples.

Triplicate cores (0.5 m long) were taken at each site in August 2008 for ^{7}Be (short-term deposition) and ^{234}Th (long-term deposition) isotope analysis, and these were transported intact back to the lab (Palinkas et al., 2005). Cores were cut into 0.5 cm sections down to 3 cm depth and 1 cm sections below that. Sections were weighed wet, dried (60° C), re-weighed, and ground. Gamma ray emissions were counted for each section on a germanium detector (Canberra) for a minimum of 24 h. Activities (measured at 477.7 and 63.3 keV for ^{7}Be and ^{234}Th, respectively) were normalized to the salt-corrected dry mass, and were corrected for decay occurring between collection and counting. Samples were then re-counted ~8 mo later to determine background activity of ^{234}Th in sediment. It was not possible to count all sections before the isotope half-lives (53 days for ^{7}Be and 24 days for ^{234}Th), so only counts performed within the half life were used.

Triplicate porewater samplers (“peepers”) were installed during the weeks of automated sampler deployment (June, August, and May) in random locations within ~10 m of respective stations. Peepers were constructed from acrylic plates, and each contained five holes centered at 5, 8, 11, 15, and 20 cm below the sediment surface (modified from Hesslein, 1976). These holes, which were covered by a polycarbonate membrane (0.2 μm) and fabric screen to protect the membrane, created reservoirs containing 10 ml of water. Peepers were filled with deoxygenated de-ionized water, assembled, and inserted into the sediment in pre-made holes. During the June 2007 and May 2008 sampling periods, three additional peepers were placed in unvegetated patches (“Edge Non”) inside the plant bed’s irregular edge region in addition to peepers within vegetated patches of the edge region (“Edge Veg”), all adjacent to the Edge station (representing four total station locations, each with triplicate samplers).

Peepers were left in the sediment ~10 d until equilibration was achieved (Hesslein, 1976), and were then sampled in the field using a 20 ml syringe and needle to puncture each membrane. Porewater samples were filtered (Acrodisc, 0.25 μm), aliquoted into 5 ml vials for NH_4^+ and PO_4^{3-} analysis, diluted with de-ionized water, placed on ice, and immediately frozen upon return to the lab. Nutrient analyses followed the same procedures as for water column samples. Additional aliquots, which were made for hydrogen sulfide analysis, were immediately fixed with diamine reagent, shaken, and stored un-chilled until subsequent analysis (modified from Cline, 1969). Within 3 mo, samples were diluted with de-ionized water and read on a spectrophotometer (Shimadzu UVmini 1240).

Statistical Analysis

Statistical analyses were performed with SAS Statistical Software v 9.1, and the significance level for all statistical tests was set at α = 0.05. Time-series data collected with automated samplers were tested for significant differences among stations for each month with multiple one-way Model II ANOVAs, where time was treated as a random factor. The ANOVA assumption of homoscedasticity was met with Levene's test, and normality of residuals was assessed visually (plotting residuals against means) and through the Shapiro-Wilk normality test. For some months and variables, it was necessary to use natural log transformations to meet ANOVA assumptions. Tukey-Kramer adjusted least-squared means were calculated, and all pair-wise comparisons were computed for each month. Transformed means and 95% confidence limits were then back-transformed.

One-way Model I ANOVAs were used to test for significant differences in porewater, sediment and epiphyte data among sites, meeting the same assumptions as above. In the cases of percent data, an arcsine transformation was often necessary to meet assumptions of homoscedasticity. Least-squared means were calculated and all pair-wise comparisons computed using Ryan's Q tests for equal sample sizes, and Tukey-Kramer HSD test for unequal sample sizes. Differences in TSS (Bare – Bed) from data taken with automated samplers (May, June, August) and grab samples (July, October) were regressed against various metrics of submersed plant presence (biomass, longest shoot length, and density) with Model I linear regression. The assumption of normality over all independent classes was met using the Shapiro-Wilk test for normality.

After retrieval, sonde data were downloaded and quality-checked for outliers. Sondes with older turbidity sensors (model 6026) reading in turbidity units of NTU were converted to NTU+ (model 6136) using the simple equation $NTU+ = 0.6486 * NTU$ (YSI Environmental, 2005). Turbidity (NTU+) was then converted to equivalent TSS (mg L^{-1}) by regressing sonde turbidity measurements against direct TSS measurements from both grab samples and concurrent measurements from automated samplers. Significant regression equations were generated separately for each instrument and each deployment and used to transform the data sonde time-series' from turbidity (NTU+) to TSS (mg L^{-1}) (Appendix I, Fig. AI.2).

To assess the interaction between suspended particles and physical processes, these TSS time-series data from sondes were linked with simultaneous measurements of wind speed, using only instances when the wind direction was between 155 and 280 degrees, the fetch directions for which the study site had significant exposure. Other wind events may have resulted in significant wave action at Bare as opposed to Bed due to sheltering from nearby land masses. It would have been preferable to use wave height instead of wind speed, but only in August and October 2008 were wave gauges deployed simultaneously with data sondes, whereas wind speed was available for every sonde deployment. Time-series records of wind speed (HPL gauge) and wave height (Bare station gauge) showed similar patterns, though wave height tended to lag behind wind speed (Appendix I, Fig. AI.3). Additionally, TSS time-series were linked with concurrent measurements of water depth for each entire deployment period. Wind speed was divided into discrete increments (0-1, 1-2, 2-3, 3-4, and 4-5 m s^{-1}) along with water depth (1.0-1.2, 1.2-1.4, 1.4-1.6, 1.6-1.8, and 1.8-2.0 m), and one-way Model I ANOVAs were performed to determine the effects of wind and water depth on TSS attenuation ($\%TSSA = 100 - \frac{TSS_{Bed}}{TSS_{Bare}} \cdot 100$) among classes by month. Tukey-Kramer-adjusted least-squared means were calculated and all pairwise differences computed. Pearson correlation analysis was used to measure the correlation between wind speed and water depth.

Results

Site Characteristics

Physical conditions at the study site varied widely over the course of this investigation. Daily maximum water temperatures were measured in mid-summer (27.3 ± 1.27 °C, mean ± SD), and daily mean salinity increased from low values in the spring (10.3 ± 0.29) to higher values in the fall (17.8 ± 0.97) (Table 2.1). During the study period, mean wind speeds tended to be high during spring months, decrease during summer, and increase again in the fall. For spring and summer instrument deployment periods, winds were directed out of the south and west, which coincided with the axis of the study transect (~200°). Fetch was maximal at the study site between 155 - 280° as wind and waves from these directions were uninterrupted by the northern shore of the Choptank River (Fig. 2.2). During the fall, winds reversed and were directed primarily out of the north and east. Mean significant wave height varied between 0.14–0.18 m by deployment, with the maximum wave height measured in July 2008 (0.66 m).

Monthly plant biomass and canopy height showed strong seasonal trends in this submersed plant bed. Both measures of bed structure reached maximum values during summer months, while shoot density tended to vary over the year (Fig 2.3). Aboveground biomass measurements made during summer months of 2008 were similar to 2007, and thus data is presented out of chronological order as a complete annual cycle. Reproductive shoots began developing in May, but the majority of shoots were still vegetative during this month. Peak aboveground plant biomass of 641 ± 21 g DW m^{-2} occurred during June and corresponded with a thick, flowering canopy that averaged 106 ± 7 cm in height (mean ± SE). Over the period from May through August, live shoots were composed of $34.90 \pm 0.34\%$ Carbon, $2.08 \pm 0.09\%$ Nitrogen, and $0.19 \pm 0.02\%$ Phosphorus (mean ± SE).

While shoot morphology changed little from June to August, shoots became more flaccid with the onset of senescence. By late August, the canopy was found leaning over in many places, reducing its “effective height” in the water column (and presumably its frictional drag). During September, aboveground biomass remained high but the canopy was lying prone on the sediment surface, thus minimizing its impact on water flow. Although the long reproductive shoots were generally still attached to their belowground tissues, the canopy's effective height had been decreased to one third (~30 - 40 cm) of its peak height.

Canopy Effects on Hydrodynamics

This *S. pectinata* bed was effective in attenuating wave energy, especially during peak plant biomass, where wave attenuation occurred during the entire deployment and persisted through high energy events (Fig 2.4). Over this deployment, wave attenuation by the plant bed was 37 ± 13.0% (mean ± SD). A comparison between concurrent wave height measurements at Bed and Bare stations during June (peak plant biomass) and September (low plant canopy) supported our assumption that attenuation within the stand was due to the presence of a plant canopy and not physical characteristics of the study site (Fig 2.5).

At the study site, vertically integrated tidal current velocities were fairly low (between 4 – 6 cm s^{-1}, maximum of 9 cm s^{-1}) both inside and outside the plant bed (Fig. 2.6). Wave orbital velocity (calculated using averages from deployment periods) exceeded tidal current velocities, averaging 26.4 cm s^{-1} during June. Though tidal current directions changed as expected, current speed was random and not related to phase of tide. In addition, vertical current profiles showed no patterns related to the presence of submersed plants (Fig. 7).

Canopy Effects on Light, Nutrients, and Sediment

Clear effects of the submersed plant bed were evident in suspended particle concentrations. Weekly means of total suspended solids (TSS) and chlorophyll-*a* (chl-*a*) measured with automated samplers decreased significantly along the transect in June and August, while in May, TSS and chl-*a* concentrations differed significantly between the Bed station and both Bare and Edge stations (Fig. 2.8, $p<0.0001$ for all months). Mean TSS concentrations outside the plant bed were high in June (15.4 mg L^{-1}) and August (14.1 mg L^{-1}) and low in May (5.8 mg L^{-1}). The greatest differences between Bare and Bed in both TSS and chl-*a* (9.2 mg L^{-1} and 4.11 $\mu g\ L^{-1}$, respectively) were observed in June, coincident with the period of peak plant biomass. In addition, %POM exhibited the inverse pattern of TSS. In May, June, and August, organic material composed a significantly ($p<0.0001$ in all cases) greater fraction of suspended particles inside the plant bed compared to outside. In June and August, the bed's edge had an intermediate suspended organic fraction. Time-series of TSS and chl-*a* displayed a persistent pattern of high concentrations outside the bed, intermediate concentrations at the edge, and lowest concentrations inside the bed during June (Fig. 2.9). As a result of reduced suspended material within the plant bed, light passing through the water column increased during June, with representative K_d values of 0.88 m^{-1} inside the bed and 1.20 m^{-1} outside (Fig. 2.10). However, during June, overall light penetration within the plant stand was low (K_d = 3.21 m^{-1}) due to shading by the dense canopy.

Concentrations of water column nutrients followed different patterns for dissolved and particulate forms. Concentrations of dissolved inorganic species (NO_3^-, NH_4^+, and PO_4^{3-}) were generally consistent among stations each month (Table 2.2). Total dissolved nutrients (TDN and TDP) showed highest concentrations within the plant bed during June, though this relationship was only significant for TDN ($p<0.0001$). On the other hand, suspended particulate nutrients (PC, PN, and PP) in

June followed significant patterns similar to suspended solids (p=0.001, p=0.0009, and p=0.007, respectively). In August, the trend remained, but was only significant for PN (p=0.038). Measurements of pH from data sondes were used as a proxy for available dissolved inorganic carbon (DIC), and *S. pectinata* can directly uptake bicarbonate, though not as efficiently as other macrophytes (Sand-Jensen, 1983 cited in Kantrud, 1990). pH was elevated within the plant stand during May (data not available for June), with a mean (± SE) of 8.6 ± 0.02 as compared to 7.9 ± 0.003 measured outside the plant stand. The maximum pH measured was 9.6 at the Bed station as compared to 8.6 at the Bare station.

Accumulation of epiphytic material exhibited seasonal patterns paralleling those of total suspended material. In July and August, accumulated epiphytic material was significantly heavier at the Bare station as compared to Edge and Bed stations when measured by total dry weight (p=0.0002 and p<0.0001, respectively) and chlorophyll-*a* (p=0.003 and p<0.0001, respectively). In contrast, the mass of accumulated material did not differ among sites in May (Fig. 2.11). Additionally, the majority of epiphytic accumulation was composed of inorganic material during July and August regardless of station, while inorganic and organic fractions were nearly equal in May (Table 2.3). During every month sampled, relatively little of the accumulated material was algal in origin. Non-algal material (detrital and inorganic) exhibited the greatest accumulation rates during June, while May rates were the lowest with August rates intermediate.

Key sediment characteristics differed among stations during the months studied. Sediment wet bulk density (WBD) was significantly different in June (p<0.0001) and August (p=0.002) where sediment sampled from the vegetated edge had the highest values of WBD (1.82 g m^{-3} in June), and sediment within the plant bed had the lowest WBD during these months (1.68 g m^{-3} in June). In contrast, there were no significant differences among stations in May (Table 2.4). Organic matter content was also significantly higher in the plant bed (1.42% in June) than at the Bare or Edge stations in May (p=0.010), June (p<0.0001), and August (p=0.003). Finally, sediment chlorophyll-*a* content did not differ significantly among stations over any month. Although differences were not statistically significant, ^{234}Th activity was elevated compared to background activity on the bed's vegetated edge in August, but not at Bare or Bed stations (Table 2.5). No elevated ^{7}Be activity was detected, indicating that fluvial material was not recently deposited in this location. The relative error in this analysis, however, was large as only two cores from each station were used.

Porewater nutrient (NH_4^+ and PO_4^{3-}) concentrations were not significantly different among stations in May or August. During the period of peak biomass in June, NH_4^+concentrations were significantly elevated at the vegetated edge (462 μM) as compared to Bare (p=0.012) and PO_4^{3-}concentrations were elevated at stations within or near the plant bed (p=0.001) (Fig. 2.12). For both NH_4^+ and PO_4^{3-}, lowest concentrations were found at Bare (120 μM and 3.5 μM, respectively). Extremely high and variable concentrations of NH_4^+ (~2.6 mM) were measured at depth (20 cm) within at the bed's vegetated edge during June (Fig. 2.13). Although differences among stations were not significant at any depth, the vegetated edge showed the highest and most variable concentrations of any station.

Feedbacks Involving Low Oxygen and Sulfide

Lower dissolved oxygen concentrations were recorded near the sediment surface within the plant bed relative to outside the bed for nearly the entire deployment period in August 2008 (Fig. 2.14). Hypoxia (O_2<2.0 mg L^{-1}) was measured inside the plant bed during 2.8% of the deployment period (38 of 1337 observations), but only 0.3% of the deployment period outside the bed (4 of 1334 observations). This was the only deployment where instrumentation was available for measurements near the sediment surface at both stations as a comparison.

Porewater hydrogen sulfide concentrations were significantly elevated in the vegetated edge region during June (396 μM) and August (318 μM) ($p<0.0001$ for both), while no significant differences were measured in May (Fig. 2.15). This trend was most prominent in June, where concentrations at the Bed station were significantly elevated (183 μM) in addition to the Edge Veg station and the largest disparity between vegetated and unvegetated areas was observed.

Canopy Architecture Effects on Waves and TSS

A strong influence of the plant canopy on wave height during summer months contributed to differences in TSS within the plant bed. The distinct seasonal impact of the plant stand on TSS concentrations was evident in several significant linear regressions relating metrics of plant growth (aboveground biomass, longest shoot length, and shoot density) to differences in directly-measured TSS (Bare – Bed) over five different months (Fig 2.16).

During peak plant biomass, canopy effects on suspended particles were highly resilient to perturbation by wind. No significant differences were present among wind speed classes, and average %*TSSA* was ~60% (Fig. 2.17A). This relationship indicates that TSS inside the bed did increase during wind events; however, these increases were more modest (and less variable) compared to conditions outside the plant stand (Fig. 2.18). During May and August (period of less prominent plant canopy), significant differences were present in TSS inside the bed relative to outside at high wind speeds ($p=0.0002$ and $p<0.0001$, respectively). During May, TSS increased at the Bed station relative to the Bare station across the entire range of wind speeds below the threshold of 4 m s^{-1}, above which TSS concentrations inside the plant bed exceeded those outside (*%TSSA*<0). During August, wind speeds >2 m s^{-1} resulted in a linear decrease in %*TSSA*, but TSS concentrations inside the plant bed remained lower than those outside. However, comparison over the full range of wind speeds was not possible as high winds rarely occurred during the June study period.

Feedbacks involving suspended particles were also resilient to perturbation by water depth during June and August study periods. TSS inside the plant bed remained stable relative to outside the bed over the entire range of water depths (1 – 2 m) (Fig. 2.17B). In May, however, a significant trend ($p<0.03$) similar to that for wind speed was observed where %*TSSA* decreased linearly with increasing water depth. At water levels >1.8 m, TSS concentrations within the plant bed exceeded those outside. Wind speed and water depth were not significantly correlated over these time-series (Pearson correlation, $p=0.40$).

Discussion and Conclusions

Plant Bed Effects on Hydrodynamics

The presence of this *Stuckenia pectinata* bed had a clear impact on wave height, significantly reducing waves within the plant stand. Despite high wave energy during many points in each deployment ($H_s > 0.5$ m), the June plant canopy reduced wave height on average within the plant stand by ~44%. This result is identical to findings from studies on meadow-forming vegetation (Fonseca and Cahalan, 1992) but contrary to findings in canopy-forming kelp beds, which move as part of the water column rather than reducing wave energy (e.g., Elwany et al., 1995). The extent of wave attenuation observed was even more significant considering that water depth often exceeded shoot length, in contrast with previous studies where shoots occupied the entire water column (e.g., Fonseca and Cahalan, 1992).

Although we expected the plants to reduce tidal current velocities, this was not observed at the study site. Wave orbital velocities greatly exceeded tidal current velocities, indicating that site hydrodynamics were primarily dominated by waves (e.g., Koch and Gust, 1999). Reproductive shoots of *S. pectinata* are thin and cylindrical for most of their length, but become highly branched approaching the water's surface (Kantrud, 1990). Given this vertical structure, we expected to find higher current speeds in the lower portion of the water column where plant surface area was minimal (e.g., Verduin and Backhaus, 2000; van Keulen and Borowitzka, 2002). This flow intensification in the lower portion of the canopy was not observed, further indicating that plant interaction with tidal currents was likely minimal at the study site.

Observed Feedbacks and Mechanisms

Wave attenuation by the *S. pectinata* canopy contributed to alterations of several key processes within the plant bed, enhancing light and nutrient availability and modifying sediment properties affecting plant growth (Fig. 2.19). These feedback effects were most apparent during the period of peak plant biomass (June) and more intermittent during other months.

Light

Concentrations of TSS were significantly reduced inside the plant bed during peak biomass, resulting in increased light penetration through the water column. Similar Chesapeake Bay studies have noted the same trends and decreases in water column light attenuation coefficients within plant beds (Moore, 2004). Reduced resuspension of deposited material (e.g., Gacia and Duarte, 2001) due to wave attenuation by the plant bed likely played an important role in the observed patterns during this period of robust plant canopy. Although tidal current speeds were slow, suspended particles still entered the plant bed through advection (and diffusion) and may have subsequently been trapped (e.g., Ward et al., 1984). The resulting increase in water clarity may stimulate photosynthesis by relieving light limitation, which would be particularly important when SAV leaves are covered with epiphytic material. For a canopy-forming species, however, this feedback effect may be less important during the June period of peak plant biomass when the majority of plant photosynthetic tissue is located near the water's surface (Van der Bijl et. al., 1989). During critical periods of plant growth (e.g., May) when the plant canopy is less well-developed, clearer water may greatly enhance plant growth.

Patterns in epiphytic growth further modulated available light for plants. Gross, largely inorganic epiphytic accumulations measured outside the study site (Fig. 2.11) and patterns present in trapping rates (Table 2.3) highlight the importance of algal biofilms as collectors of suspended particles (e.g., Van Dijk, 1993). Algal biomass and associated "trapped" material (i.e. inorganic and organic detrital) were greatly reduced within the plant stand, increasing light reaching leaf surfaces. Large-scale spatial patterns of epiphyte accumulation related to plant stand characteristics differ widely in the literature. Some studies have found a negative correlation between epiphyte accumulation and canopy density (e.g., Schulte, 2003), while other studies have indicated no relationship (e.g., Johnson et al., 2005). Previous studies generally indicate little difference in epiphytic accumulation even at large scales (e.g., Moore and Fairweather, 2006), but typically neglect distance from the plant bed's edge. One preliminary study showed that accumulation did not differ with distance from the bed's edge (Saunders et al., 2003), which mirrors the findings of this study. There are many mechanisms potentially responsible for observations of reduced epiphytic accumulation within the plant bed including physical (propagule settlement reduction, thickening of the epiphytic diffusive boundary layer), competitive (shading by plants, nutrient limitation), and faunal (grazing by plant stand-associated fauna). However, an overall conclusion cannot be drawn about the mechanism behind this reduction in growth, which was likely the combined interaction of many factors. In summary, the presence of plants positively influenced light reaching leaf surfaces through reduction of TSS concentrations and epiphytic accumulation.

Nutrients

Based on measurements of plant tissue nutrients, this *S. pectinata* bed was not limited by nitrogen or phosphorus during this study (Gerloff and Krombholz, 1966), despite relatively low water column concentrations (van Wijk, 1989c). Although water column nutrient concentrations were constant across stations, it is difficult determine if wave attenuation had an impact on plant nutrient uptake (i.e., thickened leaf diffusive boundary layer) as nutrient cycling within the bed was likely more rapid than outside (e.g., Caffrey and Kemp, 1990). Sediment porewater is also a valuable source of NH_4^+ (e.g., Lee and Dunton, 1999) and PO_4^{3-} for aquatic macrophytes (Barko et la., 1991). Measurements of porewater nutrient concentrations from this study suggest that the accumulation and subsequent decomposition of particulate organic material within the bed greatly augmented these pools (e.g., Short, 1987), which has been observed in other canopy-forming beds from this estuary (Bartleson, 2004). Measurements of porewater pools did not take into account that plant uptake was likely large (e.g., Wigand et al., 2001), and therefore the contribution of trapped organic material decomposition to these pools may have been underrepresented.

Although this SAV stand was not limited by N or P, reduced water mixing within the plant stand may have contributed to dissolved inorganic carbon (DIC) limitation. Elevated pH measurements in May at the Bed station supported this concept. The maximum within-bed pH measured in this study (9.6) was slightly above the maximum measured (9.4) in another nearby canopy-forming plant bed (Bartleson, 2004). The extreme productivity of this plant bed may have resulted in DIC limitation, as *S. pectinata*'s does not utilize bicarbonate as readily as many other macrophytes (Sand-Jensen, 1983 cited in Kantrud, 1990), and carbonate and bicarbonate dominate the DIC species at these high pH values. Therefore, reduced mixing at leaf surfaces and quiescent conditions within the bed possibly had the deleterious effect of DIC limitation. In spite of this, the plant bed effectively accumulated a massive amount of above- and belowground biomass, indicating that DIC limitation did not majorly inhibit growth. In conclusion, while porewater nutrient pools were augmented by organic particle trapping and subsequent decomposition (forming a positive feedback), reduced turbulence within the plant bed may have resulted in minor DIC limitation during peak plant biomass.

Sediments

At the Bed station, sediment WBD was significantly lower than any other location. This, coupled with a larger proportion of sediment organic material, indicated that resuspension and transport of autochthonous material out of the plant bed was minimal during peak plant biomass (e.g., Gacia and Duarte, 2001) and that lighter allochthonous organic material may be deposited deep within the plant bed. Sediment organic content in this bed was on the lower end of what has been found in many healthy seagrass beds (Koch, 2001) and was additionally lower than is thought to be deleterious for this species (<26 mg C g^{-1} or ~2.6%) (van Wijck et al., 1992). Nevertheless, microbial decomposition of organic material resulted in elevated (>300 μM) concentrations of sediment porewater hydrogen sulfide in some vegetated areas (Fig. 2.15). Significantly elevated sulfide values in conjunction with station differences in sediment organic matter may indicate rapid turnover of organic material within the plant bed. Thresholds of sulfide toxicity vary by species and depend on ambient conditions, but concentrations >1 mM negatively impact seagrass growth in general (e.g., Koch, 2001). However, concentrations substantially less than this (~0.4 mM) have been shown to reduce photosynthesis, stressing plants (e.g., Goodman et al., 1995). In *S. pectinata*, sulfide levels >0.48 mg g^{-1} (~21 mM) are reported to reduce plant growth (van Wijck et al., 1992), but other harmful effects may occur at much lower levels. While sulfide concentrations approaching 750 μM were measured, they tended to occur towards to bottom of the root zone (20 cm), and did not persist from month to month (data not shown). Though elevated, porewater sulfide levels were not likely large enough to significantly reduce plant growth, though sulfide-associated stress may have occurred.

Rapid decomposition of organic material within the bed and reduced water mixing appeared to stimulate community respiration (e.g., D'Avanzo et al., 1996), leading to frequent but brief hypoxic events measured near the sediment surface in August (Fig. 2.14). Oxygen depletion has been measured in beds of floating-leaved macrophytes (e.g., Caraco and Cole, 2002; Goodwin et al., 2008) and is known to be deleterious to seagrasses (e.g., Holmer and Bondgaard, 2001). *S. pectinata* is tolerant of low oxygen conditions in freshwater systems, and anoxic sediment can even stimulate tuber germination (Dixon et al., 2006). While hypoxic events recorded in this study could have contributed to reduced plant growth, their duration was likely too short to cause lasting damage.

Controls on Feedback Development

Plant Canopy

Strong seasonal patterns in feedbacks due to the changing plant canopy were measured in this *S. pectinata* bed. Limited data have suggested that cylindrical seagrasses do little to reduce sediment movement (Fonseca and Fisher, 1986). Under the variable wave-dominated field conditions of this study, however, plant biomass and height of canopy (longest shoots) exerted strong control on patterns of suspended material within this plant stand (Fig. 2.16). The significant negative relationship between TSS reduction and shoot density was likely due to the high variability of shoot density over the year, seemingly out of sync with aboveground biomass production. Shoot density has been cited by many researchers as highly important in structuring water flow through plant stands (e.g., Gambi et al., 1990; Peterson et al., 2004; Hendriks et al., 2008; Widdows et al. 2008). However, results from this study indicate that for canopy-forming vegetation experiencing mainly oscillatory flow conditions, the effect of shoot density on feedbacks is overshadowed by the more prominent effects of canopy height and aboveground biomass.

One curious result was the relatively small impact this SAV bed had on suspended material during late May (Fig. 2.8, Fig. 2.16), despite a canopy architecture almost identical to June. Overall suspended material concentrations were much lower during May and were mainly organic in composition, which may partially explain this discrepancy. However, previous studies have shown that highly branched structures (i.e. reproductive shoots in June) are much more effective at trapping particles than cylindrical structures (i.e. vegetative shoots in May) (Harvey et al., 1995). Therefore, the sheer length of canopy-forming shoots may not be the only plant property impacting hydrodynamics As a consequence, seasonal impacts on suspended particle concentrations may be enhanced in species with multiple, alternating shoot types or prominent reproductive structures (e.g., Ackerman, 1997).

Canopy Effects: Resilience to Perturbation

The mitigating influence of plant beds on resuspension during high-energy storm events has long been known (Ward et al., 1984), and recent studies have focused on quantifying this economically important property of submersed plant beds (e.g., James and Barko, 1994 cited in Madsen et al., 2001; Granata et al., 2001). In the present study, *S. pectinata* effects on TSS attenuation were resilient to perturbation by high winds during the period of peak plant biomass (June). This suggests that the plant canopy effectively enhanced particle sinking and reduced shear stress at the sediment surface, minimizing associated sediment resuspension (Fig. 2.17A). During June, the slight (though not well-resolved) trend of increasing *%TSSA* with increasing wind speed suggests that low-turbidity conditions were maintained even during high winds within the plant bed. August measurements showed a pattern similar to those in late May, where the suspended material concentrations inside the plant bed gradually approached those outside with increasing wind speeds (>2 m s^{-1}). During the May period of lower biomass and shorter canopy, high winds resulted in more suspended material inside the bed as compared to outside. The source of this additional suspended material is likely autochthonous and previously-deposited organic particles as well as material trapped on plant leaves in algal epiphyte matrices. Sediment grain size within the plant bed may be finer, and thus more easily resuspended, resulting in an "under-estimation" of resilience to perturbation. These results are consistent with findings from freshwater canopy-forming species of similar biomass and morphology (James et al., 2004).

Water levels elevated above canopy height (>1.2 m) were expected to reduce the capacity of the plant canopy to attenuate wave energy, and result in higher input of suspended particles into the bed (e.g., Ward et al., 1984). Instead, variations in water level over the entire June and August time-series' had little impact on %*TSSA* (Fig. 2.17B). This result suggests that average-sized waves (~10 cm) are effectively attenuated at all observed water levels. During the more minimal-canopy period in late May (canopy height<90 cm), the pattern in %*TSSA* was similar to that of wind speed, indicating a combination of reduced capacity to attenuate waves and increased particulate inputs from overlying water at water depths greater than canopy height. Although water depth and wind speed were not highly correlated, there is a relationship between these two variables, and their complex interaction with submersed plant beds would benefit from further attention.

Feedbacks at the Plant Bed's Edge

While canopy effects on hydrodynamics and associated feedbacks were strong and consistent in the robust inner portion of the plant bed, conditions at the bed's edge were very different. Previous researchers have suggested that the edge of a seagrass bed is a dynamic region characterized by increased deposition of suspended particles (den Hartog, 1971 cited in Fonseca et al., 1982). At relatively coarse scales, numerical model simulations suggest that the seaward perimeter of submersed plant beds is an active site of sediment accumulation (Chen et al., 2007); however, scant evidence of particle trapping in natural bed edges exists in the literature. Over the course of this study, some interesting edge effects were observed that contribute to a whole-bed understanding of feedbacks.

The hydrodynamics at the plant bed's edge are thought to be complex and variable, but few measurements exist in natural systems. In August when wave gauges were available for deployment outside, at the edge of, and inside the *S. pectinata* bed (Fig. 2.2), weekly mean (± SD) significant wave heights were 0.14 ± 0.055 m, 0.16 ± 0.053 m, and 0.12 ± 0.044 m, respectively. While waves were attenuated within the plant bed as expected, wave heights were greatest at the edge of the bed (by ~2 cm). This phenomenon has been previously suggested based on a modeling study (Mendez et al., 1999) and observed in one other field study (Bradley and Houser, 2009). The proposed mechanism is that the leading edge of vegetation acts as an impenetrable "step" to waves, increasing wave heights and resulting in some wave reflection. Because water depth was slightly different between Bare and Edge stations, shoaling may have contributed to the observed pattern. However, using average water depths and wave height at the Bare station, expected wave height at the Edge station could be calculated using $\frac{1}{g} H_{s,Bare} \cdot c_{Bare} = \frac{1}{g} H_{s,Edge} \cdot c_{Edge}$, simplified to $H_{s,Edge} = H_{s,Bare} \cdot \left(\frac{h_{Bare}}{h_{Edge}} \right)^{\frac{1}{4}}$. Therefore, expected wave heights at the Edge station are 0.14 m, and shoaling only explains about one third of the observed 15% increase in wave height. It is likely that the effects of the June plant canopy on hydrodynamics at the bed's edge were even more pronounced, and further study of natural plant communities is necessary elucidate this phenomenon.

If wave momentum is immediately reduced at the bed's edge, large and heavy grains might be expected to fall out of suspension fairly quickly. Observations of fine-scale sediment properties in this study provide evidence for particle-trapping at the edge. Significantly higher WBD of surface sediments in vegetated patches of the bed's edge (Edge Veg) relative to the unvegetated area (Bare) (Table 2.4) suggests that deposition of larger suspended particulate material may be focused primarily in this patchy edge region. Although evidence is not conclusive, isotopic signatures also support this claim. The elevated ^{234}Th signature at the bed's edge suggests recent deposition of previously suspended sediments, while Bed and Bare stations do not show this same signature. Finally, despite the decrease in water column chl-*a* within the plant bed, the proportion of suspended organic material (relative to TSS) steadily increased with distance into the bed (e.g., Moore, 2004), further implicating the bed's edge as a zone of intense deposition of coarser-grain suspended particles.

Previous studies have shown that porewater ammonium pools increase along a transect moving from unvegetated regions to the densely-vegetated inner bed (Kenworthy et al., 1982), but the findings from this study contradicted this result. In contrast, we observed elevated (though highly variable) porewater nutrient and sulfide concentrations at the plant bed's vegetated edge (Edge Veg). The most striking example occurred for hydrogen sulfide in June and August (Fig. 2.15), where significantly higher concentrations were found in vegetated patches compared to adjacent unvegetated patches (Edge Non) and the plant bed (Bed). This result is even more surprising given that percent organic matter in edge sediments was lower than inside the plant bed. One possible explanation for these observations is that water clarity in the edge region tends to be lower than within the inner bed. Consequently, plants at the bed's edge might have lower photosynthetic rates, resulting in reduced porewater NH_4^+ uptake (Caffrey and Kemp, 1990) and less radial O_2 loss from roots to balance sulfide intrusion (Lee and Dunton, 2000; Holmer et al., 2005). While there may indeed be an impact of reduced light availability at the edge, concurrent measurements of water column light attenuation inside the bed (K_d=0.88 m^{-1}) and in the edge region (K_d=0.98 m^{-1}) along with measurements of suspended material suggest that light levels at the edge were not largely different from those inside the plant bed. Another explanation could be that during peak plant biomass in June, the majority of suspended particulate material is deposited at the bed's edge, and decomposition of organic components modifies porewater nutrient and sulfide pools. However, the mechanisms behind this observation are unclear and depend on the complicated balance between rates of plant uptake, nutrient cycling, and deposition.

These results indicate that the edge region (especially the seaward perimeter, though no measurements were made in this location), experiences water and sediment quality less favorable for plant growth than the dense inner region of the plant bed. Therefore, the edge region functions as a buffer, where hydrodynamic modification and subsequent water clarity improvement occurs during summer months, primarily benefitting the inner bed. The destruction of this edge region would likely impact the entire plant bed, reducing the ability of feedbacks to modify water quality.

Feedbacks and Habitat Quality

Feedback effects of the *S. pectinata* bed played a major role in modifying habitat conditions through a range of mechanisms, both positive and negative. Ultimately, continued growth and survival of this and other plant beds depend on the balance between positive and negative feedbacks. In this context, it is useful to compare quantitative data inside and outside the bed for key indices of habitat quality to ascertain whether submersed plants could survive under conditions existing outside the bed.

Mean TSS levels measured during June were elevated slightly above the maximum value (15 mg L^{-1}) associated with acceptable habitat for SAV in the mesohaline region of Chesapeake Bay (Dennison et al., 1993). This indicates that summer water clarity may have been insufficient to support bed survival in the absence of growth-promoting feedbacks. Furthermore, the reduction of epiphytic growth (and associated trapped particles) within the plant bed additionally modified light conditions. The light attenuation coefficient for epiphytic material could be calculated with $K_e = 0.07 + 0.32 \cdot \left(\frac{B_e}{B_{de}} \right)^{-0.88}$ where $B_{de} = \frac{gDWepi}{gDWSAV}$ and $B_e = \frac{mgchla}{gDWSAV}$ represent total epiphyte mass and algal mass, respectively. The percent of light passing through the water column is $PLW = e^{K_d * z} \cdot 100$ assuming a depth of 0.3 m (the average height of the water column over the upper plant canopy). The percent of light reaching the leaf surface is then $PLL = e^{K_e * B_{de}} \cdot PLW$ (Kemp et al., 2004). Using epiphyte accumulations and directly measured K_d from June, approximately 50% of incident light reached the leaf surface within the plant bed, as opposed to 0.6% for a plant growing outside the bed without the benefits of feedbacks. The light climate outside the bed was clearly not sufficient to support the growth of most submersed plants, which require at least 15% of incident light (Kemp et al., 2004) or even *S. pectinata*, which is fairly tolerant of low light conditions (~4%) (Bourne, 1932 cited in Howard-Williams and Liptrot, 1980). The largely non-algal composition of epiphytic accumulations measured outside the plant bed implies that TSS reduction within the stand not only increases water column light penetration, but also has the pronounced secondary effect of increasing light at the leaf surface.

In conclusion, this *Stuckenia pectinata* bed significantly reduced wave energy within the plant stand, which contributed to a substantial reduction in concentrations of suspended particulate material. Growth of algal epiphytes was also retarded during peak plant biomass, likely due to a combination of physical and competitive interactions. The interplay of suspended particles and algal epiphyte matrices was of great importance in regulating light reaching plant leaves. Trapping and subsequent decomposition of particulate organic material led to increases in pools of sediment porewater NH_4^+ and PO_4^{3-}, which augmented low water column nutrient concentrations and helped plants circumvent limitation. Autochthonous and allochthonous organic inputs to the bed also resulted in an accumulation of sediment porewater sulfide within the stand, but concentrations were not high enough to significantly reduce plant growth. Reduced mixing associated with wave attenuation resulted in low oxygen conditions within the plant stand, but hypoxic events were likely too intermittent to negatively impact plants. While DIC limitation was another probable outcome of reduced mixing within the plant bed, this stand managed to attain a robust canopy by June. Plant canopy impacts on hydrodynamics and TSS concentrations varied seasonally with canopy height and bed biomass, and were most resilient to perturbation during periods of peak plant biomass. Feedback effects also differed based on location within the plant stand; the bed’s edge region (an important buffer zone) experienced variable hydrodynamic conditions and a buildup of porewater NH_4^+ and sulfide. Positive feedbacks affecting light penetration resulted in vigorous plant growth which could not otherwise have occurred under the conditions of poor water clarity and heavy epiphytic growth that characterize this system.

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Tables

Table 2.1: Summary of physical measurements over the 2007 and 2008 periods of instrument deployment.

				Wind[&]			Wave height[+]	
Deployment	Dates	Salinity*	Temperature* (°C)	Direction (° true)	Mean Speed ($m\ s^{-1}$)	Max Speed ($m\ s^{-1}$)	Mean (m)	Max (m)
June/July 07	6/25/07 - 7/02/07	11.0 (0.07)	27.3 (1.27)	214 (24.6)	1.80 (0.752)	5.07	-	-
August 07	8/20/07 - 8/27/07	14.9 (0.20)	25.9 (1.68)	103 (25.9)	1.86 (0.787)	5.26	-	-
May 08	5/1/08 - 5/10/08	-	-	258 (21.4)	2.36 (1.110)	6.46	0.17 (0.091)	0.50
May/June 08	5/23/08 - 6/5/08	10.3 (0.29)	21.4 (1.64)	278 (23.3)	2.44 (0.982)	5.22	-	-
June/July 08	6/25/08 - 7/11/08	-	-	283 (22.2)	1.89 (0.895)	5.14	0.18 (0.087)	0.66
August08	8/8/08 - 8/22/08	11.5 (0.24)	26.5 (0.87)	331 (21.6)	2.20 (1.151)	5.40	0.14 (0.055)	0.36
September 08	9/5/08 - 9/11/08	-	-	151 (20.5)	2.53 (1.400)	8.19	0.16 (0.092)	0.59
October 08	10/16/08 - 10/23/08	17.8 (0.97)	17.3 (2.48)	22 (19.5)	2.63 (1.991)	8.65	0.18 (0.096)	0.47

All values are mean (SD).

*Based on measurements from the data sonde deployed at the Bare station.

[&] Measured at a long-term land-based station (Horn Point Weather Station).

[+] Measured by the pressure-sensing gauge deployed near the Bare station.

Table 2.2: Summary of water column dissolved and particulate nutrient concentrations from automated samplers at each station by month.

	May 2008			June 2007			August 2007		
	Bare	Edge	Bed	Bare	Edge	Bed	Bare	Edge	Bed
NO_3^-	-	-	-	0.26 (0.03)	0.59 (0.21)	0.28 (0.04)	-	-	-
NH_4^+	1.67 (0.12)	1.38 (0.08)	1.41 (0.10)	1.39 (0.36)	0.93 (0.14)	1.73 (0.25)	2.44 (0.21)	2.81 (0.22)	3.07 (0.23)
PO_4^{3-}	-	-	-	0.23 (0.03)	0.19 (0.03)	0.17 (0.02)	0.15 (0.01)^{ab}	0.19 (0.02)^{a}	0.13 (0.01)^{b}
TDN	-	-	-	23.91 (0.63)^{a}	25.75 (0.57)^{ab}	28.48 (0.69)^{b}	28.93 (0.84)	30.15 (0.69)	29.38 (0.98)
TDP	-	-	-	0.5 (0.02)	0.49 (0.02)	0.54 (0.04)	0.52 (0.05)	0.50 (0.05)	0.47 (0.05)
PC	-	-	-	120.68 (9.13)^{a}	87.07 (8.46)^{b}	69.82 (10.01)^{b}	113.00 (6.30)	89.98 (8.03)	88.26 (8.21)
PN	-	-	-	20.42 (1.28)^{a}	17.19 (1.30)^{ab}	13.16 (1.22)^{b}	16.89 (0.56)^{a}	14.08 (1.12)^{ab}	13.57 (1.08)^{b}
PP	0.35 (0.01)	0.39 (0.03)	0.31 (0.04)	0.92 (0.06)^{a}	0.80 (0.04)^{ab}	0.68 (0.05)^{b}	0.84 (0.04)	0.77 (0.04)	0.69 (0.06)

All values are means (SE).
Superscript letters indicate significant differences among stations within each month ($p<0.05$) and lack of letters indicate no significant difference.

Table 2.3: Estimates of epiphytic composition on artificial substrates at all three stations over summer months.

			Organic*				
Month	Station	Inorganic	Total	Algal[&]	Detrital	Non-Algal	Trapping rate[+]
May 2008	Bare	0.41 (0.10)	0.46 (0.088)	0.021 (0.0078)	0.44 (0.080)	0.85 (0.17)	0.085 (0.017)
	Edge	0.62 (0.42)	0.64 (0.31)	0.033 (0.0148)	0.61 (0.30)	1.23 (0.71)	0.12 (0.071)
	Bed	0	0.53 (0.055)	0.046 (0.0022)	0.49 (0.053)	0.49 (0.053)	0.049 (0.0053)
July 2007	Bare	54.04 (10.16)	5.25 (0.94)	0.28 (0.056)	4.97 (0.94)	59.01 (11.03)	9.83 (1.84)
	Edge	4.54 (0.42)	2.21 (0.31)	0.037 (0.013)	2.17 (0.31)	6.71 (0.19)	1.12 (0.031)
	Bed	2.88 (0.37)	1.49 (0.12)	0.021 (0.0019)	1.47 (0.12)	4.34 (0.48)	0.72 (0.081)
Aug 2007	Bare	40.05 (20.19)	3.34 (0.12)	0.15 (0.013)	3.18 (0.11)	43.23 (20.16)	6.18 (2.88)
	Edge	1.72 (0.33)	0.90 (0.12)	0.019 (0.0023)	0.88 (0.11)	2.60 (0.41)	0.37 (0.059)
	Bed	2.79 (1.02)	1.12 (0.24)	0.027 (0.0032)	1.10 (0.24)	3.89 (1.26)	0.56 (0.18)

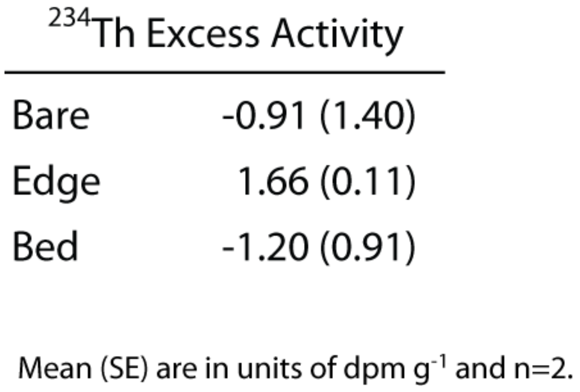
All units (except trapping rate) are accumulated masses in units of g DW m^{-2} artificial substrate.
*Estimated by loss on combustion.
[&] Estimated assuming C:chl-a ratio of 50:1 (Cloern et al., 1995).
[+] Rates (units of g DW m^{-2} d^{-1}) estimated using duration of deployment (7 d in June, 6 d in August, 10 d in May).

Table 2.4: Summary of sediment properties (wet bulk density, percent organic matter, and sediment chlorophyll-*a*) by month at each station.

		Bare	Edge Non	Edge Veg	Bed
May 2008 (3*)	WBD (g cm^{-3})	1.84 (1.77 - 1.90)	1.79 (1.69 - 1.88)	1.82 (1.72 - 1.93)	1.77 (1.61 - 1.94)
	Organic (%)	0.84 (0.64 - 1.03)^{ab}	0.65 (0.49 - 0.81)^{a}	0.72 (0.56 - 0.87)^{a}	1.10 (0.94 - 1.25)^{b}
	Chl-*a* (mg m^{-2})	-	-	-	-
June 2007 (6*)	WBD (g cm^{-3})	1.77 (1.74 - 1.81)^{a}	-	1.82 (1.79 - 1.85)^{b}	1.68 (1.64 - 1.72)^{c}
	Organic (%)	0.72 (0.66 - 0.77)^{a}	-	0.74 (0.66 - 0.81)^{a}	1.42 (1.27 - 1.57)^{b}
	Chl-*a* (mg m^{-2})	0.86 (0.37 - 2.09)	0.49 (0.16 - 0.83)	0.54 (0.13 - 0.95)	0.51 (0.36 - 0.65)
Aug 2007 (3*)	WBD (g cm^{-3})	1.87 (1.83 - 1.91)^{a}	-	1.88 (1.82 - 1.94)^{a}	1.69 (1.52 - 1.85)^{b}
	Organic (%)	0.90 (0.29 - 1.51)^{a}	-	0.76 (0.61 - 0.90)^{a}	1.52 (1.16 - 1.88)^{b}
	Chl-*a* (mg m^{-2})	0.67 (0.32 - 1.03)	-	0.46 (0.14 - 0.78)	0.52 (0.30 - 0.75)

*Indicates number of samples.
Values are means with 95% confidence intervals in parentheses.
Superscript letters denote significant differences ($p<0.05$) among sites within months and lack of letters indicates no significant difference

Table 2.5: Excess activity of ^{234}Th at the time of collection for each station in August 2007.



	^{234}Th Excess Activity
Bare	-0.91 (1.40)
Edge	1.66 (0.11)
Bed	-1.20 (0.91)

Mean (SE) are in units of dpm g^{-1} and n=2.

Figures

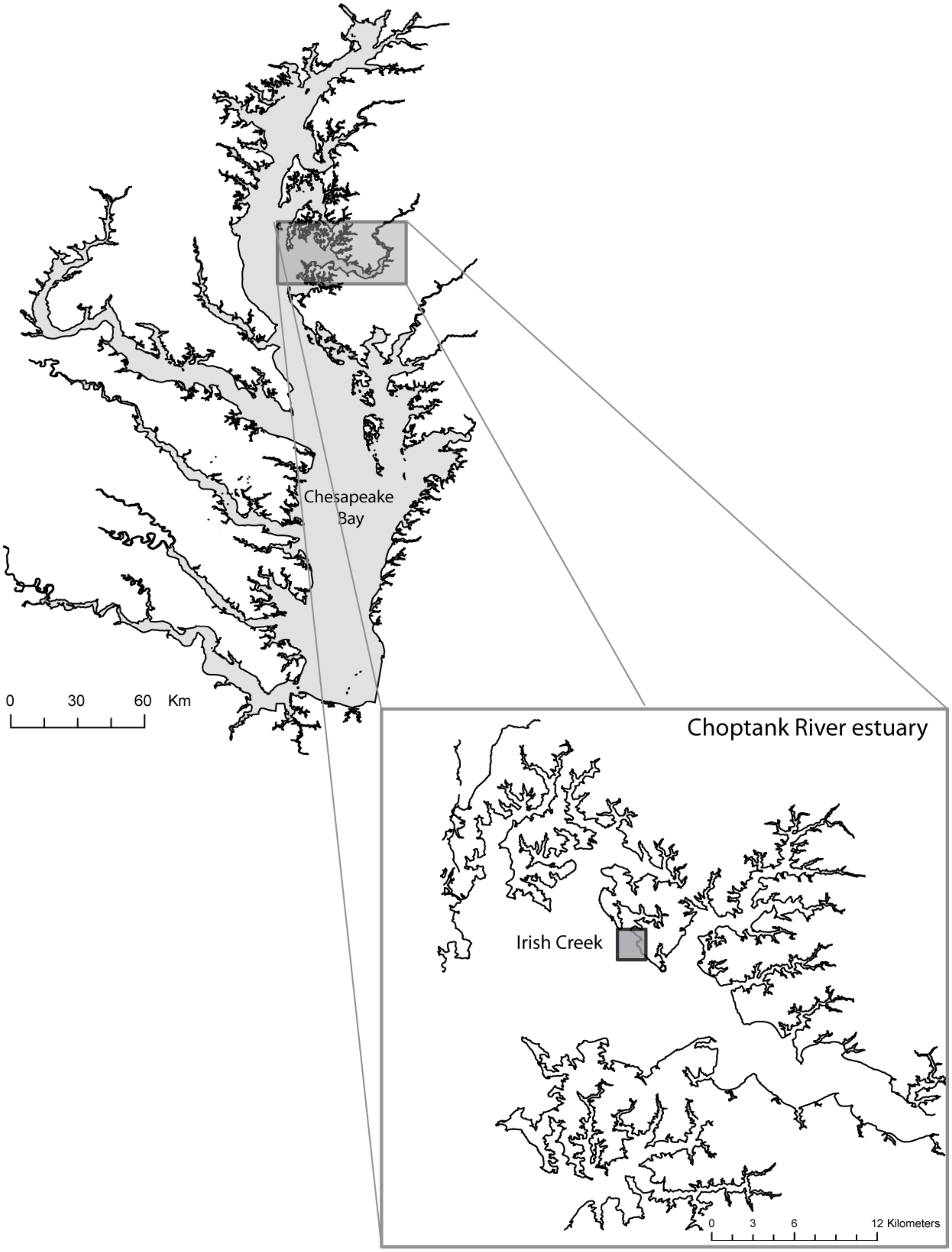


Figure 2.1: Location of the *Stuckenia pectinata* study site at the mouth of Irish Creek in the Choptank River estuary.

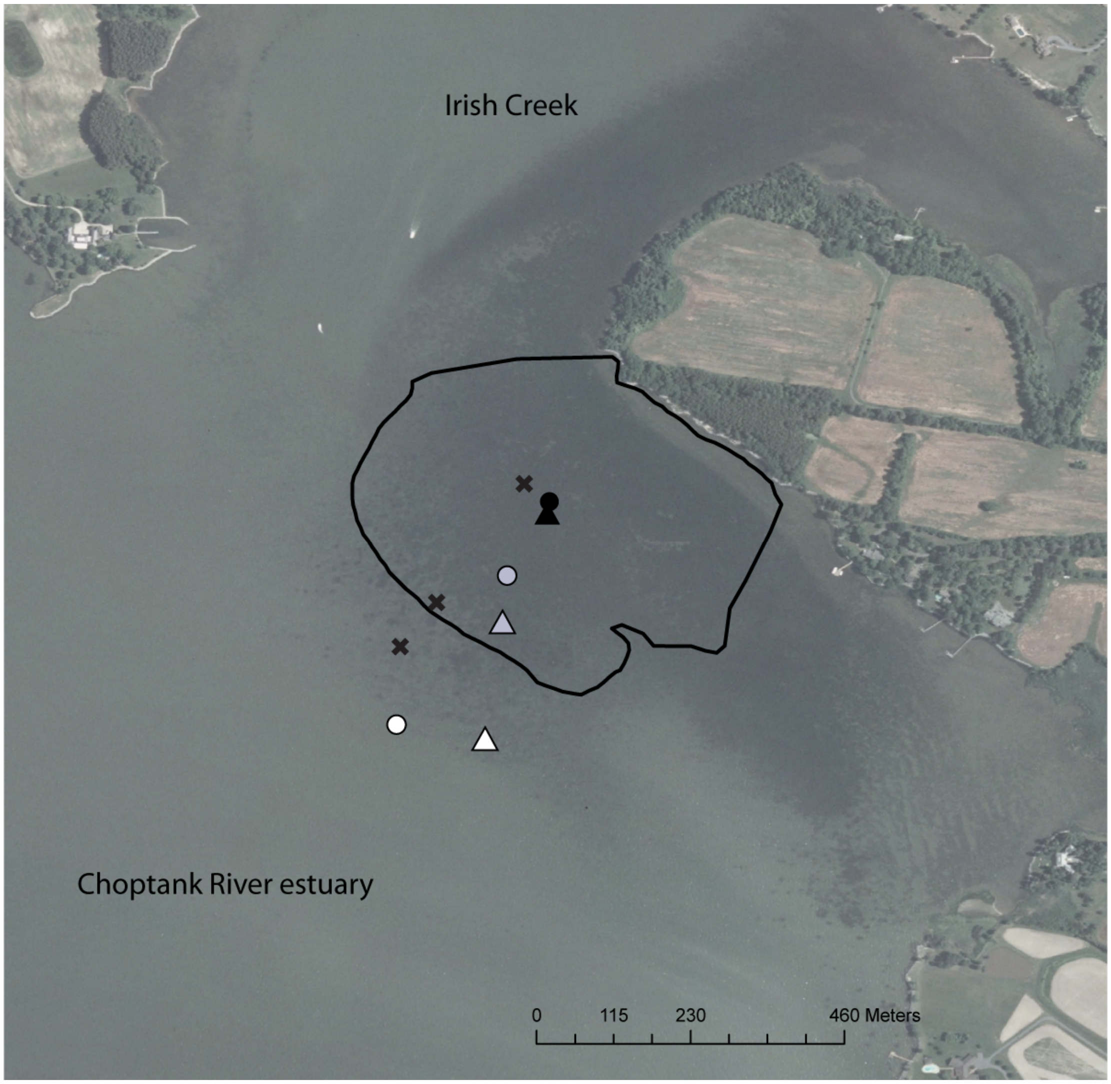


Figure 2.2: Sampling platform locations at the Irish Creek study site (plant bed outlined in black). Bed (black), Edge (grey), and Bare (white) stations are shown for 2007 (circles) and 2008 (triangles). The background aerial photograph was taken prior to 2007. Solid black X's indicate the locations of Bare, Edge, and Bed station wave gauges (when deployed) in 2008.

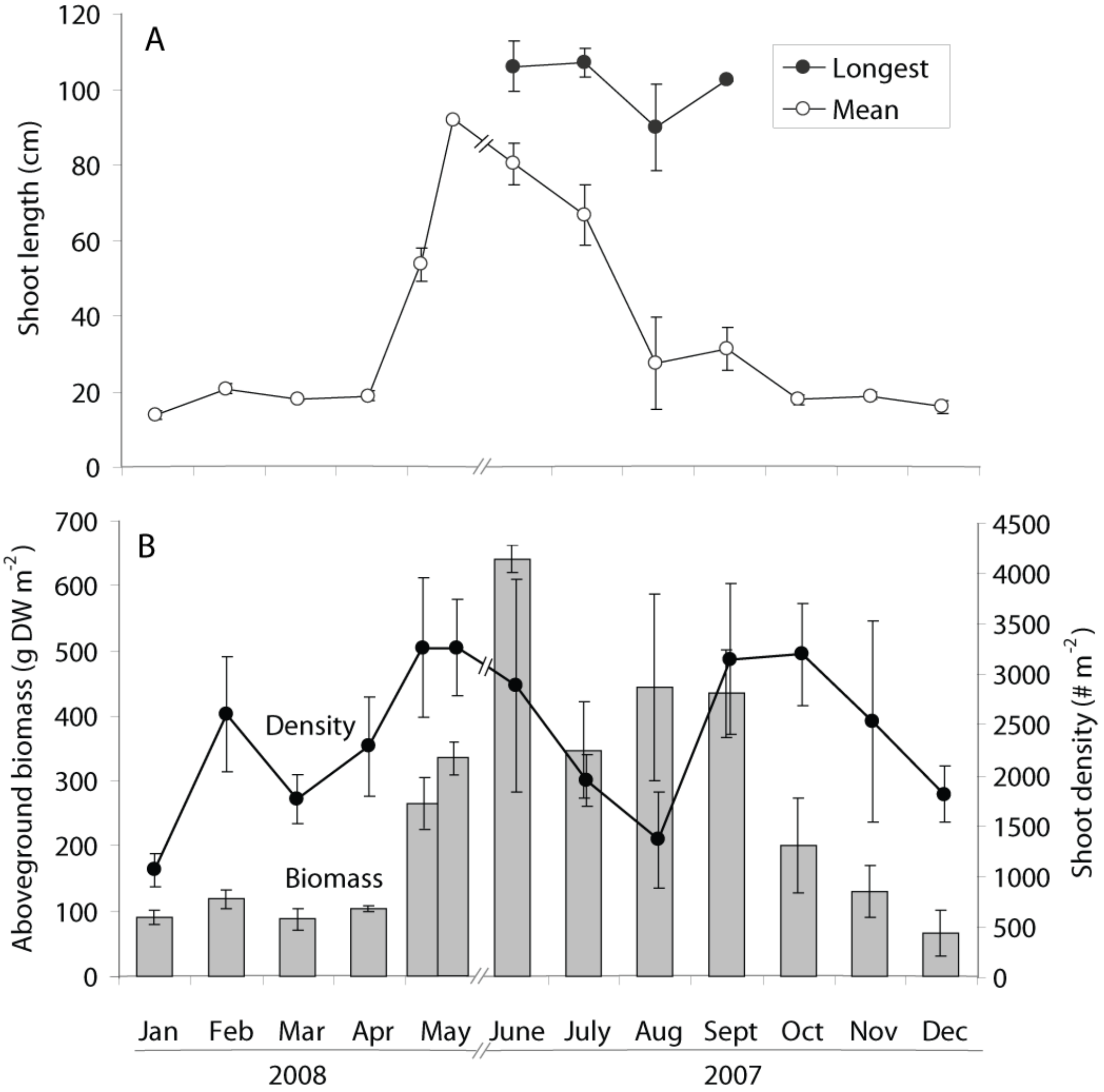


Figure. 2.3: Selected measures of canopy presence during the study period. Samples were taken monthly, except in May (two samples). All values are mean ± SE. Total mean (all shoots) and mean longest (reproductive shoots only) shoot lengths (A). Grayscale bars indicate aboveground live plant biomass, and points are shoot density with n=3 (B).

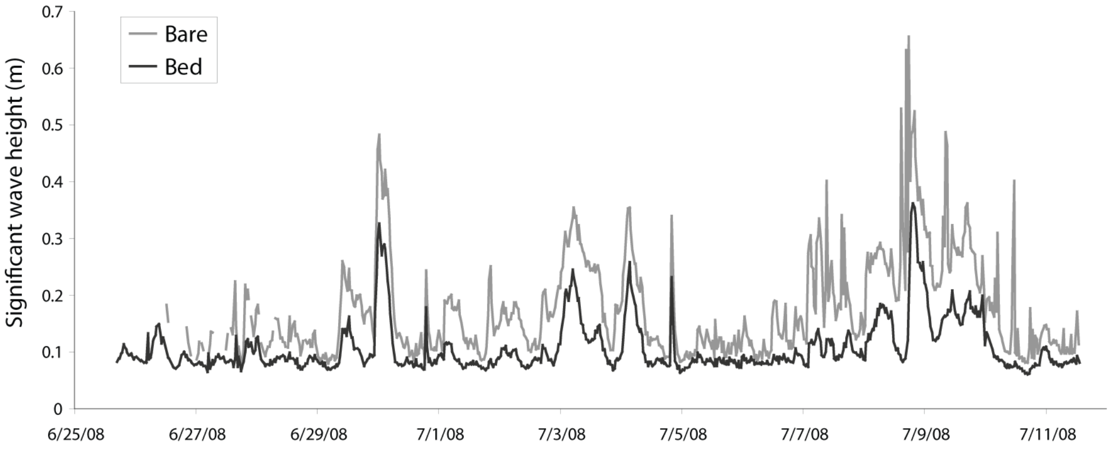


Figure 2.4: Significant wave height (m) inside (black) and outside (gray) the plant bed during June/July period of peak plant biomass.

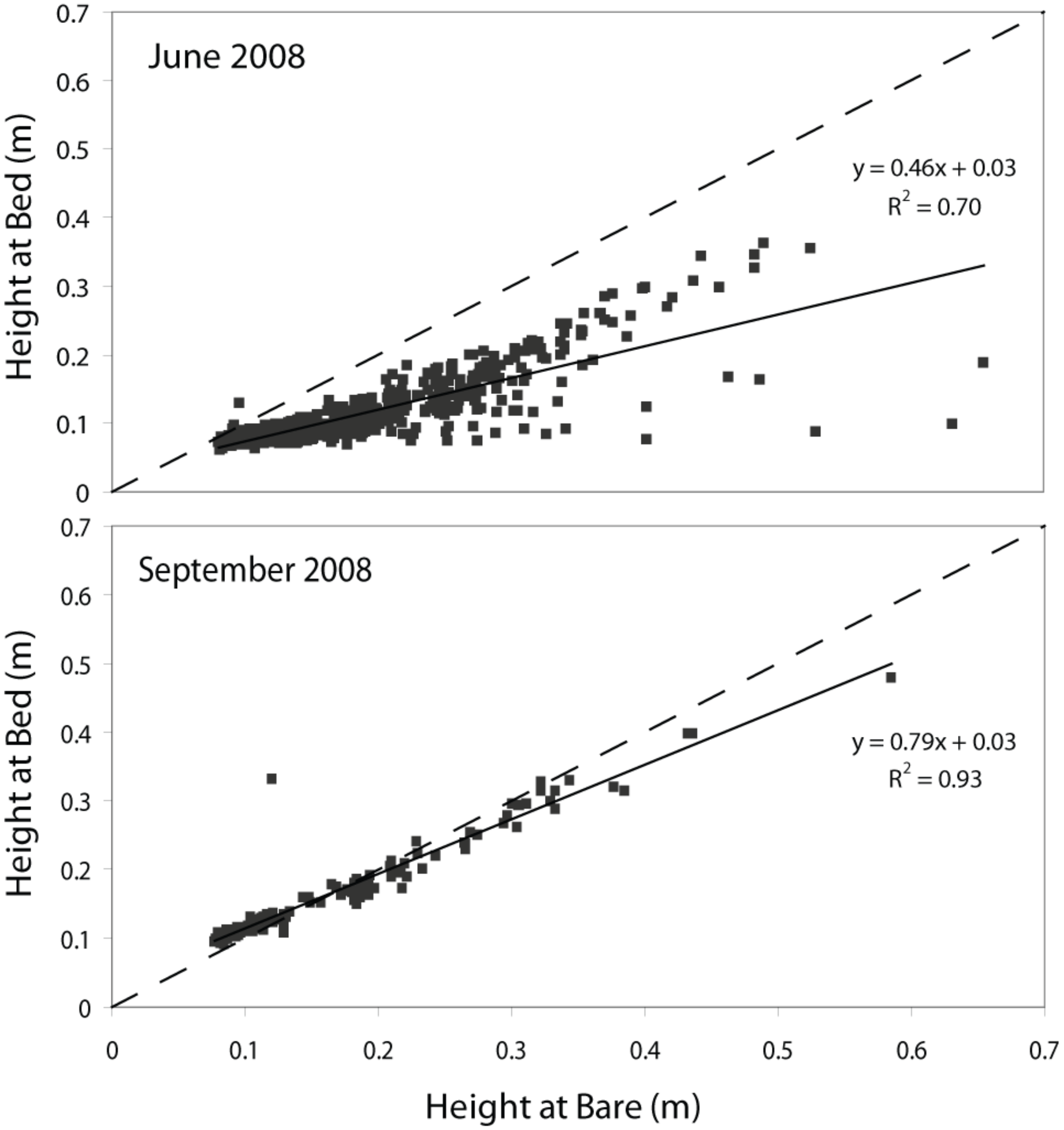


Figure 2.5: Wave attenuation by the plant canopy in June (peak plant biomass) and September (low plant canopy). Dashed lines represent a 1:1 relationship between Bare and Bed station measurements of significant wave height (m).

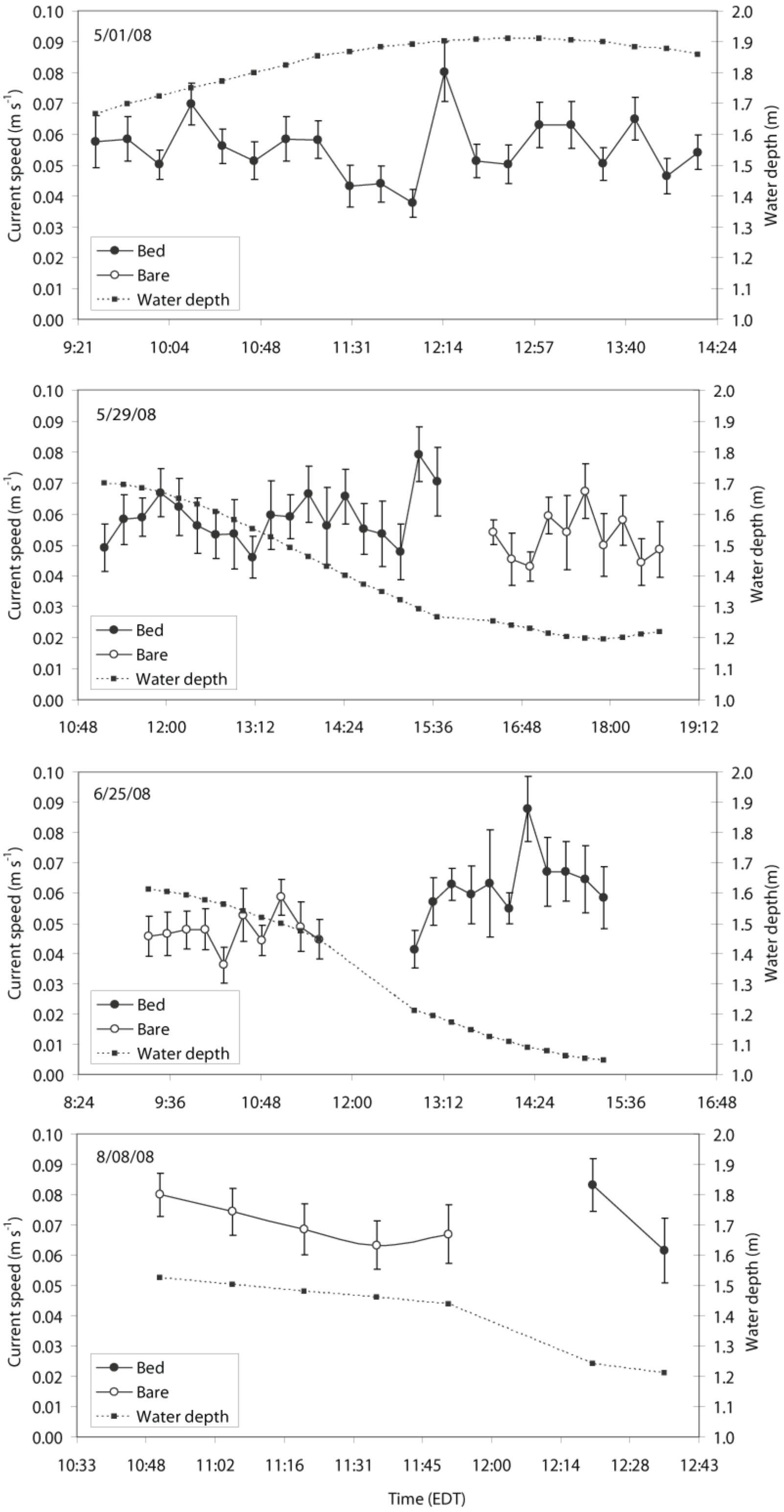


Figure 2.6: Time-series of depth-integrated tidal current speeds measured at Bed and Bare stations along with water depth over four ADCP instrument deployment periods. Error bars indicate standard error based on number of vertical measurements.

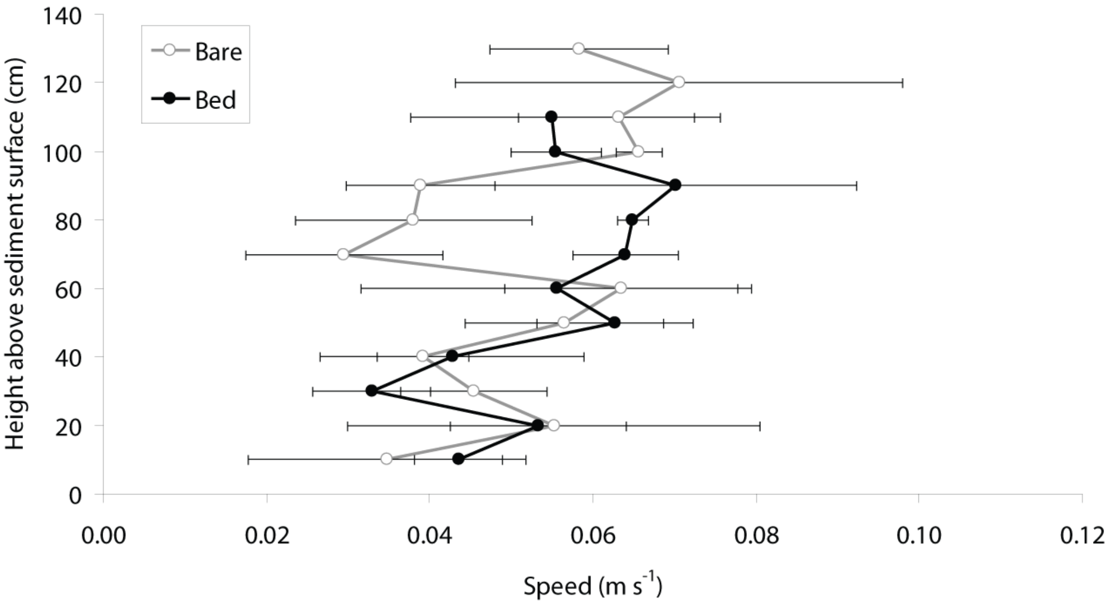


Figure 2.7: Representative vertical current profiles inside (black circles) and outside (white circles) the plant bed during a falling tide in June 2008 (peak plant biomass). Values are mean ± SE (n = 4).

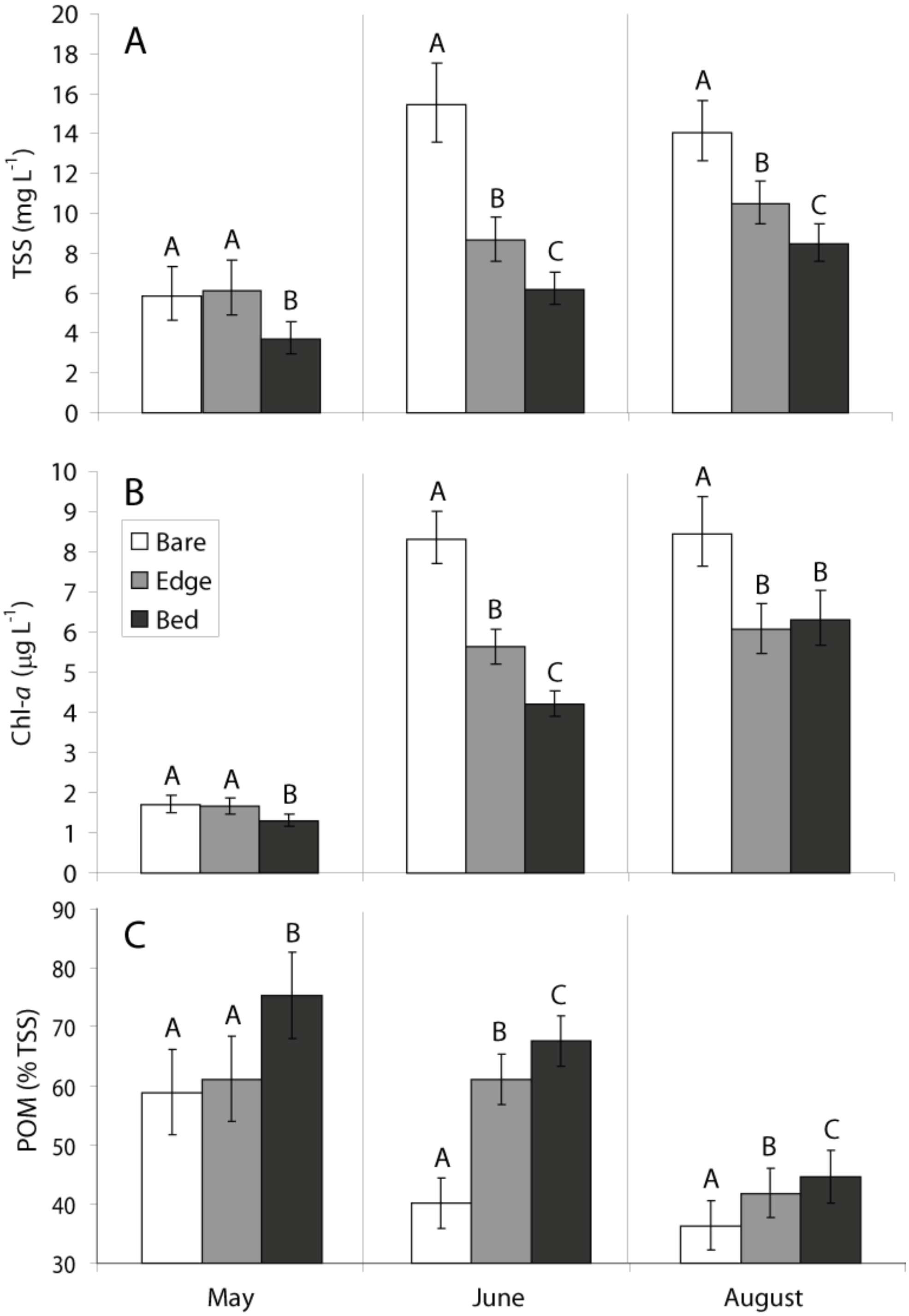


Figure 2.8: Weekly least-squared means of TSS (A) chl-*a* (B), and POM (C) collected with automated samplers from Bare (white), Edge (gray), and Bed (black) by month. Error bars indicate the 95% confidence intervals around means and letters indicate significant differences among stations within May (n=55), June (n=78), and August (n=42).

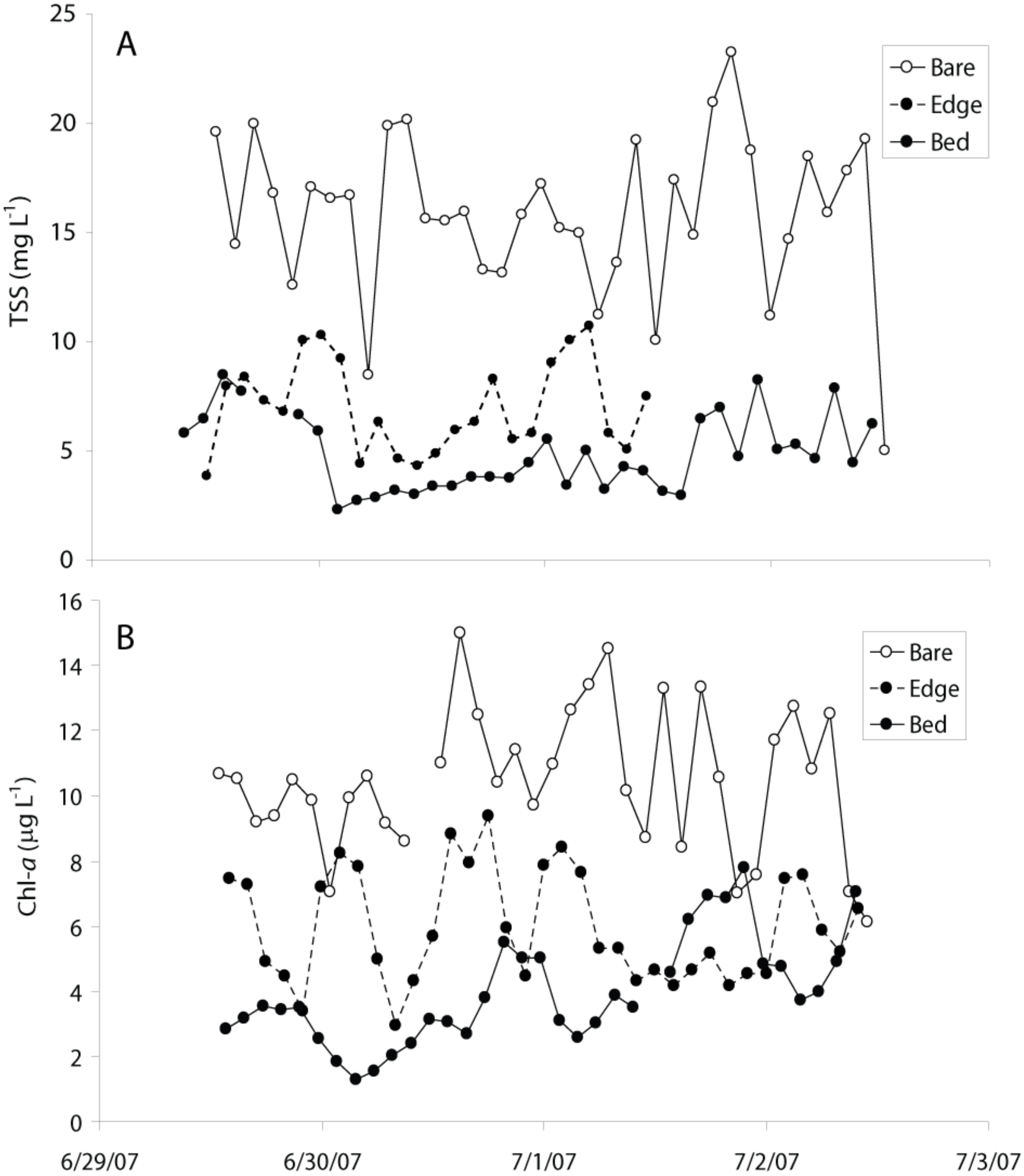


Figure 2.9: Time-series of TSS (A) and chl-*a* (B) concentrations measured with automated samplers at Bare (white), Edge (gray), and Bed (black) stations during June (period of peak plant biomass).

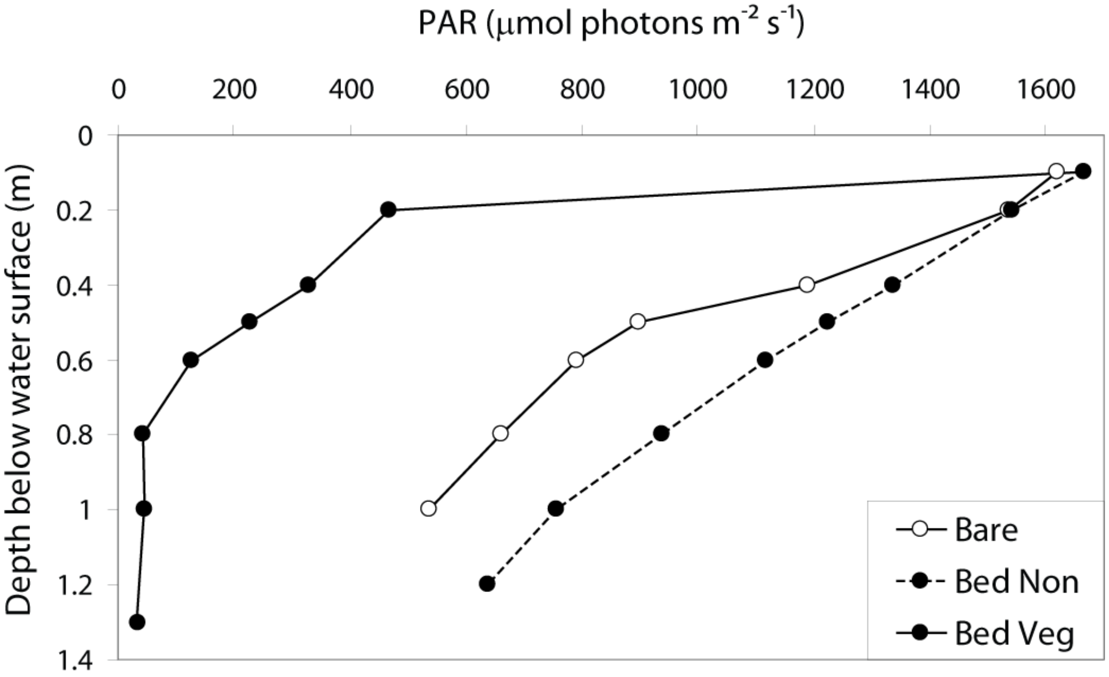


Figure 2.10: Concurrent vertical profiles of photosynthetically active radiation (PAR) measured outside the plant bed (Bare, K_d=1.20 m^{-1}), inside the plant bed (Bed Veg, K_d=3.21 m^{-1}), and in a de-vegetated patch within the bed (Bed Non, K_d=0.88 m^{-1}) during June.

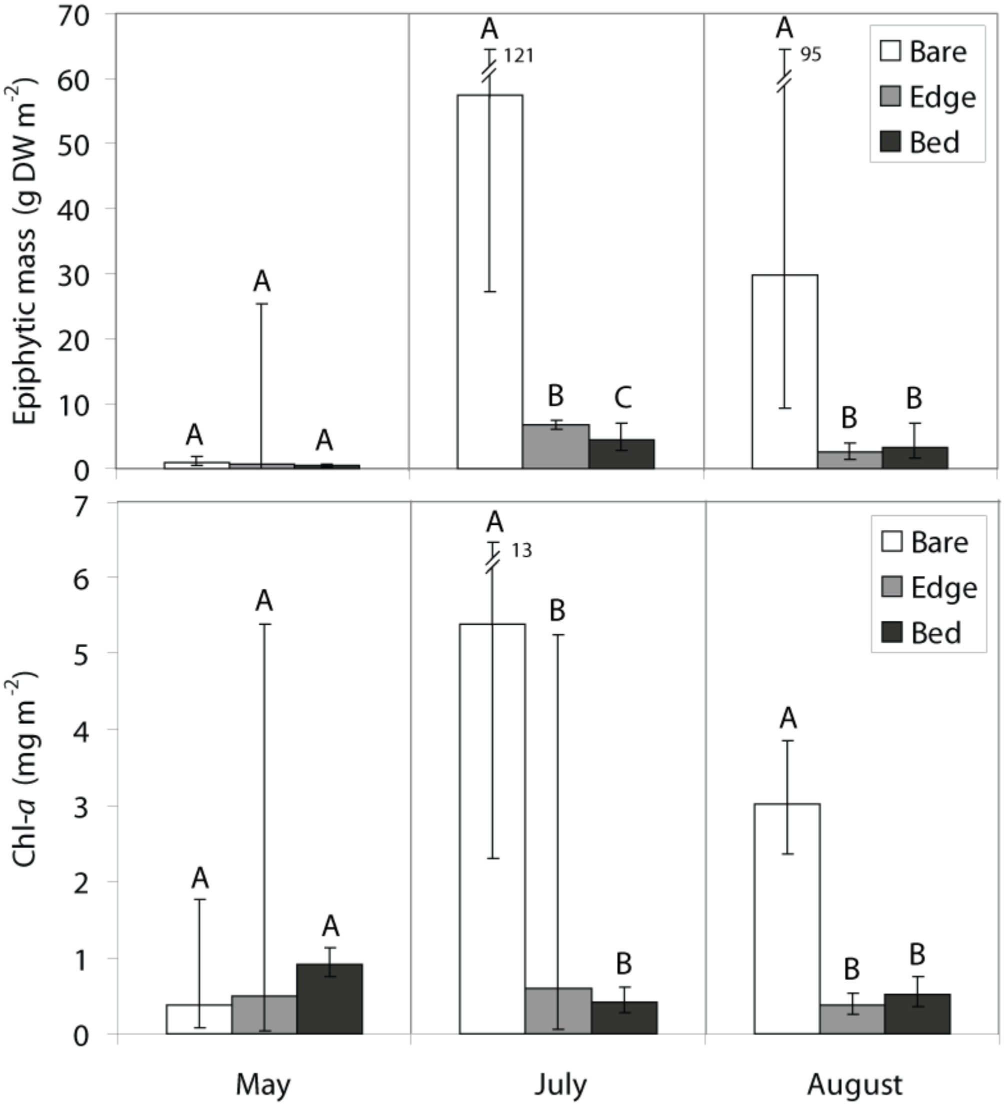


Figure 2.11: Accumulation of epiphytic material on artificial substrates measured in weight of dry material (top) and chl-*a* (bottom) per surface area during May (n=3), July (n=3), and August (n=5). Error bars indicate the 95% confidence interval around back-transformed means. Letters indicate significant differences among stations within each month.

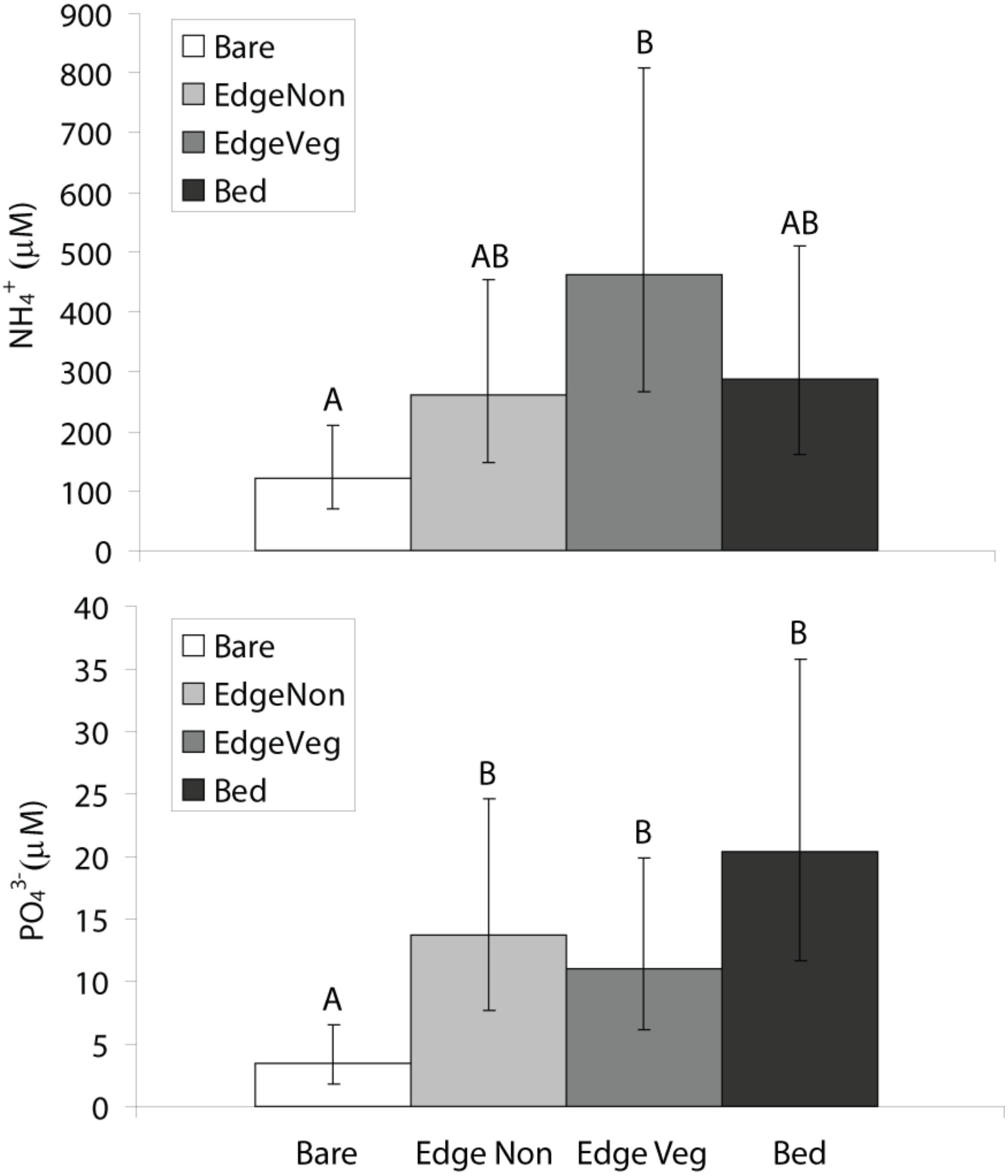


Figure 2.12: Depth-averaged (0 - 20 cm) porewater nutrient concentrations (NH_4^+, top; PO_4^{3-}, bottom) from porewater samplers (n=3) during peak plant biomass in June. Values are means with 95% confidence limits, and letters indicate significant differences among stations.

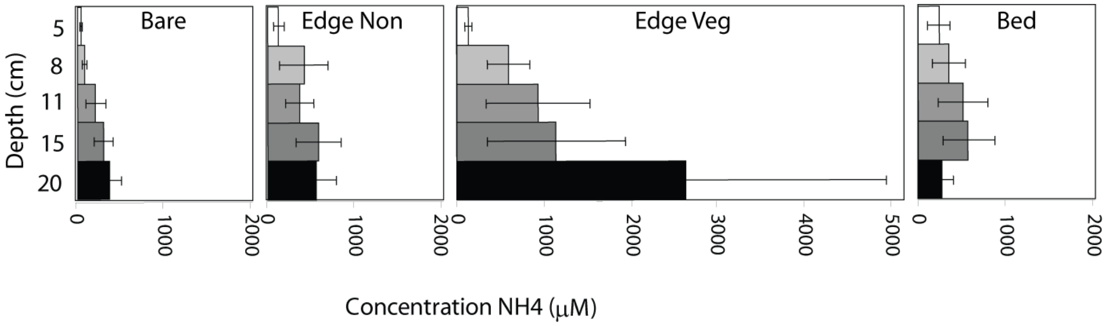


Figure 2.13: Vertical profiles of mean dissolved porewater NH_4^+ (μM) for all four stations at depth below sediment surface (cm) during June. Error bars indicate standard error. There were no significant differences among stations within depths.

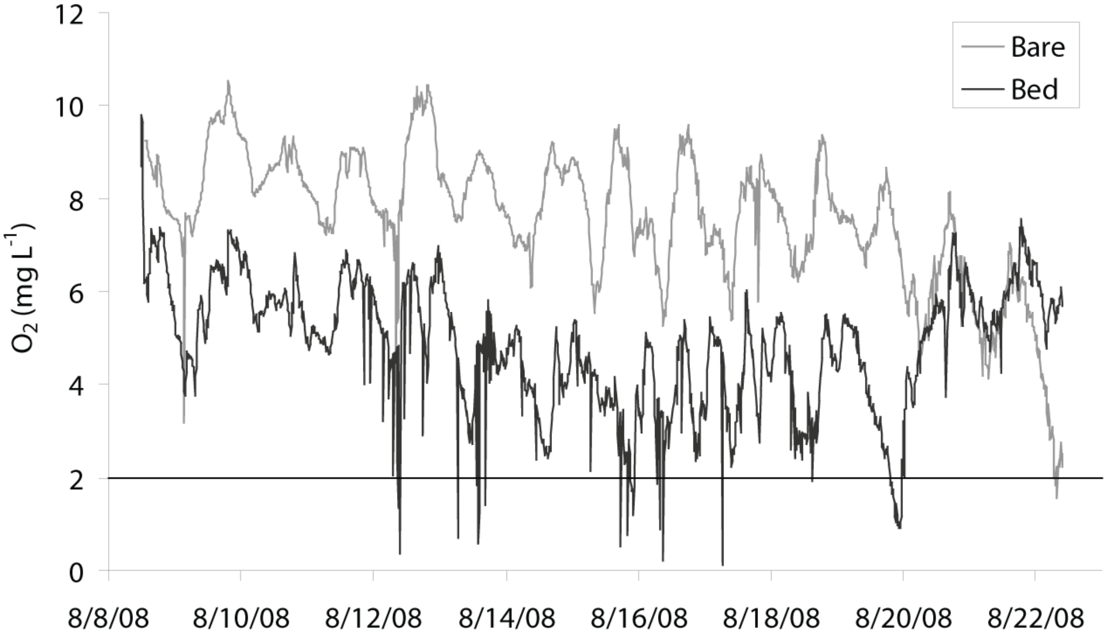


Figure 2.14: Time-series of dissolved oxygen concentrations measured by data sondes deployed during August near the sediment surface at Bare (light gray) and Bed (dark gray) stations. Concentrations below the black line (2.0 mg L^{-1}) are considered hypoxic.

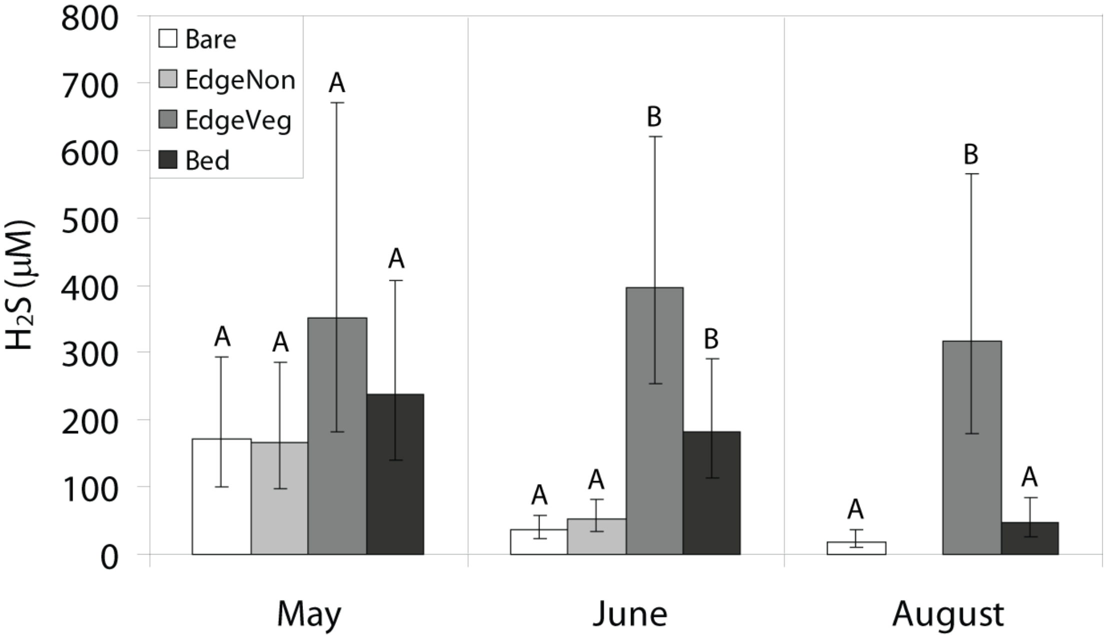


Figure 2.15: Depth-averaged (0 - 20 cm) sediment porewater sulfide concentrations (μM) from porewater samplers during all three deployments (n = 3). Values are least-squared means with 95% confidence limits, and letters indicate significant differences among stations within months.

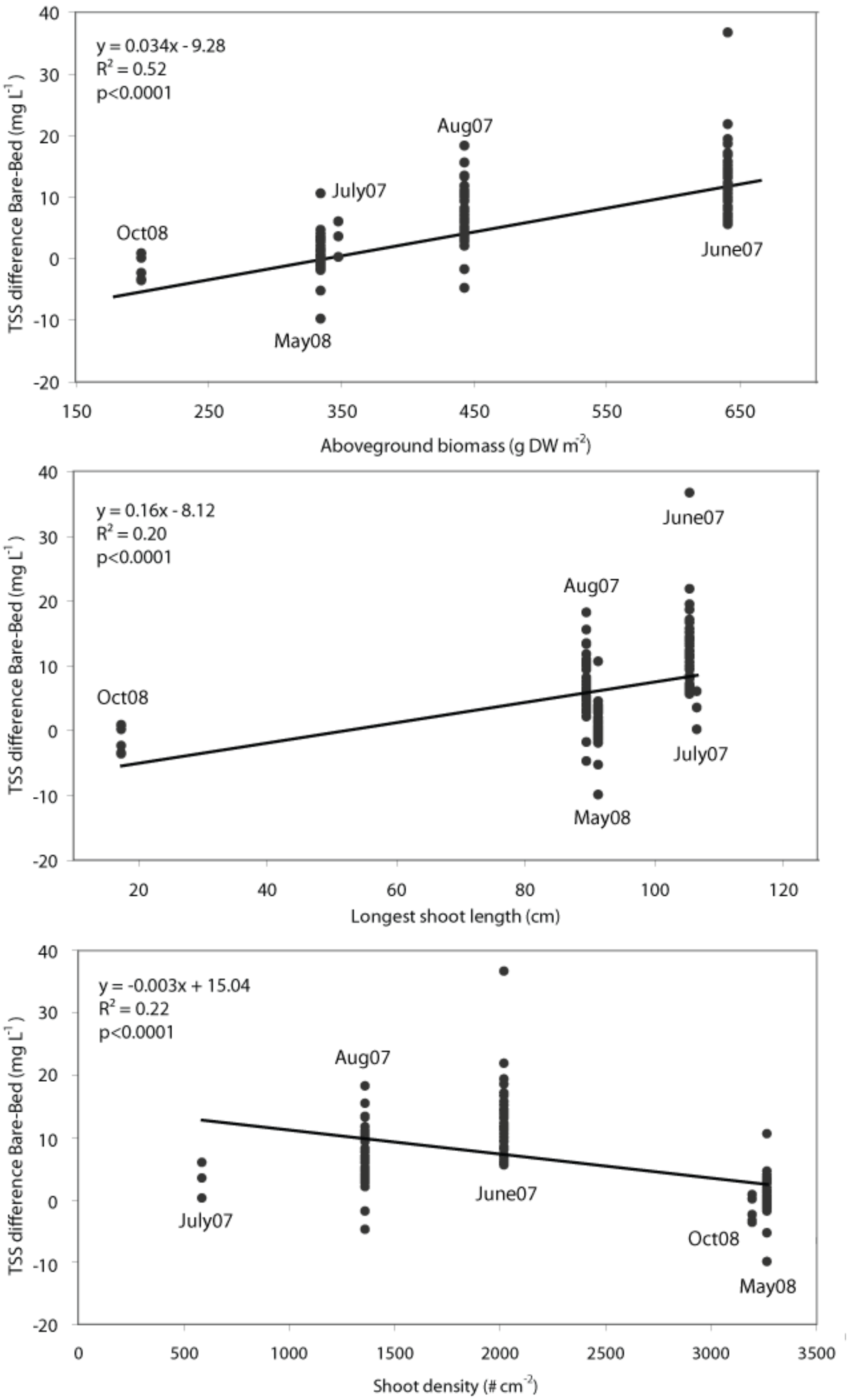


Figure 2.16: Linear regressions of difference in TSS concentrations (Bare-Bed) against metrics of plant presence (aboveground biomass, longest shoot length, and shoot density). TSS values were measured directly from concurrent samples taken by automated samplers (June, August, May) and by hand (July, October). Number of samples (n) differed each month (June=41, August=29, July=3, May=35, and October=6).

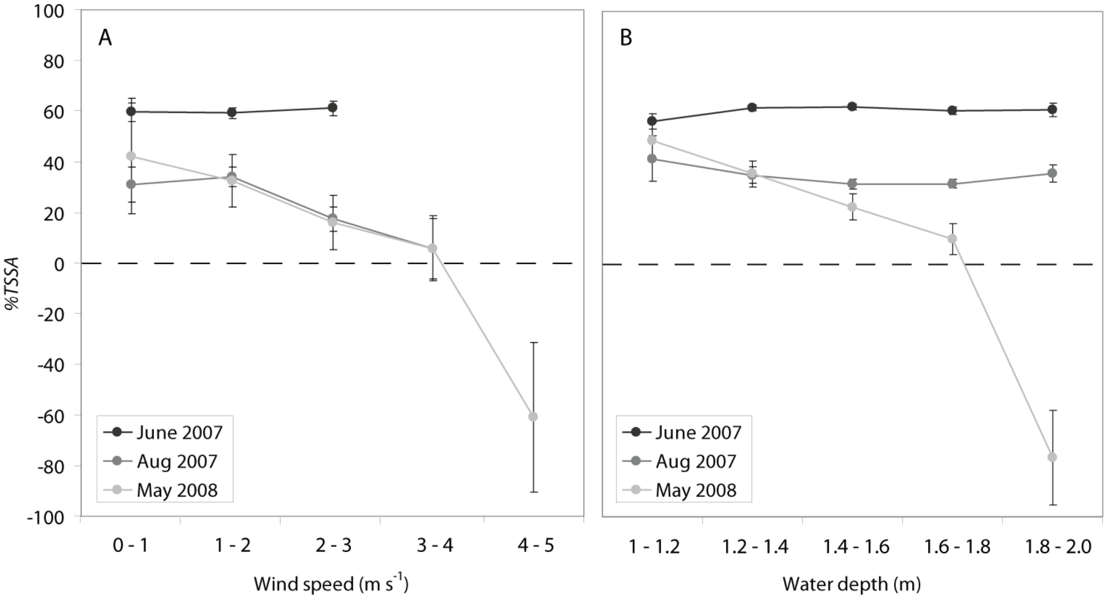


Figure 2.17: Resilience of feedbacks to perturbation by wind (A) and water depth (B) in June (black), August (gray), and May (light gray). %*TSSA*=100-TSSBed/TSSBare*100, where TSS values come from data sondes at Bare and Bed stations. Values are means and error bars represent 95% confidence limits. The dashed line at 0% represent TSS (Bare) = TSS (Bed). Wind data only includes measurements when wind direction was between 155 - 280 degrees, while water depth includes the entire TSS time-series.

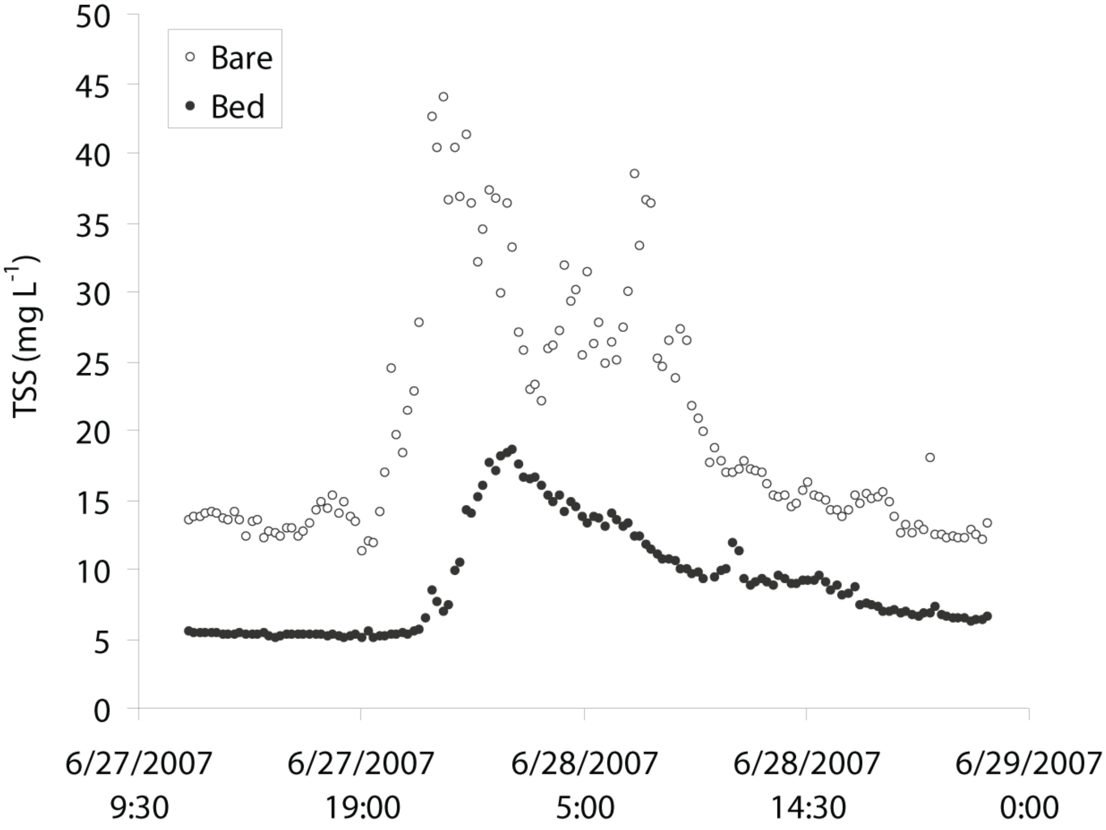


Figure 2.18: Example time-series illustrating a wind event during the June instrument deployment period. Values are converted TSS (mg L^{-1}) from Bare (white) and Bed (black) station data sondes.

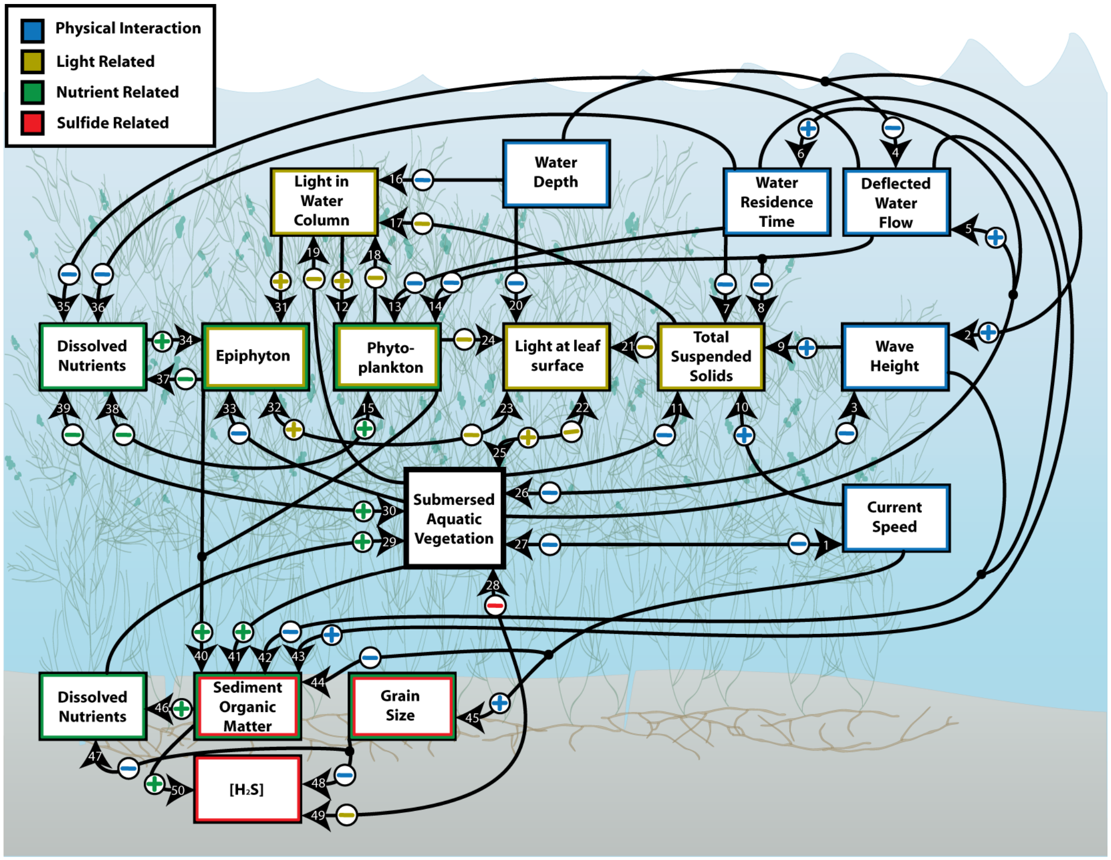


Figure 2.19: Conceptual diagram summarizing key feedback processes resulting from ecosystem engineering in a canopy-forming submersed plant bed. The growth of SAV is principally driven by factors associated with the availability of dissolved nutrients (green) and light (yellow) and by factors related to the accumulation of sediment organic matter and byproducts of decomposition (e.g., H_2S, red). Many of these factors are strongly influenced by feedbacks resulting from physical effects of plant bed friction on water flow (blue). Changes in a given variable tend to influence other variables (black arrows) in either positive (plus) or negative (minus) ways. The colors on the plus/minus symbols refer to which variables are involved in the feedback (i.e., nutrients, light, physical forces, H_2S levels). Supplement to Fig 2.19 summarizes all interactions.

Supplement to Fig. 2.19: Summary of key feedback processes resulting from ecosystem engineering in a canopy-forming submersed plant bed

Dense stands of SAV reduce current velocities (1) and wave heights (3) due to frictional drag from the plant canopy. Additionally, water flow is deflected around the plant stand (5) and water residence time within the stand increases (6). Deeper water (e.g., high tide) can work against wave attenuation (2) and water flow deflection (5) by decreasing the proportion of the water column occupied by SAV. Large waves (26) and fast currents (27) can directly constrain SAV growth.

As a result of flow modification TSS decreases within the plant stand due to decreased advection (8), particle settling (7), reduced resuspension (9, 10), and collisions with plant stems (11). Phytoplankton are also affected by flow modification directly (13, 14). A decrease in TSS and phytoplankton within the plant stand results in increased light penetration through the water column (17, 18), which increases light at the leaf surface (21, 24). Increased light penetration results in more available light for phytoplankton (12) and epiphyton (31, 32), varying with water depth (16, 20). Epiphyton also directly reduce light reaching leaf surfaces (23), which impacts SAV (25).

Dissolved water column nutrients, which improve growth of phytoplankton (15), epiphyton (34), and SAV (30), are affected by water flow modification. Less advection of dissolved nutrients into the bed (35) increases competition (36) between phytoplankton (13, 38), epiphyton (37), and SAV (39). SAV biomass increases competition for light in addition to nutrients, as leaves shade the water column (19) and other plants (22). However, denser SAV growth reduces epiphyte colonization through reduced advection of epiphyte propagules into the bed and mechanical removal through leaf rubbing (33).

Organic material accumulates within the plant bed due to algal and SAV biomass (40, 41) as well as allochthonous deposited material (42, 43, 44). This can reduce sediment grain size within the plant bed (45), which decreases sediment permeability (47, 48). Decomposing organic matter contributes to dissolved porewater nutrient pools (46), providing additional nutrients for SAV (29). However, phyto-toxic hydrogen sulfide can accumulate in sediment porewater (50), decreasing plant photosynthesis (28). Radial oxygen loss within the rhizosphere (49), which depends on photosynthetic rates, can balance sulfide intrusion into plant lacunae.

Chapter 3: Effects of canopy-forming submersed plant beds on spatial patterns of water clarity in a shallow coastal system

Abstract

This study describes how submersed plant beds influence spatial distributions of key water quality variables and how this influence is affected by the size and shape of the plant stand. A *Dataflow VI* flow-through water sampling system, providing fine-scale measurements along cruise tracks of a small boat, was used to investigate patterns in selected water quality variables (turbidity, chlorophyll-a, temperature, dissolved oxygen, and pH) across a robust stand of the canopy-forming submersed plant *Stuckenia pectinata*. Detailed maps of water quality were generated using spatial interpolation of measured variables via kriging. Within this relatively large and dense plant bed, water quality conditions were significantly altered during summer months of peak plant biomass. Turbidity in particular showed interesting patterns, with a striking decrease over the first 100 m inside the bed's perimeter, suggesting that the trapping of suspended particles was focused in this region. Plant bed effects on water clarity were then related to canopy height, shoot density, and cross-shore bed width by comparison among a suite of nearby beds dominated by the morphologically similar species, *Ruppia maritima*. Wide and dense stands with tall canopies showed significantly reduced turbidity and increased light penetration, while narrow and sparse stands with low canopies often showed elevated turbidity compared to conditions outside the stand. These results suggest that minimum bed size for significant improvement of water quality within the plant stand varies with

shoot density, providing tentative restoration guidelines for minimum size and density needed for self-sustaining plant beds.

Introduction

Seagrasses and other submersed aquatic vegetation (SAV) form globally important communities which have been recognized as providing many significant ecosystem services (Costanza et al., 1997). SAV beds represent valuable coastal habitats that provide food and refugia for a variety of commercially important benthic and pelagic animals (e.g., Lubbers et al., 1990; Hemminga and Duarte, 2000; Seitz et al., 2005). Many coastal waters worldwide, including large ecosystems like Chesapeake Bay, have unfortunately experienced degraded water clarity due to increased anthropogenic loading of sediment and nutrients (Kemp et al., 2005). In Chesapeake Bay and other shallow coastal ecosystems, decreased light penetration due to suspended sediment and algal biomass as well as overgrowth of epiphytes on leaf surfaces have led to large-scale declines in submersed plants during recent decades (Kemp et al., 1983; Duarte, 1995).

Though many different submersed plant species have historically occurred in Chesapeake Bay (Stevenson and Confer, 1978), some of the most striking are the canopy-formers, which produce meter-long vertical shoots that are often visible at the water surface. Many of these canopy-forming SAV species are important food sources, particularly for waterfowl, which graze on plant leaves, inflorescences, rhizomes, and tubers (Perry et al., 2007). Two important canopy-forming SAV species in Chesapeake Bay are *Ruppia maritima* and *Stuckenia pectinata*, the former of which continues to be widely distributed and the latter of which has a more limited geographic distribution in the estuary (Moore et al., 2000; Orth et al., 2009). These species are characterized by their seasonally contrasting growth forms with tall (>100 cm) flowering reproductive shoots in mid-summer and shorter (30-40 cm) vegetative shoots during the remainder of the growing season (Kantrud, 1990; Silberhorn et al., 1996).

Although highly sensitive to poor water clarity, submersed plants modify water flow substantially within the plant stand, resulting in positive feedbacks that can improve local habitat quality (Koch, 2001; de Boer, 2007). The ability of these plants to attenuate waves and currents depends on the architecture of the stand, including shoot density, canopy height, and plant bed size and shape. High shoot density has been shown to retard water flux into and through the bed due to increased friction associated with plant biomass (e.g., Peterson et al., 2004; Hendriks et al., 2008). In comparison with meadow-forming species, canopy-forming SAV are particularly effective in attenuating wave and current energy (Fonseca and Cahalan, 1992; Verduin and Backhaus, 2000). The plant canopy’s ability to retard water flow increases sharply as shoot height approaches the water surface (Nepf and Vivoni, 2000), in contrast to the stronger “skimming flows” that occur over meadow-forming SAV beds (Koch and Gust, 1999; Widdows et al., 2008). Plant bed size and shape are likely to be important characteristics that control water flow within stands; however, their influence has not been explicitly quantified (e.g., Fonseca and Koehl, 2006). Because distance travelled into a meadow results in progressive extraction of fluid momentum by plant interaction (Gambi et al., 1990), wider plant beds would be expected to have a greater effect on water flow modification.

Modification of water flow by plant beds reduces turbidity through increased sinking of suspended particles (Palmer et al., 2004; Huang et al., 2008), direct adhesion to plant leaves (Agawin and Duarte, 2002; Hendriks et al., 2008) and reduced resuspension (Fonseca and Fisher, 1986; Gacia and Duarte, 2001). This has the effect of increasing water clarity within the plant stand, resulting in improved habitat quality relative to outside conditions (e.g., Ward et al., 1984; Moore, 2004). Increased light penetration within plant beds is expected to result when canopy architecture has a large impact on water flow (e.g., Vermaat et al., 2000).

Although considerable attention has been paid to SAV in Chesapeake Bay (e.g., Orth et al., 2002), feedbacks have not been incorporated into management and restoration strategies. The use of ecosystem-modifying species as cost-effective and sustainable restoration solutions has recently been emphasized in the theoretical literature (Byers et al., 2006), and the spatial arrangement of plants in aquatic environments is gaining recognition as an important consideration for ecosystem management (Halpern et al., 2007). For example, submersed plant bed characteristics that result in decreased turbidity and increased light penetration could be considered in establishing minimum stem density and bed size needed for restoration of plant species with different canopy architectures.

The majority of research on quantifying impacts of shoot density, canopy height, and bed size on water flow and clarity has been done using flumes and models (e.g., Verduin and Backhaus, 2000; Abdelrhman, 2003) or cylindrical mimics in place of live plants (e.g., Nepf, 1999; Bouma et al., 2007) and has considered these attributes of plant beds singly as opposed to in concert. Little work has focused on attributes that regulate the tendency of SAV beds to modify local water clarity in natural systems, despite implications for management and restoration of these important systems. Thus, the goals of this study were: (1) to describe spatial patterns in water clarity associated with a Chesapeake Bay bed of the canopy-forming SAV species, *Stuckenia pectinata*; and (2) to compare feedbacks associated with water clarity over a range of SAV beds dominated by *S. pectinata* or *R. maritima* with various canopy heights, shoot densities, and sizes. This study addresses the hypothesis that taller canopies, denser plant stands, and larger beds have the greatest impact on concentrations of suspended material and thus higher light penetration within the plant stand.

Methods

Study Sites

This study took place in the Choptank River estuary during summers of 2007 and 2008. In 2008, the Honga River estuary was included to increase the number of study sites. Both systems are Maryland tributaries on the eastern shore of Chesapeake Bay, located approximately 85 and 140 km from the Bay mouth, respectively (Fig. 3.1). SAV beds in this study were dominated by one of two species, *Ruppia maritima* or *Stuckenia pectinata*, both of which are canopy-forming plants of similar morphology (Stevenson and Confer, 1978). SAV beds dominated by

R. maritima tend to be more ephemeral than *S. pectinata* stands, with large year-to-year variability (e.g., Silberhorn et al., 1996).

Plant beds examined in this study were initially located using maps of SAV cover from the previous year created as part of the Chesapeake Bay Monitoring Program's SAV aerial mapping (http://web.vims.edu/bio/sav/) conducted by the Virginia Institute of Marine Science (VIMS). Reconnaissance surveys of candidate sites, which were conducted by boat during June, consisted of a visual assessment of canopy height and crown density. Two canopy height groups were defined for plant beds based on reproductive status. Stands were either "vegetative", with shoot lengths between 20 and 50 cm, or "reproductive", with flowering shoots that often reached the water surface (lengths of 60–100 cm). Crown density categories were based on the VIMS SAV scale (e.g., Orth et al., 2009): 1 (<10% coverage), 2 (10-40% coverage), 3 (40-70% coverage), or 4 (70-100% coverage). If the presence of SAV could not be determined during boat surveys due to poor water clarity, a long-handled garden rake was used to collect representative shoots (which were usually vegetative).

Six beds were surveyed in the Choptank in 2007, and only three of these returned in 2008 (Fig. 3.2A). In 2008 we chose three additional Choptank beds and five beds from the Honga (Fig. 3.2B), totaling 15 study locations. All beds surveyed were dominated by *R. maritimia* with the exception of Bridge Creek, which was a mix of the two species, and Irish Creek, which was dominated by *S. pectinata*. Different plant beds varied in size, density, and canopy height, but it was not possible to sample every combination of these factors, as bed selection was severely limited by poor water clarity in both years.

***Dataflow* mapping**

A *Dataflow VI* system (Madden and Day, 1992; Lane et al., 2007) was used to conduct fine-scale surface-water mapping of selected water quality variables from a small outboard motor boat for areas within and surrounding submersed plant beds. The underway sampling system consisted of an overboard PVC water intake located 0.6 m beneath the water's surface, through which water was drawn with a submersible pump. Water then flowed through plastic tubing and was sampled by a data sonde (Yellow Springs Instruments, Inc., Model 6600) equipped with a series of sensors for turbidity (model 6136), chlorophyll (model 6025), dissolved oxygen (model 6562), conductivity/temperature (6560), and pH (model 6561), all programmed to record every four seconds. A GPS unit (Garmin 178C Sounder) and portable computer (Panasonic Toughbook) running *Dataflow* software recorded the GPS coordinates of each instrument reading. Sampled water was expelled from the system via plastic tubing on the opposite side of the boat (Fig 3.3). Clogging of the intake pipe did occur during *Dataflow* mapping, due to plant material becoming lodged against a trap inside the intake. To minimize time spent clogged, the system was equipped with a paddle-wheel flow sensor (+GF+ Signet) and horn alarm, which would sound if flow became reduced (<3.0 L min^{-1}).

Rather than motoring through SAV beds, we either poled the boat with long wooden stakes or allowed it to drift over the beds to minimize resuspension of particles attached to leaves and destruction of the bed. This approach resulted in data recordings every 0.5–4 m with highly irregular cruise tracks, especially when high wind and wave conditions made for difficult maneuvering. For each cruise track, the boat was oriented with the intake port leading in the direction of travel to minimize sampling of water disturbed by the boat's keel.

Peak biomass for *R. maritima* occurred later in the season (July and early August) than for *S. pectinata*, and cruises were scheduled to map the beds at all stages of growth. Mapping was conducted a total of nine times (June and August 2007; May, July, and September 2008) in the *S. pectinata* bed, six times (July and August 2007; June, July, and September 2008) in the Choptank River *R. maritima* beds, and twice (July and September 2008) in the Honga River *R. maritima* beds. Cruises consisted of a series of tracks cross-shore and/or along-shore that sampled both inside and outside the bed, repeatedly traversing the bed's edge. During each mapping, GPS coordinates of bed edges and presence of grass were periodically recorded as verification of bed area; however, poor water clarity complicated this effort, especially in late summer.

Triplicate water samples of 60 - 180 ml were collected and filtered in the field (Whatman GF/F, 0.45 μm) several times per sampling cruise to verify chlorophyll-*a* (chl-*a*) calibration and to relate turbidity (NTU+) to total suspended solids (TSS, mg L^{-1}). Chl-*a* filters were wrapped in aluminum foil and frozen until subsequent analysis. Within one year of collection the samples were thawed, extracted in 100% acetone, sonicated, filtered, and read on a fluorometer (Turner Designs, Model 10-AU). TSS concentrations were determined by filtering a known volume of water through pre-weighed and ashed (4 h at 550 °C) filters. Filters were rinsed with deionized water to remove salt, and then dried (3 d at 60° C) and reweighed. In addition, vertical PAR (photosynthetically active radiation) profiles were taken during mapping (LI-COR, LI-193SA hand-held 2π sensor) for calculation of diffuse down-welling light attenuation coefficients (K_d).

Spatial Analysis

Following cruises, data files were downloaded and exported to Excel 2003 (Microsoft Office) spreadsheets, where formatting and quality control checks were performed using previously developed QA/QC algorithms (Mark Trice, pers. comm., Maryland's Department of Natural Resources). This procedure filtered data for outlying values in all sampled variables, helping to identify spurious data associated with clogging of the system intake (e.g., Boynton et al., 2007). Event-related turbidity patches such as those associated with commercial shellfish dredging and cownose ray (*Rhinoptera bonasus*) feeding activity were occasionally present at several sites during *Dataflow* cruises. Cruises with such disturbances or with an insufficient number of tracks crossing the bed (≤ 3) were removed from further analyses.

After QA/QC protocols were completed, data were imported into ArcMAP (ESRI, v.9.2) as point shapefiles. The 2007 data defining SAV bed outlines in the Choptank and Honga Rivers were downloaded from the VIMS Chesapeake Bay SAV monitoring website (http://web.vims.edu/bio/sav/gis_data.html) and imported into ArcMAP. Bed crown densities and perimeters defined from aerial photography were compared to our *in situ* observations, and VIMS bed attributes were modified accordingly. In almost every case, VIMS SAV maps matched the field observations.

The shortest distances between data points and the deep (seaward) edge of each SAV bed were calculated using the *Near Analysis* function, part of the ArcMAP Proximity toolset.

Finally, the shapefiles were spatially interpolated to produce raster maps of variables measured by the *Dataflow* system using the Geostatistical Analyst extension in ArcMAP, following a modified version of a previously developed procedure used to generate water quality maps (Dave Wilcox, pers. comm., VIMS). First, prediction surfaces were generated with ordinary kriging, which bases interpolation on influences of neighboring values. The search neighborhood used had four sectors and was elliptical, including 2-25 neighbors. Model fit was improved by visual assessment of the semivariogram and covariance plots, followed by modification of lag size and number of lags. For many interpolations, the default lag values resulted in poor model fit, in which case values were revised based on the principle that the product of number of lags and lag size must be approximately half the distance between the furthest two points to be interpolated (ESRI, 2001). Post-interpolation, default and modified model fits were compared using error values given as part of the kriging output, and prediction maps were exported as raster files.

Statistical Analysis

Statistical analyses were conducted using SAS v9.1, with the significance level set at $\alpha = 0.05$. For each cruise, the overall mean turbidity values within ($turb_{in}$) and outside ($turb_{out}$) each plant bed were calculated by pooling measured values and used to determine the bed's *Turbidity Attenuation* (*%TA*) as

$\%TA = 100 - \frac{turb_{in}}{turb_{out}} * 100$. A Model I multiple regression was then computed using a stepwise selection method with *%TA* as the dependent variable and canopy height (categorical), density (categorical), and cross-shore width (continuous) as independent variables. The independent variable was normally distributed for any value of the dependent variables and variances were homogeneous, meeting the regression assumptions. The default significance level for variable inclusion in the model was $p = 0.15$. Correlation between the independent variables was assessed through the calculation of Pearson correlation coefficients. Water quality variables were also pooled in 25 m increments inwards from the plant bed's seaward edge and the percent difference from outside-bed conditions was determined as above. A Model I multiple stepwise regression was also computed as above with standard deviation of within-bed turbidity as the dependent variable.

Measurements of turbidty were converted to TSS by regressing direct TSS measurements from grab samples against concurrent measurements of turbidity taken by the data sonde (Appendix I, Fig. AI.4). Total average light attenuation coefficients were calculated for the interior of each bed based on transformed turbidity and chl-*a* data from the *Dataflow* instruments with the equation $K_d = 0.32 + 0.016 * chla + 0.094 * TSS$ (Gallegos, 1994; Kemp et al., 2004). A Model I least-squares regression of K_d against the product of cross-shore bed width and crown density was computed, and the R^2 value was calculated. A similar linear regression was also calculated for *%TA* using the same independent variable.

Results

The Irish Creek *S. pectinata* study site had a large impact on all variables measured during the summer months. Turbidity and chlorophyll-*a* maps showed marked decreases with distance inwards from the bed's seaward perimeter (Fig. 3.4A,B), while dissolved oxygen (O_2), temperature, and pH increased with distance inwards from the perimeter (Fig. 3.4C-E). A single representative *Dataflow* transect of turbidity into the plant bed showed a clear linear region of turbidity reduction, beginning ~60 m within the bed's seaward edge (Fig. 3.5). Mean (± SE) turbidity before this sharp drop-off was 7.4 ± 0.1 NTU+, and levels were reduced to 3.3 ± 0.03 NTU+ over a distance of ~40 m. When all measurements within the bed were pooled by 25 meter increments inwards from the bed's seaward perimeter, the region of sharp linear turbidity reduction remained (%*TA* increased), and turbidity continued to decrease at a slower rate past 100 m inwards, eventually reaching 50% of values measured outside the plant bed (Fig. 3.6A). Chl-*a*, which was also attenuated with distance inwards from the plant bed's perimeter, had a more gradual slope than turbidity. %*TA* began increasing linearly ~125 m inside the plant bed and eventually reached 25%. On the other hand, O_2, temperature, and pH all increased with distance inwards from the bed's seaward perimeter (%*TA* decreased), and O_2 and pH slightly decreased at maximum distances (approaching the bed's shoreward perimeter) (Fig. 3.6B).

Individual submersed plant beds surveyed in this study showed variable impacts on water clarity during June and July periods of peak plant biomass (Table 3.1). For many plant stands, turbidity levels were reduced to well below values outside the bed (%*TA*>>0); however, others were more turbid within the bed compared to outside (%*TA*<0). For late season cruises (late August, September) there was little difference between turbidity "inside" and "outside" the areas occupied by SAV beds in June and July (Appendix II, Fig AII.1-15). During this late season period when plant canopies had been reduced or eliminated, turbidity patterns were much less variable, with values tending to be slightly higher "inside" relative to values "outside" with a mean (± SE) *%TA* of -12 ± 11%.

In general, wide and dense *R. maritima* and *S. pectinata* beds exhibited decreased average turbidity within the plant stand relative to average outside conditions during summer months. The best multiple regression model (adj. R^2=0.34, p=0.02) included crown density and cross-shore bed width, but not canopy height and was described by the equation $\%TA = 7.7 * density + 0.1 * width - 30.7$ (Fig. 3.7). Although canopy height and crown density were significantly but weakly correlated (Pearson correlation, r=0.46, p=0.035), crown density and cross-shore bed width were not significantly correlated.

Despite the exclusion of canopy height from this regression model, reproductive and vegetative beds had different impacts on water clarity. The product of cross-shore width and crown density provided a single, combined variable that succinctly characterized the impact of plant beds on water clarity. The trend of greater turbidity attenuation by larger and denser beds was significant for reproductive beds (R^2=0.51, p=0.009), while no significant relationship existed for vegetative beds and turbidity within was slightly greater than outside (%*TA*<0) (Fig. 3.8). The variability of turbidity measurements around the mean within plant beds showed significant, opposite patterns for vegetative and reproductive beds (ANOVA, $p<0.05$) (Fig. 3.9). In short, vegetative beds, variability tended to increase with increasing density; whereas in tall, reproductive beds, variability decreased with increasing density.

The impact of turbidity attenuation on light penetration was obvious in the relationship between calculated light attenuation coefficients (K_d) and (cross-shore bed width) x (crown density). There was generally good agreement between light attenuation coefficients measured directly and those estimated from concurrent *Dataflow* samples (Appendix I, Fig. AI.5), and estimated values included chl-*a* concentrations as well as TSS concentrations. In vegetative beds, no significant relationship was found between K_d and (cross-shore bed width) x (crown density), and K_d was slightly elevated above 1.5 m^{-1}. For reproductive canopies, however, average within-bed light penetration increased as beds became larger and denser. At (cross-shore bed width) x (crown density)>700, light attenuation within reproductive beds decreased below 1.5 m^{-1}.

Discussion and Conclusions

Feedbacks in a Dense Reproductive Plant Bed

Although many studies have reported reduction in suspended material within plant stands (e.g., Ward et al., 1984; Granata et al., 2001; Moore, 2004), *Dataflow* maps from the Irish Creek *Stuckenia pectinata* site provide a unique, graphic, and quantitative illustration of how a large and dense SAV bed with a tall canopy can strongly influence local water quality conditions (Fig. 3.4A-E). Strong spatial gradients for all measured variables visible in maps indicate that conditions within this submersed plant bed were relatively quiescent during sampling periods. Elevated within-bed pH and O_2 levels indicate high plant productivity in addition to reduced water mixing during this period of peak plant biomass. The steep linear decrease in turbidity coupled with relatively stable chl-*a* concentrations over the first ~100 meters within the bed's seaward perimeter (Fig. 3.6) could indicate the deposition of larger suspended particles within this transition region, followed by the more gradual deposition of lighter organic material deeper into the bed's interior. The frictional effects of the tall plant canopy in early summer are further revealed by comparison with turbidity maps obtained in the fall when plants were senescing (Appendix II, Fig. AII.1). Although turbidity values were generally lower in early fall, water sampled in the area of previous *S. pectinata* occupation had elevated turbidity compared to water "outside" the bed. This could indicate resuspension of previously deposited material in the absence of a full plant canopy or high concentrations of organic particles associated with the degradation of senescent plant biomass. Additionally, wave shoaling and shoreline erosion may have increased in the absence of a plant canopy.

Spatial Patterns

Some interesting spatial patterns were observed across the suite of SAV beds in the study region. Comparison between cruises during peak plant biomass and later in the season supported our assumption that spatial patterns in water clarity were not due to inherent physical characteristics of the site, but instead resulted from the presence of submersed plant beds (Appendix II, Fig. AII.1-15). Beds that were wider with greater crown density and tall reproductive canopies tended to attenuate turbidity most strongly over the plant stand, while turbidity levels within smaller and lower density beds were often higher than those outside the bed (Table 3.1). The most likely cause of higher turbidity within small beds was resuspension of epiphytic material coating plant leaves (e.g., Koch, 2002); we observed (but did not quantify) heavy epiphytic growth at most *R. maritima* sites during the summer cruises. Epiphytic accumulations, autochthonous plant material, and previously deposited allochthonous material could all be easily resuspended due to the reduced ability of small, narrow beds to attenuate wave and tidal current energy.

Additionally, the minimal capacity of these narrow, low density plant beds to buffer shorelines from wave energy may have resulted in shoreline erosion, increasing within-bed turbidity (e.g., Koch et al., 2009). During sampling, we visually observed shoreline erosion occurring at the Smoke Point site (Appendix II, Fig. AII.12). This particular site (where *%TA* approached -60%), was an outlying point in several regressions (Fig. 3.7, 8). *Dataflow* maps suggest that erosion was occurring in many other narrower, less dense sites (Appendix II, Figs. AII.3, 7, 10, 11), whereas denser and wider beds showed no signs of increased near-shore erosion (Appendix II, Figs. AII.1, 2).

The relationship between all sampled plant beds and *Turbidity Attenuation* was significant but showed considerable variability (Fig. 3.7). One possible explanation for high variability in this study is that the hydrodynamic regime may have varied greatly among study sites. Additionally, canopy height did not add significance to this multiple regression model, most likely due to the limitations associated with available beds, as discussed below. Nevertheless, the influence of larger and denser reproductive beds with (cross-shore bed width) x (crown density)>750 on hydrodynamics and subsequent reduction of within-bed turbidity, was strongly apparent from this study (Fig. 3.8). A previous study using many of the same site locations found that in reproductive beds, crown density was negatively correlated with epiphyte biomass and positively correlated with silt fraction of sediment (Schulte, 2003), which is consistent with the relationship between *%TA* and density found in this study. Based on the relationship between bed parameters and *%TA*, beds with crown density=4, needed a minimum cross-shore bed width of 190 m to reduce overall within-bed turbidity below values outside the bed. For lower densities, beds needed to be increasingly wide for turbidity attenuation to take place (density=3, width=250; density=2, width=375; and density=1, width=750).

Habitat Criteria

Wide and dense beds significantly reduced turbidity within the plant stand, which resulted in increased light penetration (Fig. 3.10). The (cross-shore bed width) x (crown density) threshold for K_d was the same as for *%TA*, despite the fact that K_d was calculated with chl-*a* in addition to turbidity. This could suggest that in these systems, light attenuation by suspended particles (non-algal) is more relevant than attenuation by phytoplankton. However, the majority of beds surveyed (13 of 21) experienced average light penetration during summer months that exceeded published maximum habitat threshold values ($K_d > 1.5$ m^{-1}, Dennison et al., 1993). Despite these low light conditions, SAV managed to survive and even produce reproductive shoots in some cases. One obvious explanation is error in estimation of K_d based on measured *Dataflow* variables. While this likely has little impact on trends related to bed parameters, the true average light penetration may have been slightly higher than the estimated values. Another potential explanation for this incongruity is that although turbidity was not reduced over the entire bed, regions of low turbidity did exist in these narrower and less dense beds, and perhaps this intermittent light availability was sufficient for plant growth. Variability was not significant among vegetative beds, indicating that these short canopies interact relatively little with water flow, except perhaps in the case of highest crown density (Fig. 3.9) (e.g., Chen et al., 2007). However, significantly high variability in low density reproductive beds indicated some interaction with water flow and the potential for patchy regions of reduced turbidity. In addition, poor water quality during the summer months (when the majority of aboveground plant material has already accumulated) may have little impact on bed development (e.g., Moore et al., 1996).

Mapping Surface Water Quality over SAV Beds

Many fine-scale patterns in water quality within SAV beds were revealed through the use of *Dataflow*, which would have been difficult to resolve using traditional Eulerian sampling methods. In general, there are relatively few studies that present fine-scale maps of surface water quality in shallow near-shore areas (e.g., Herrera-Silvera et al., 2004; Lane et al., 2007), and no previously published mapping studies for areas occupied by submersed plants. Although some previous studies have related plant bed characteristics to water quality variables, dissolved oxygen is most often measured (e.g., Caraco and Cole, 2002; Bartleson, 2004) rather than turbidity. The absence of water clarity studies over SAV beds may be related, in part, to difficulties associated with boat propulsion and sampler intake-clogging. While some disturbance of plants (and their associated algal epiphytes) did occur during sampling in the present study, this disturbance would have resulted in an underestimation of SAV bed effects on reducing levels of turbidity and chl-*a*.

The effort in this study to relate turbidity attenuation to bed size, density, and height was constrained by character covariance among the beds that occurred in the study area. For example, most large beds found were also dense with tall reproductive canopies, while smaller beds encountered here tended also to be sparse with shorter vegetative canopy structure. In general, we were unable to locate low-density reproductive beds, and vegetative beds typically did not occur at the highest widths and densities. This made a full comparison among bed characteristics (complete block design) impossible.

Management and Restoration Implications

The incorporation of feedbacks and associated improvement in SAV habitat has the potential to greatly improve restoration and management strategies including model prediction, transplantation schemes, and restoration efficiency. In shallow coastal systems, water movement is not purely unidirectional or uniform, and feedback effects become much more unpredictable. However, a simple spatial understanding of SAV bed properties that facilitate feedback development can add to our understanding of bed success, improving predictive power in SAV habitat models (e.g., Cerco and Moore, 2001; van derHeide et al., 2007; Best et al., 2008). Cost-effectiveness of SAV restoration efforts (e.g., Fonseca et al., 1998) may be optimized by incorporating turbidity conditions at the planting site into transplantation decisions such as shoot density or bed width (van Katwijk et al., 2009). The efficiency of restoration efforts may be increased by avoiding transplantation in areas which do not have adequate space for feedback development (e.g., narrow regions) or where bed size would have to be excessively large to reap the benefits of feedbacks based on local water clarity conditions. Finally, restoration site choice could be streamlined by avoiding locations where turbidity levels are elevated such that positive feedback effects would be inadequate to provide sufficient light penetration for plant survival. In conclusion, the spatial patterns of feedbacks impacting light availability in SAV beds may help inform current restoration strategies in Chesapeake Bay and other degraded coastal systems worldwide, but further studies incorporating water clarity, bed parameters, and hydrodynamics are necessary.

In conclusion, clear patterns in turbidity and chl-*a* measurements at the Irish Creek *S. pectinata* study site indicated that the majority of suspended material deposition occurred within a short distance of the bed's edge (<100 m). Distinct patterns in pH, temperature, and O_2 also revealed effects of the plant stand. These results reaffirm the large impact a robust canopy-forming bed can have on local water quality and implicate the edge region as a dynamic transition zone between degraded conditions outside the bed and improved conditions within. A comparative study including a broad suite of SAV beds (most of which were dominated by *R. maritima*) revealed that variations in canopy height, crown density, and cross-shore width were important in controlling bed effects on water clarity. Larger and denser beds with tall canopies tended to show improved water clarity (and little variability) within the plant stand. Consequently, these beds showed improved light penetration, with light attenuation coefficients reduced below a maximum threshold for SAV habitat suitability criteria. In contrast, beds with short canopies had little impact on water clarity and often showed higher turbidity values inside the bed compared to outside. The use of *Dataflow* instrumentation within submersed plant beds allowed quantification of fine-scale spatial patterns in water quality and provided a unique comparison of water clarity conditions over a broad range of SAV beds.

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Tables

Table 3.1: Overall means of turbidity (NTU+) inside and outside all study sites and *Turbidity Attenuation* (%*TA*) during summer and fall *Dataflow* cruises.

Site	Date	Canopy*	Species#	Density$	Width (m)	Location&	Mean (NTU+)	*%TA*
Irish Creek	6/26/2007	Repro	Sp	4	340	Out	6.7	25
						In	5.0	
Irish Creek	6/27/2007	Repro	Sp	4	340	Out	7.6	46
						In	4.1	
Irish Creek	9/11/2008	None	-	-	-	Out	1.7	-118
						In	3.7	
Bridge Creek	7/1/2008	Repro	Sp, Rm	4	470	Out	5.4	37
						In	3.4	
Bridge Creek	9/11/2008	None	-	-	-	Out	5.2	9
						In	4.7	
Cat Cove	7/25/2008	Repro	Rm	2	241	Out	6.1	-16
						In	7.0	
Cat Cove	9/12/2008	None	-	-	-	Out	6.2	21
						In	4.9	
Chapel Creek	7/24/2007	Repro	Rm	3	442	Out	13.2	26
						In	9.7	
Chapel Creek	6/26/2008	Veg	Rm	1	442	Out	5.2	-3
						In	5.3	
Chapel Creek	8/29/2007	None	-	-	-	Out	2.8	20
						In	2.3	
Cooks Cove	7/26/2007	Repro	Rm	4	407	Out	6.6	22
						In	5.1	
Cooks Cove	8/29/2007	None	-	-	-	Out	4.3	5
						In	4.1	
Deep Neck	6/26/2008	Veg	Rm	3	184	Out	11.6	6
						In	10.8	
Deep Neck	7/1/2008	Veg	Rm	3	184	Out	8.5	18
						In	7.0	
Deep Neck	9/11/2008	None	-	-	-	Out	6.4	2
						In	6.3	
Drum Point	6/26/2008	Veg	Rm	3	87	Out	5.4	-5
						In	5.7	
Drum Point	7/1/2008	Veg	Rm	3	87	Out	6.1	1
						In	6.0	
Drum Point	9/11/2008	None	-	-	-	Out	6.6	-11
						In	7.3	
Hambleton Isl.	7/24/2007	Veg	Rm	1	207	Out	10.7	8
						In	9.8	
Kirwans Neck	7/21/2008	Repro	Rm	3	191	Out	3.8	15
						In	3.3	

Leadenham Crk.	7/24/2007	Repro	Rm	3	112	Out	9.1	-18
						In	10.7	
Leadenham Crk.	6/26/2008	Veg	Rm	1	105	Out	9.5	-10
						In	10.4	
Leadenham Crk.	8/29/2007	None	-	-	-	Out	3.3	-46
						In	4.8	
Mulberry Pt.	7/24/2007	Veg	Rm	2	74	Out	8.4	-21
						In	10.1	
Mulberry Pt.	6/26/2008	Veg	Rm	1	37	Out	6.9	-2
						In	7.0	
Smoke Pt.	7/25/2008	Repro	Rm	2	273	Out	7.2	-56
						In	11.2	
Smoke Pt.	9/12/2008	None	-	-	-	Out	3.8	-7
						In	4.0	
Transplant	7/26/2007	Veg	Rm	4	214	Out	7.6	-22
						In	9.2	
Transplant	7/1/2008	Repro	Rm	3	124	Out	5.3	9
						In	4.8	
Transplant	9/11/2008	None	-	-	-	Out	6.7	-3
						In	6.8	
Wallace Crk.	7/21/2008	Repro	Rm	4	204	Out	8.0	9
						In	7.3	
Wallace Crk.	9/12/2008	None	-	-	-	Out	5.7	0
						In	5.7	
Wheatley Pt.	7/21/2008	Repro	Rm	2	85	Out	8.8	-8
						In	9.5	
Wheatley Pt.	9/12/2008	None	-	-	-	Out	6.3	-13
						In	7.2	

*Canopy height was defined as tall and reproductive ("Repro") or short and vegetative ("Veg") during the growing season. "None" indicates a senescing canopy during early fall cruises.

#Species was either *Ruppia maritima* (Rm) or *Stuckenia pectinata* (Sp). Hyphens indicate senesceing fall canopy.

$Crown density follows the VIMS scale: 1=0-10%, 2=10-40%, 3=40-70%, and 4=70-100%.

&During early fall cruises, "In" and "Out" refer to the location of the bed perimeter during the prior growing season.

Figures

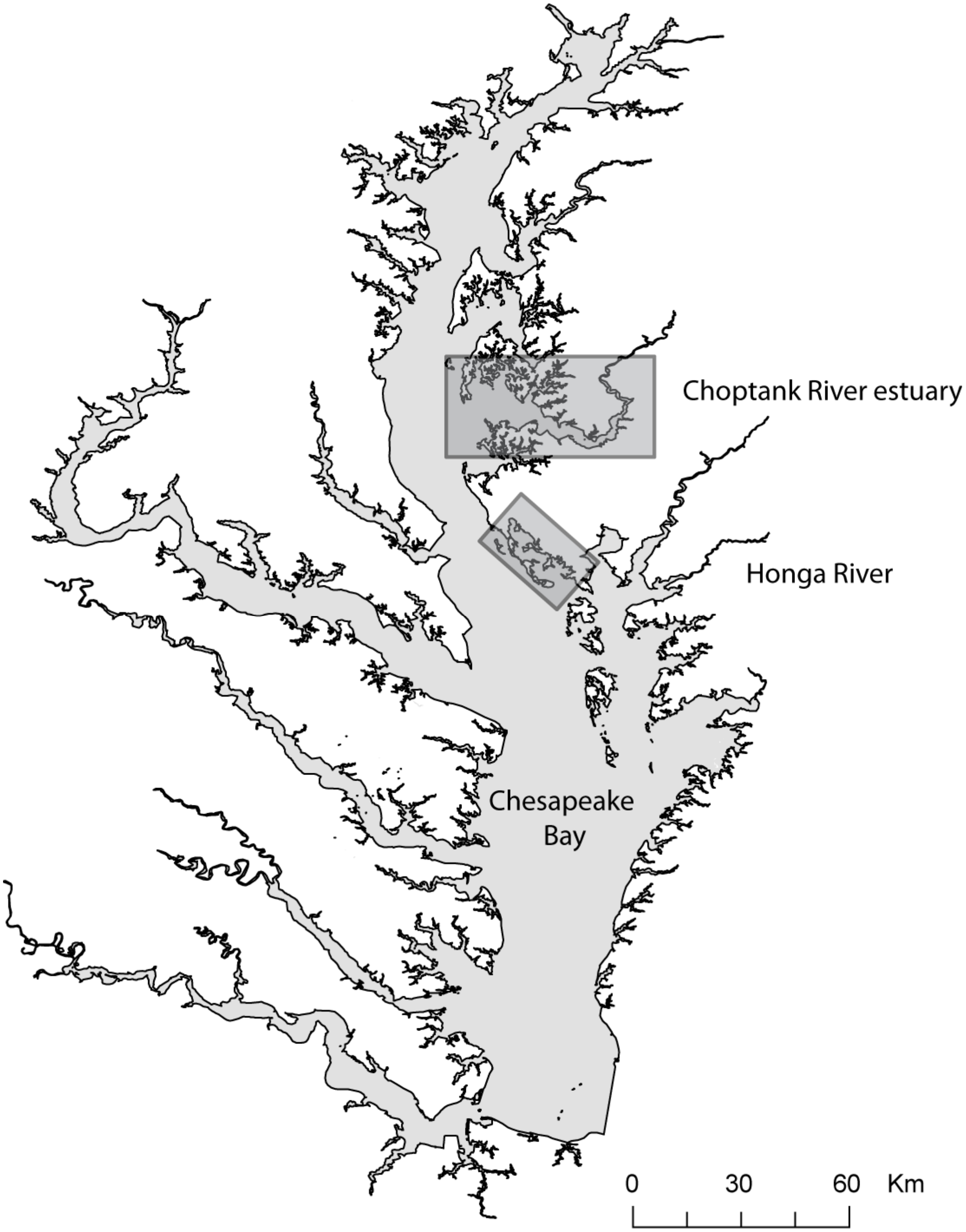


Figure 3.1: Location of study sites for 2007 and 2008 Dataflow cruises.

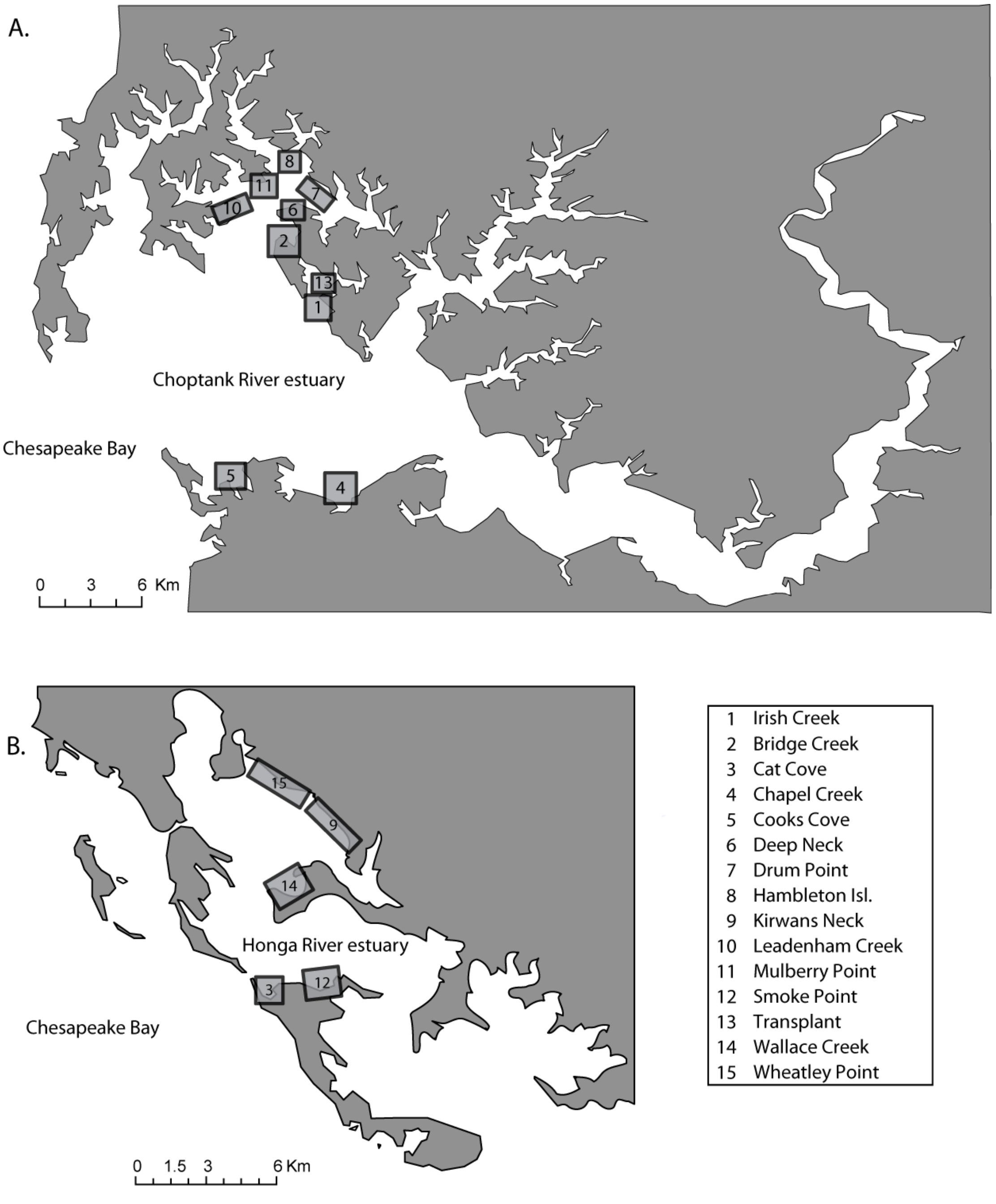


Figure 3.2: Location of study sites in the Choptank River (A) and Honga River (B) estuaries.

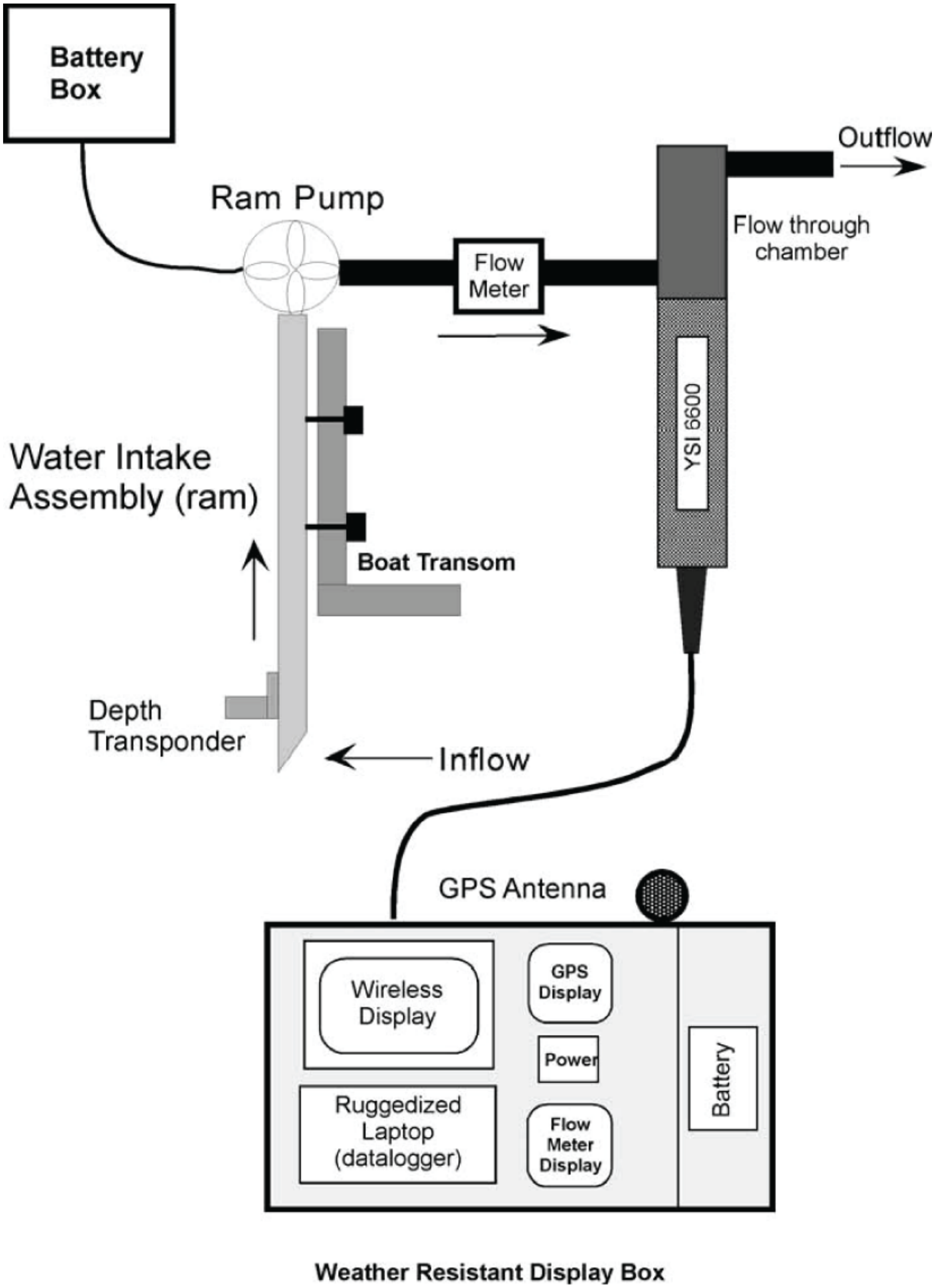


Figure 3.3: Diagram of *Dataflow VI* setup (from Boynton et al., 2007) showing all instruments and tubing. Arrows indicate the direction of water flow through the system.

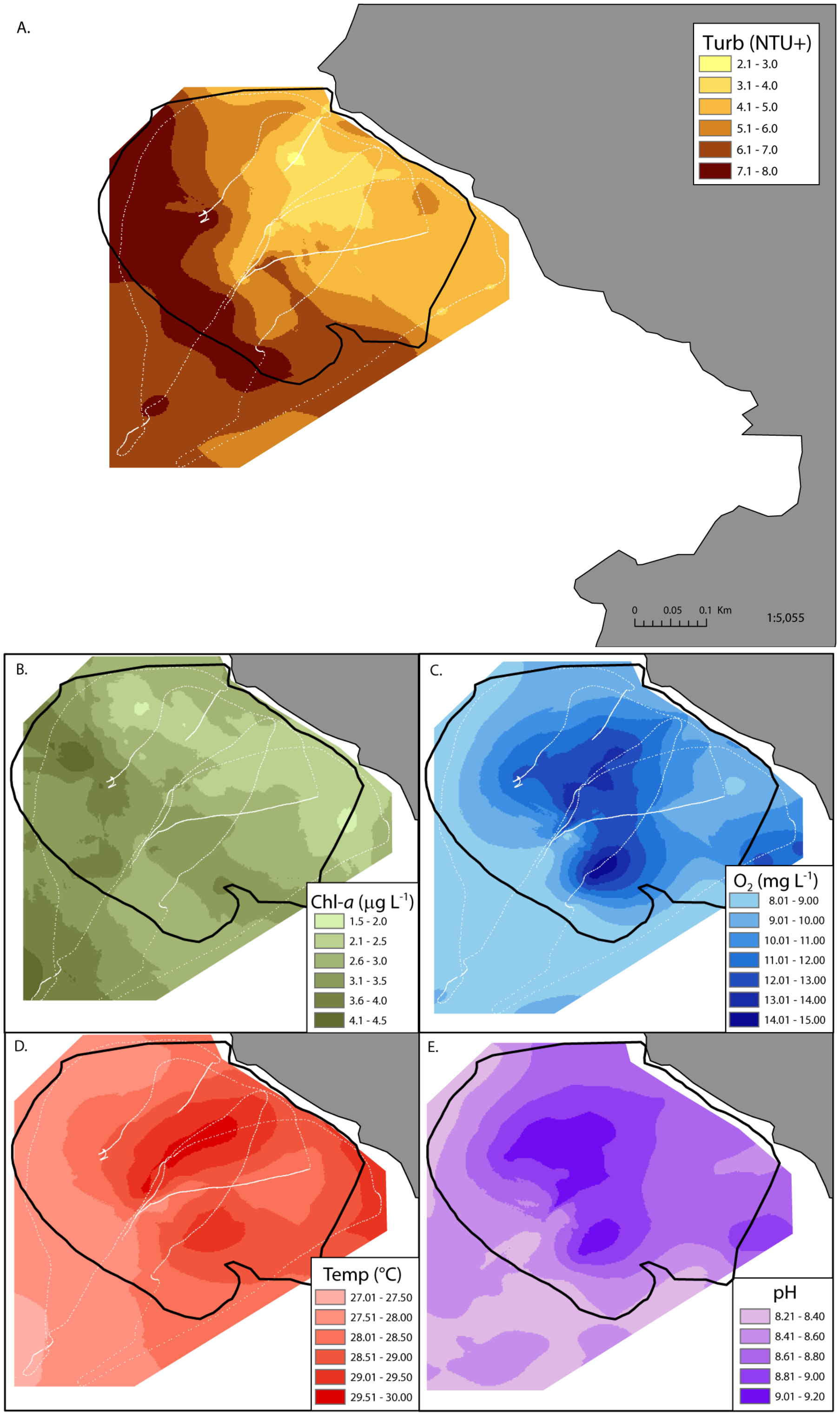


Figure 3.4: Interpolated maps produced at the Irish Creek study site Dataflow cruise on 6/26/07 (peak plant biomass). Maps include turbidity (A), chlorophyll-*a* (B), dissolved oxygen (C), temperature (D), and pH (E). Black lines delineate the plant bed perimeter, and white dots indicate the cruise track.

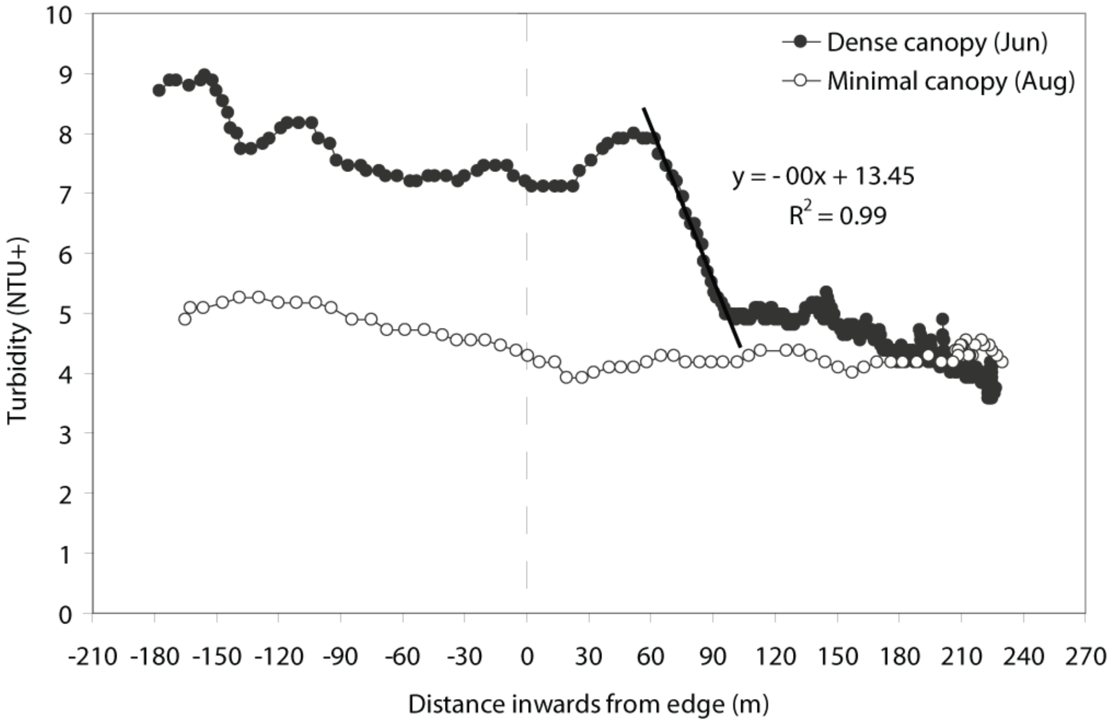


Figure 3.5: *Dataflow* transect at the Irish Creek site during June (dense canopy) and late August (minimal canopy). The transect was aligned with the automated sampler platforms. The plant bed's edge is located at distance = 0 and positive values are increasing distance into the bed. The black line represents the slope of the initial turbidity decline within the bed, described by the significant equation ($p<0.05$) and regression coefficient shown.

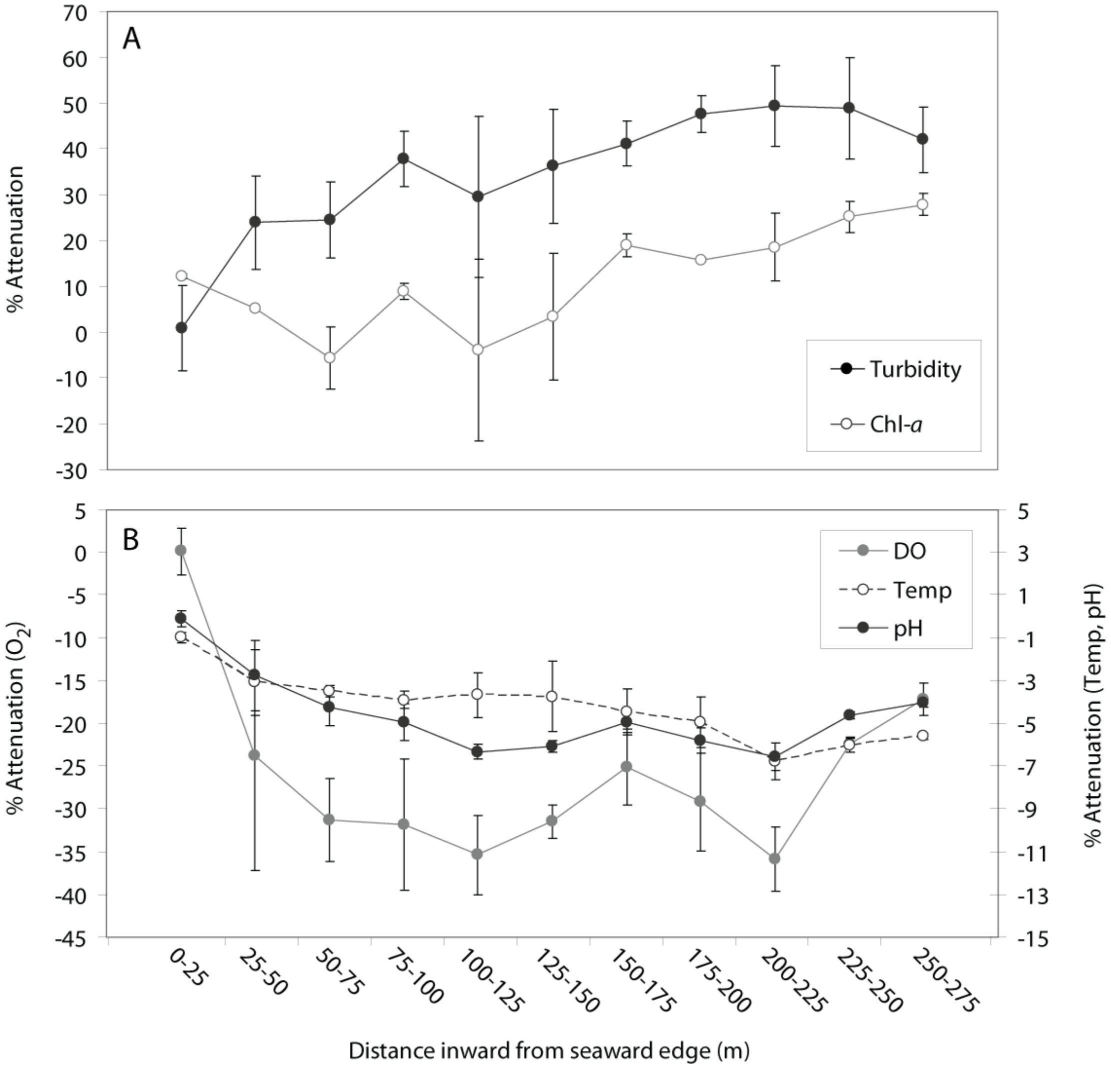


Figure 3.6: Mean (± SE) attenuation of turbidity, chl-*a* (A), O_2, temperature, and pH (B) from Irish Creek Dataflow cruises (n=2) in 25 m increments inward from the bed's seaward perimeter (distance=0). Percent attenuation represents the pooled increment compared to conditions outside the bed (e.g., $\%Attenuation(O_2) = 100 - \frac{O_{2(0-25)}}{O_{2(out)}} \cdot 100$. Thus, if values inside the plant bed exceed those outside, %Attenuation < 0.

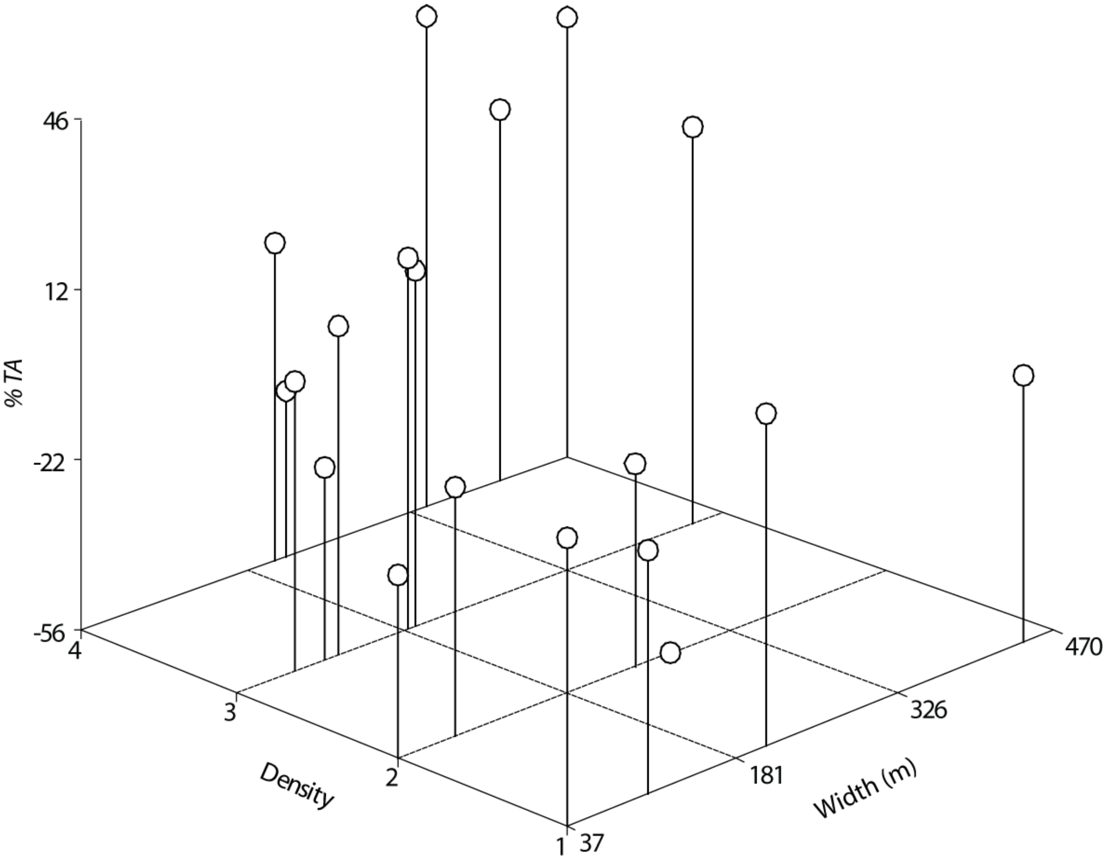


Figure 3.7: Multiple regression of *Turbidity Attenuation* (%*TA*) against crown density (VIMS scale) and cross-shore bed width for all sites surveyed during summer Dataflow cruises. The relationship is described by the equation $\%TA = 7.7 \cdot density + 0.1 \cdot width - 30.7$ (adj. $R^2 = 0.34$, p=0.02).

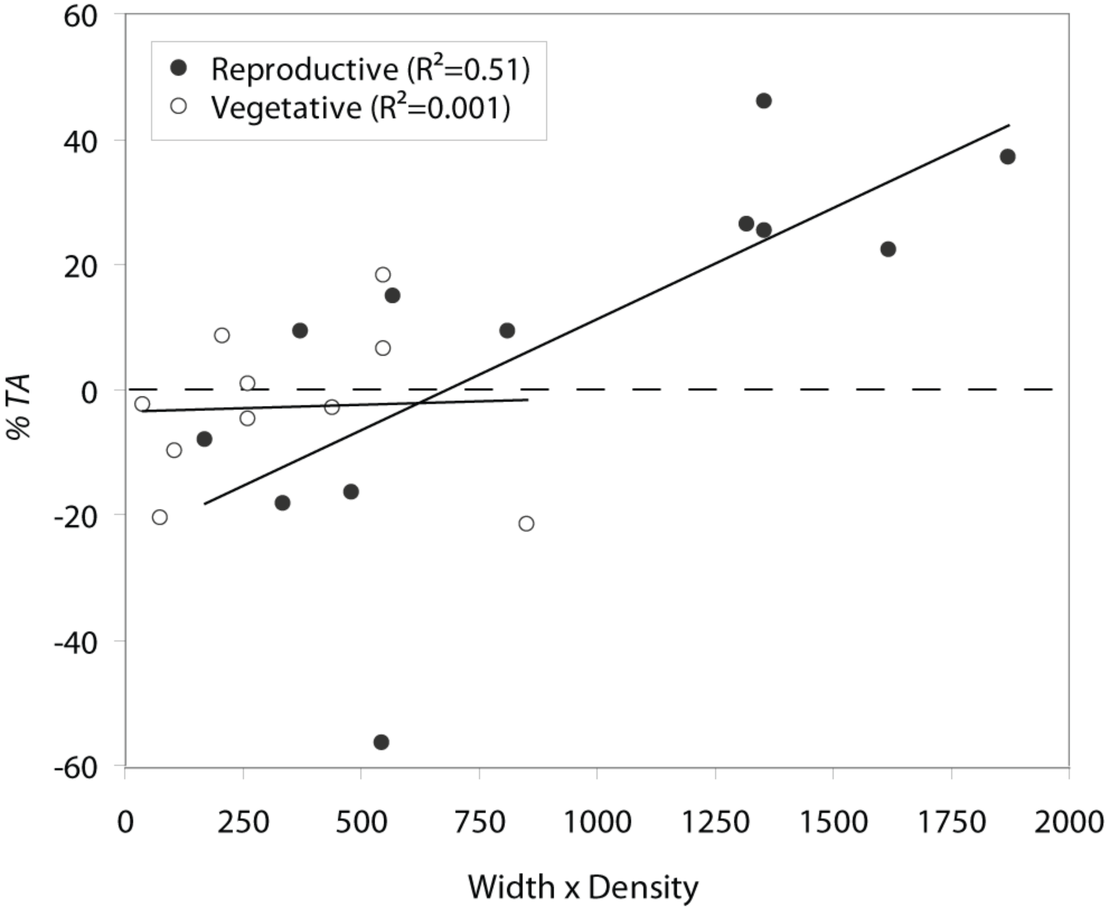


Figure 3.8: Linear regression of *Turbidity Attenuation* (%*TA*) by (cross-shore bed width (m)) x (crown density) for reproductive (y = 0.04x - 24.3, p=0.009) and vegetative (y = 0.001x - 3.5, p=0.92) summer plant beds. The dashed line (%*TA*=0%) indicates average turbidity inside is equal to average turbidity outside.

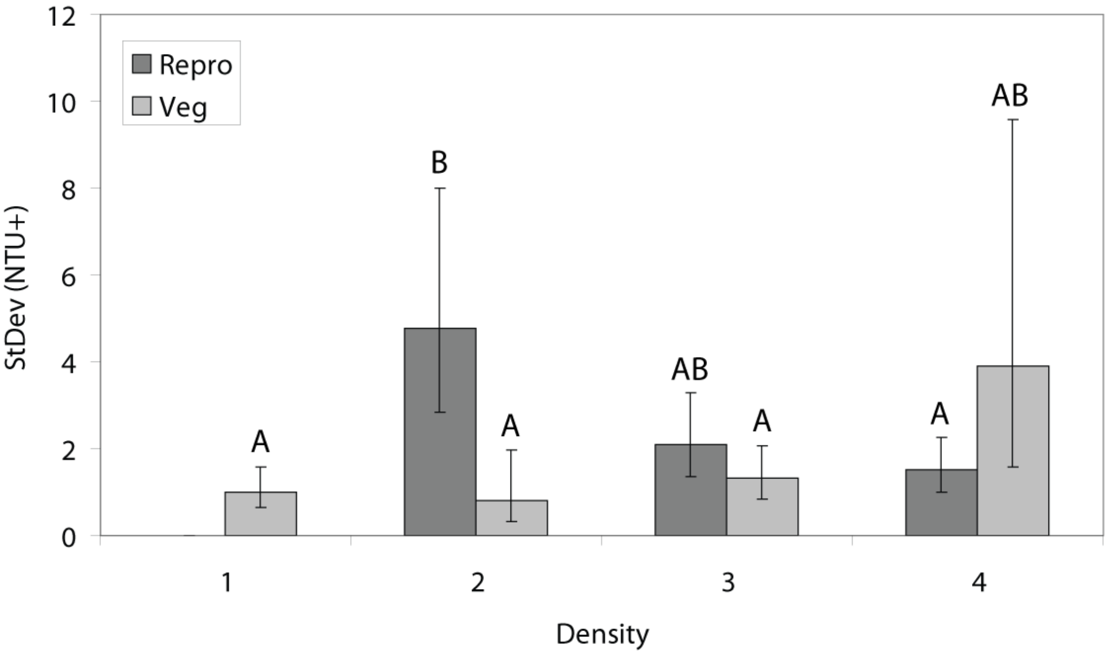


Figure 3.9: Standard deviation in turbidity values within plant beds by crown density (VIMS scale) and canopy height. Error bars indicate 95% confidence limits around the mean and letters indicate significant differences among means (ANOVA $p<0.05$).

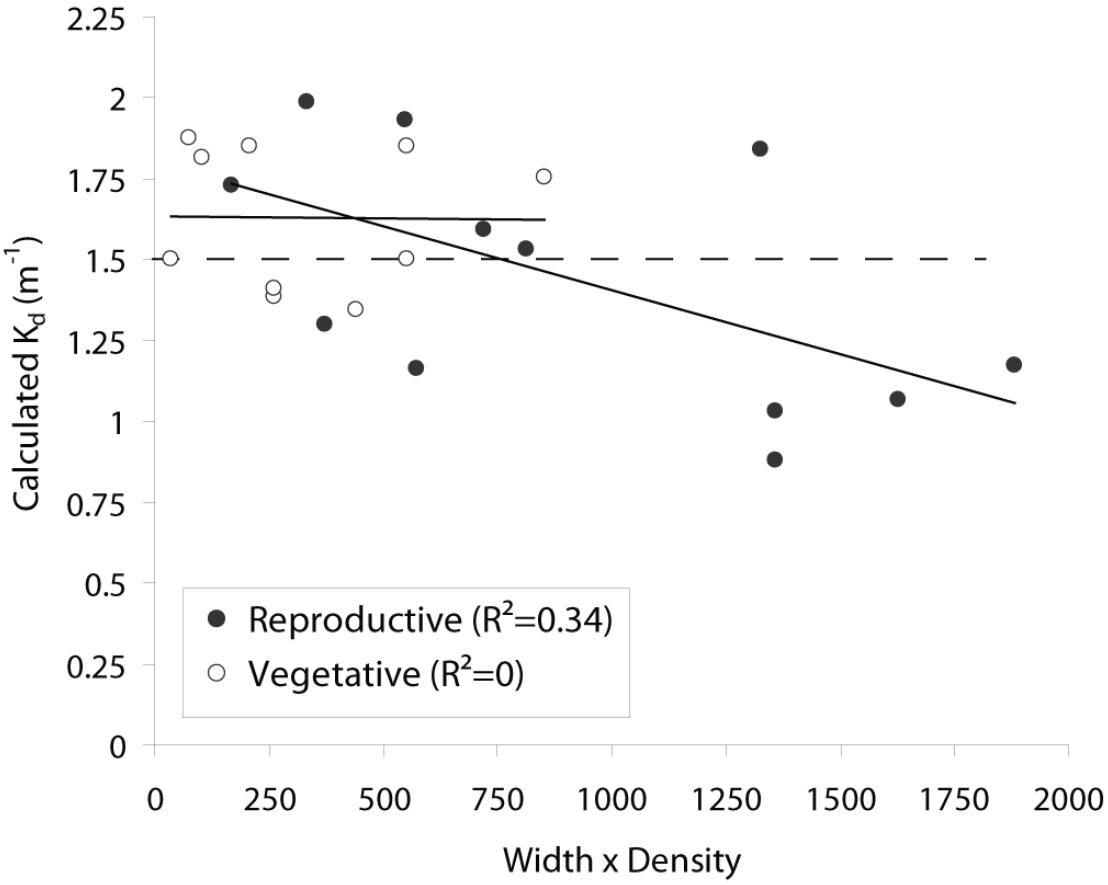


Figure 3.10: Linear regression of estimated light attenuation coefficients (K_d) within short vegetative (y=1.63, p=0.96) and tall reproductive (y=-0.0004x+1.80, p=0.048) submersed plant beds against (Cross-shore bed width (m)) x (crown density). Dashed line (K_d=1.5) indicates maximum SAV habitat light requirement threshold (Dennison et al., 1993).

Synthesis and Implications

The persistence of a robust stand of the canopy-forming species *Stuckenia pectinata* in the Choptank River estuary presented a unique opportunity to study interactions between this plant bed and its surrounding environmental conditions. In Chapter 1 of this thesis, seasonal variations of the *S. pectinata* bed structure were quantified in relation to seasonally-changing water quality conditions. This plant bed developed a tall canopy (>1 m) and produced unprecedented levels of aboveground biomass for Chesapeake Bay (641 g DW m^{-2}) by June. Additionally, this bed generated high densities of reproductive propagules (vegetative and sexual) and maintained moderate aboveground plant tissue throughout the year. Net daytime rates of ecosystem production peaked during May (329 mmol O_2 m^{-2} d^{-1}) when plant biomass was rapidly accumulating. Habitat criteria for the mesohaline region suggest that summer water quality conditions were marginal for plant survival, and local disturbance due to cownose ray activity caused further degradation of water clarity. Evidently, rapid growth of this plant stand during the spring period of high light penetration helped protect the bed from the poor water quality conditions and physical disruption (e.g., cownose rays) during summer months.

In addition to its highly competitive spring growth strategy, this plant stand improved local habitat conditions through interaction with hydrodynamics. In Chapter 2, I investigated wave attenuation by the plant canopy and associated feedbacks impacting light and nutrient availability, and sediment suitability in this plant stand. Modification of hydrodynamics and subsequent feedbacks showed strong seasonality, becoming most prominent and difficult to perturb in June (peak plant biomass). During this period, waves within the stand were attenuated 44%, which contributed to significant decreases in suspended particulate material concentrations through trapping and reduction of resuspension. Epiphytic algal growth was also diminished within the plant bed, which directly increased light reaching leaf surfaces; additionally, the trapping of suspended particles in heavy epiphytic growth compounded low light conditions outside the bed. The decomposition of autochthonous and allochthonous material within the plant bed contributed to elevated sediment porewater nutrients, which supplemented low concentrations of water column nutrients. Reduced mixing within the stand also contributed to potential DIC limitation, periodic bottom-water hypoxia, and elevated porewater sulfide levels. Though unlikely, these negative feedback effects may have reduced plant growth or stressed plants during this month. During the poor water quality conditions of summer months, light levels outside the plant bed would not have been sufficient to support SAV growth without the benefit of positive feedback effects.

As modification of hydrodynamics and subsequent impacts on suspended particles are known to vary depending on plant structure, spatial patterns in water clarity within this *S. pectinata* bed were compared to those in a suite of other nearby plant beds to quantify the effects of bed size, density, and canopy architecture. In Chapter 3, interpolated maps were produced using a *Dataflow* flow-through system, and strong patterns in water quality were evident within the *S. pectinata* plant bed. In general, wide and dense SAV beds with a tall canopy had the greatest impact on water clarity. The threshold for reduced average turbidity within the stand compared to levels outside was (cross-shore width) x (crown density) > 750, with the widest and densest beds showing turbidity levels reduced by ~30%.

The combined findings from these studies reinforce several important points. First, strategies in plant growth exhibited by this plant bed (Chapter 1), along with its canopy-forming morphology (Chapter 2), and spatial extent (Chapter 3) resulted in substantially improved habitat conditions. Based on the estimation of light availability to leaves without the benefits of positive feedbacks, SAV would not be able to survive the degraded summer water quality conditions of the Choptank River estuary. In this instance, the benefits of ecosystem engineering seemed to vastly outweigh the stresses based on the simple observation of robust plant growth. However, if habitat conditions were slightly different (e.g., higher initial organic content in sediments), it is possible that feedback effects could push the system over a tolerance threshold (e.g., sediment porewater hydrogen sulfide concentration), reducing plant growth when feedbacks are most pronounced. Further work in ecosystem modeling may help determine the thresholds of local conditions and plant morphology under which hydrodynamic modification by submersed plants could negatively impact their growth.

Additionally, the submersed plant bed’s edge region seems to be critical for initial wave attenuation (Chapter 2) and subsequent suspended particle settlement (Chapter 2, 3). Based on findings from these studies, the edge region (<100 m from bed perimeter) serves as a transition zone between suspended material concentrations outside the bed to more stable within-bed concentrations. Of course, this value depends on multiple SAV bed properties explored in these chapters including density, width, and biomass. Destruction of this transition region or width reduction in general of natural plant beds may have implications for habitat quality within the entire bed. As armoring of shorelines in heavily-populated coastal areas increases and global sea level rise continues, potential SAV habitat may be reduced to a narrow margin. Thus, growth-promoting feedback development may be less likely to occur, especially under degraded water quality conditions, negatively impacting SAV communities in many coastal systems.

Finally, this work has implications for management and restoration of SAV in Chesapeake Bay and other coastal regions. The recognition of feedbacks as prominent features in plant beds is key, and preliminary information on width and density relationships that promote feedbacks is crucial for restoration efforts. For species with small-scale reproductive strategies (i.e. rhizome elongation or tuber production), the incorporation of the "nursery bed effect" into restoration strategies may be highly successful and cost-effective. As degraded water quality conditions in this system are not likely to be alleviated in the near future, management and restoration of SAV communities should focus on highly productive species with early-season growth strategies, which can successfully compete under ambient conditions.

Appendix I: Relationships between measured and estimated variables

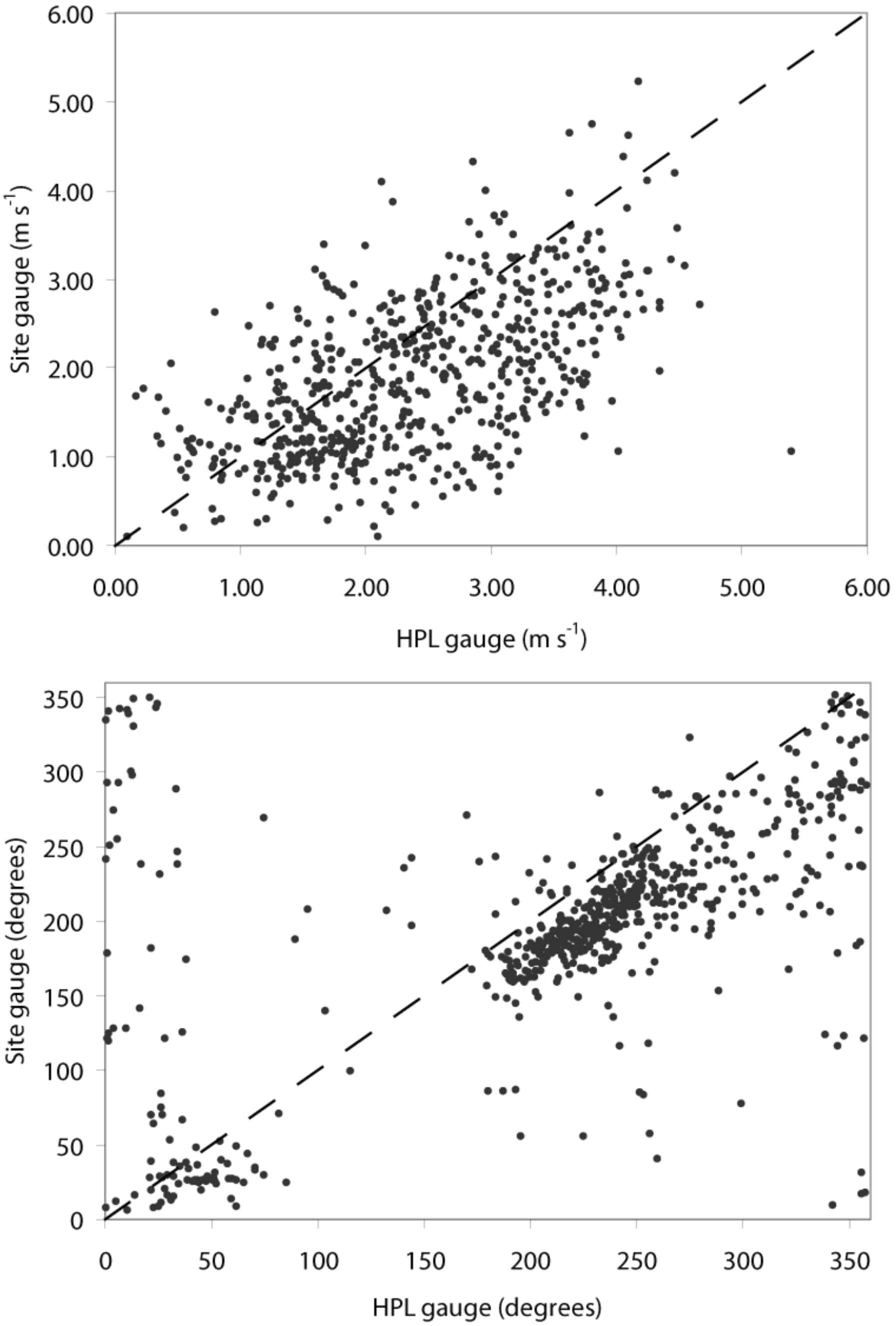


Figure AI.1: Relationships between long-term land-based measurements (HPL gauge) and measurements from this study (Site gauge) of wind speed (above) and direction (below) during May 2008. Dashed lines indicate a 1:1 relationship between gauges.

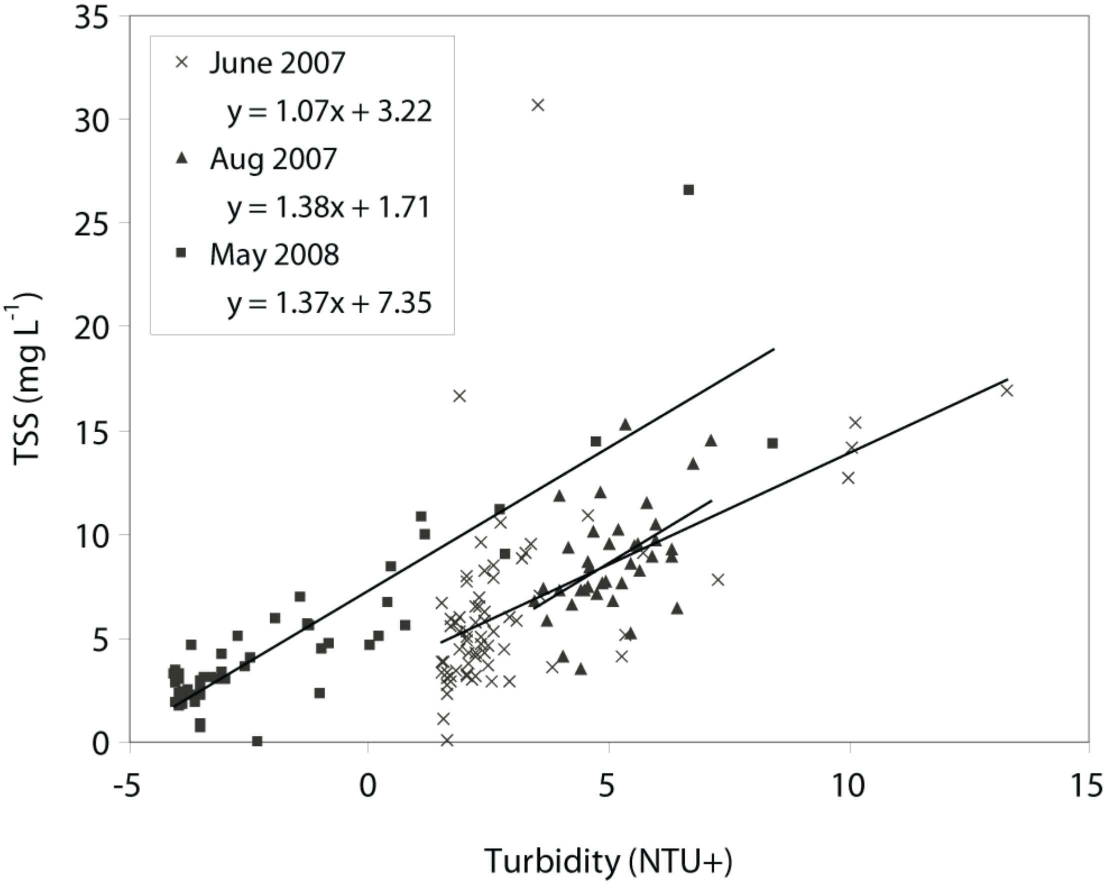


Figure AI.2: Linear regressions relating turbidity measured with data sondes to TSS measured directly at the Bed station for June (R^2=0.29, p<0.0001), August (R^2=0.24, p=0.0017), and May (R^2=0.78, p<0.0001).

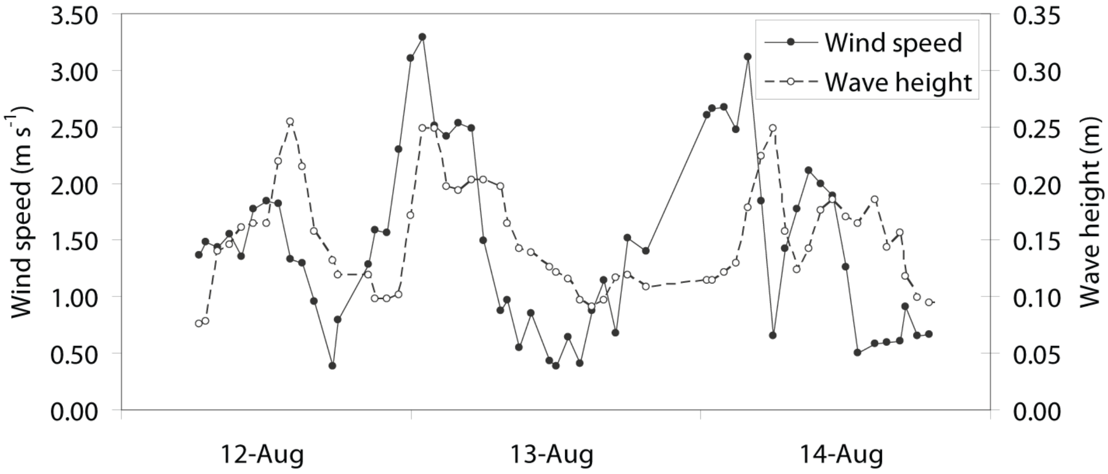


Figure AI.3: Time-series example of wind speed (HPL wind gauge) and significant wave height measurements (Bare station) during part of the August 2008 instrument deployment period. Only periods when winds were blowing from between 155 and 280 degrees (significant fetch directions) are included.

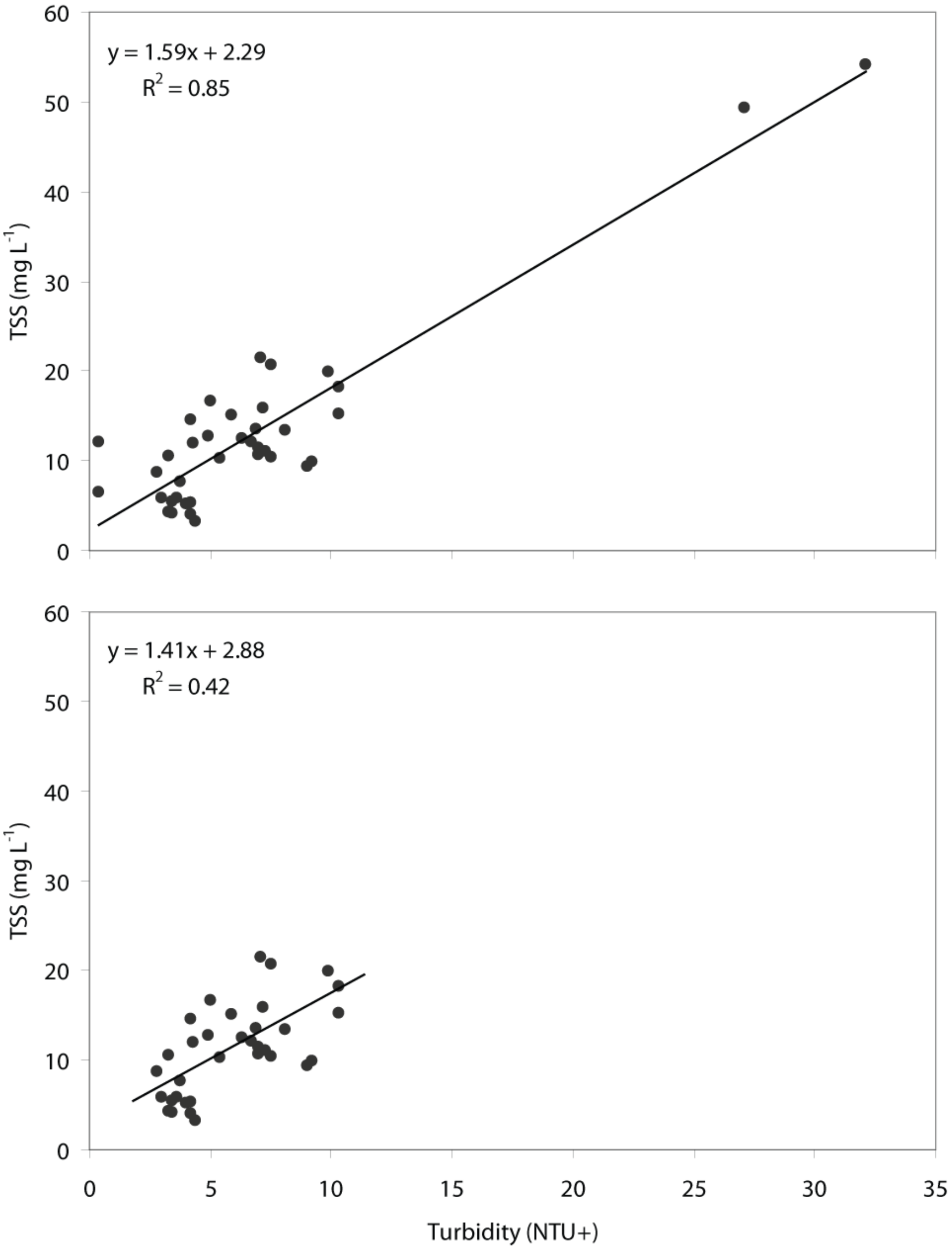


Figure AI.4: Significant ($p<0.05$) linear regressions relating turbidity (NTU+) to TSS (mg L^{-1}) using data collected with the *Dataflow* system and during quality control checks in tanks of estuarine water. The upper figure includes all concurrent samples, while the lower figure shows the regression without outlying points for comparison. The regression equation (upper figure) was used to convert turbidity to TSS for calculation of light attenuation.

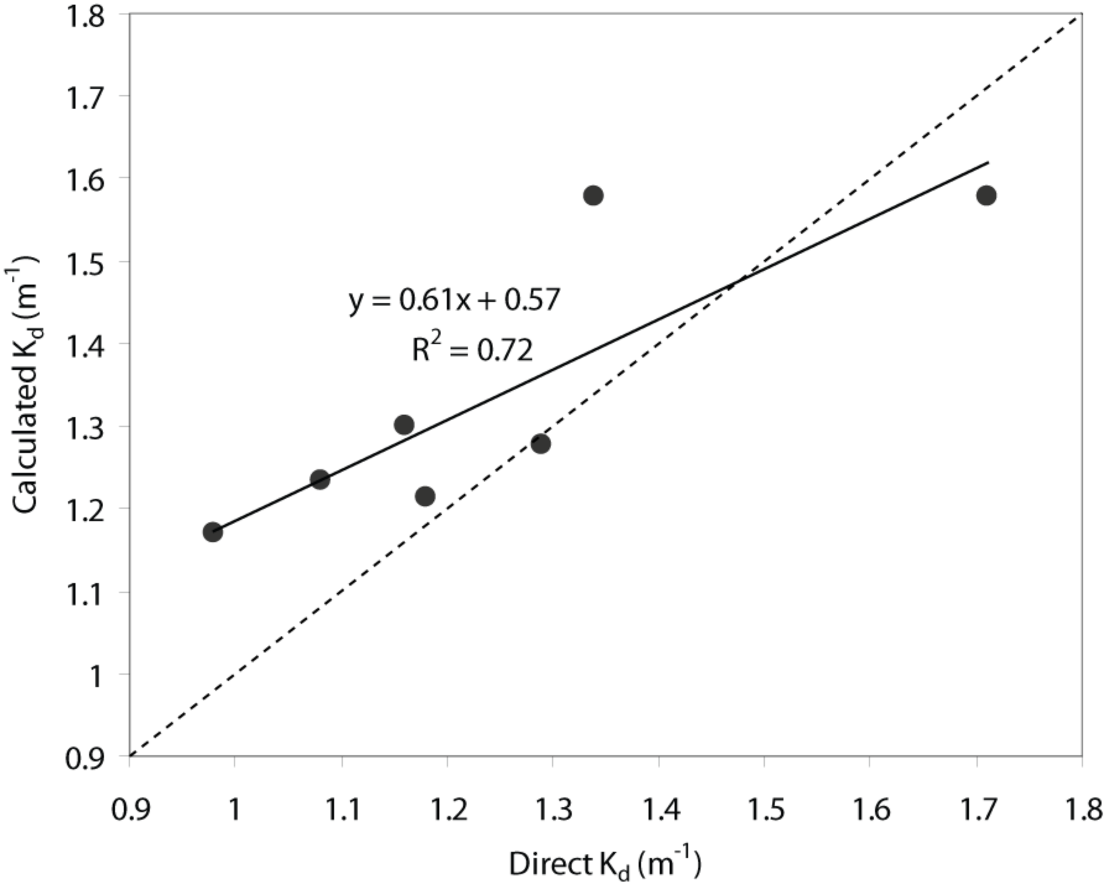


Figure AI.5: Comparison of direct and calculated estimates of light attenuation coefficients (K_d) during *Dataflow* cruises ($p=0.016$). Direct were measured with vertical PAR profiles, while estimates come from TSS and chl-*a* concentrations converted from concurrent measurements by the data sonde. The dashed line indicates 1:1 relationship.

Appendix II: Interpolated maps of turbidity created using a *Dataflow VI* flow-through sampling system in submersed plant beds

Figures AII.1-15: Interpolated turbidity maps created with *Dataflow VI* instrumentation. Turbidity contours (brown shades) were generated via a kriging procedure in ArcGIS software. Each maps shares the same legend, shown below (Fig AII.0). Black lines indicate submersed plant bed perimeters during summer months (May-July). August and September cruises were during a "low canopy" period where plants had little presence within the water column and the bed perimeter indicates the plant bed location during summer months for comparison. White lines indicate the boat's cruise track. Refer to Table 3.1 for specifics on each plant bed.

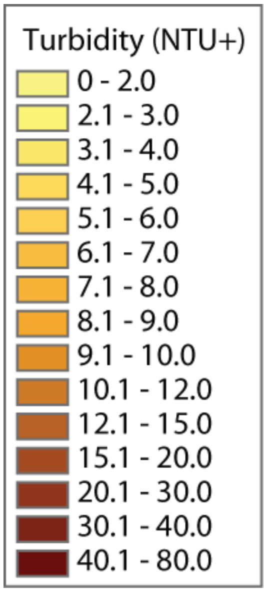


Figure AII.0: Turbidity (NTU+) legend used by all interpolated maps shown below (Figs. AII.1-15).

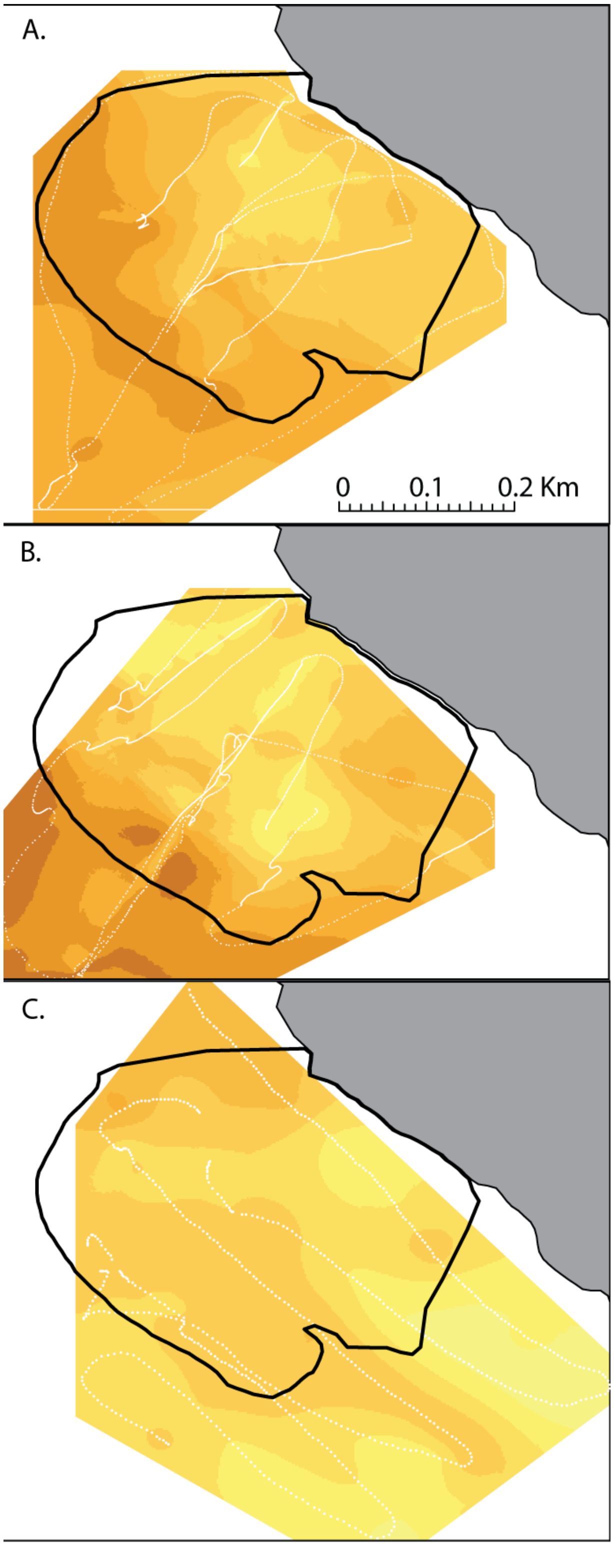


Figure AII.1: Irish Creek on 6/26/2007 (A), 6/27/2007 (B), and 9/11/2008 (C).

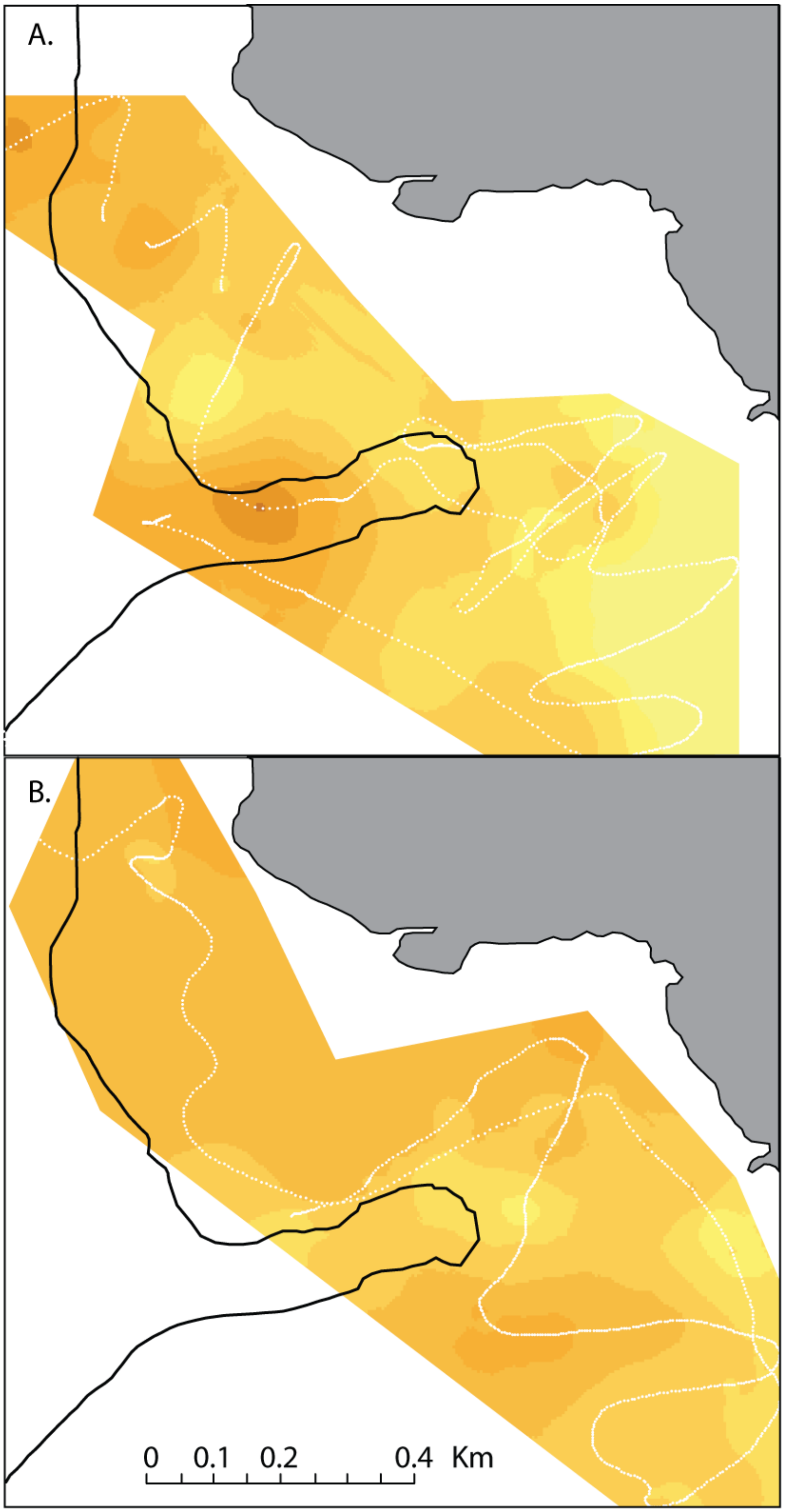


Figure AII.2: Bridge Creek on 7/1/2008 (A) and 9/11/2008 (B).

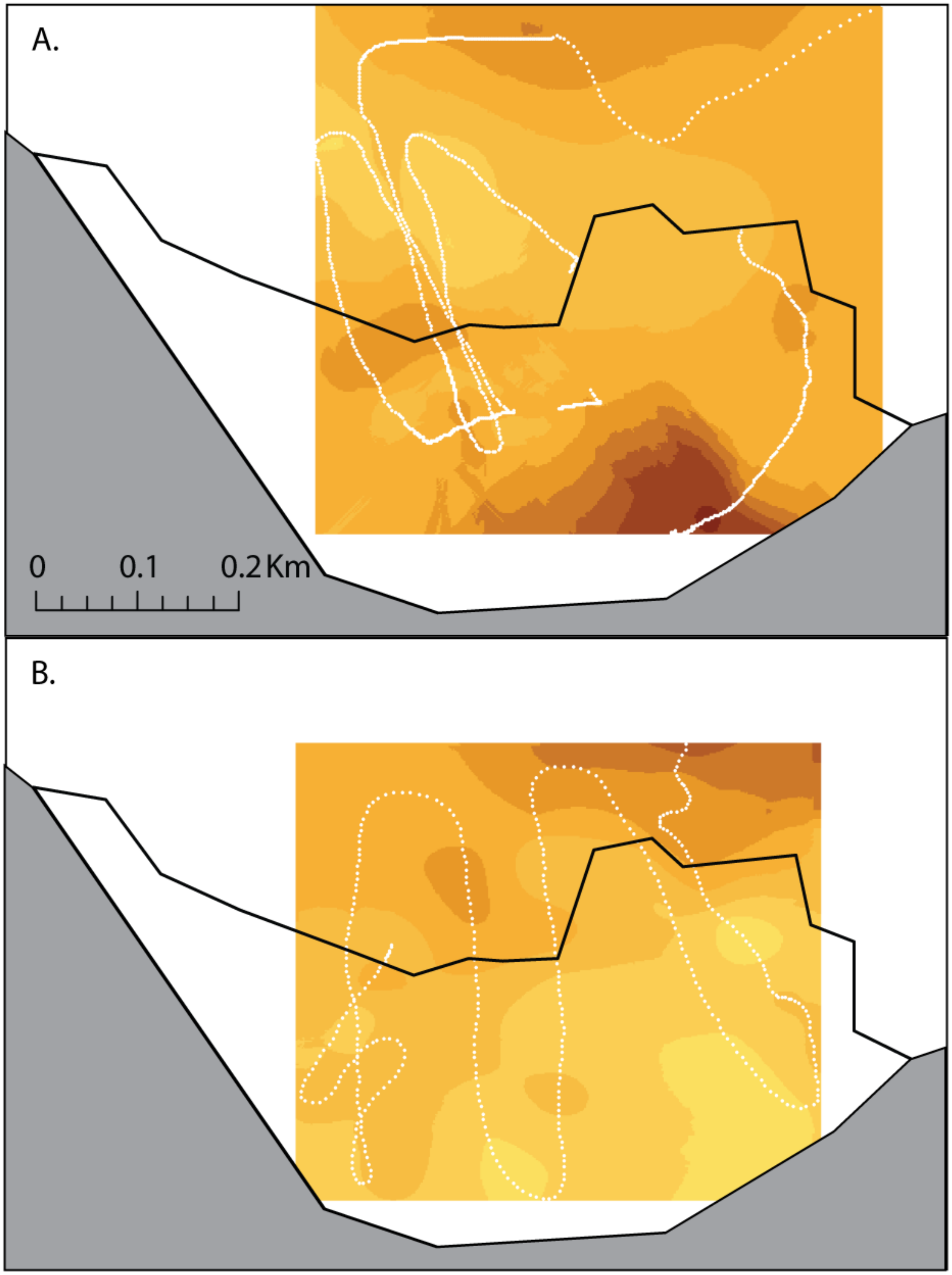


Figure AII.3: Cat Cove on 7/25/2008 (A) and 9/12/2008 (B).

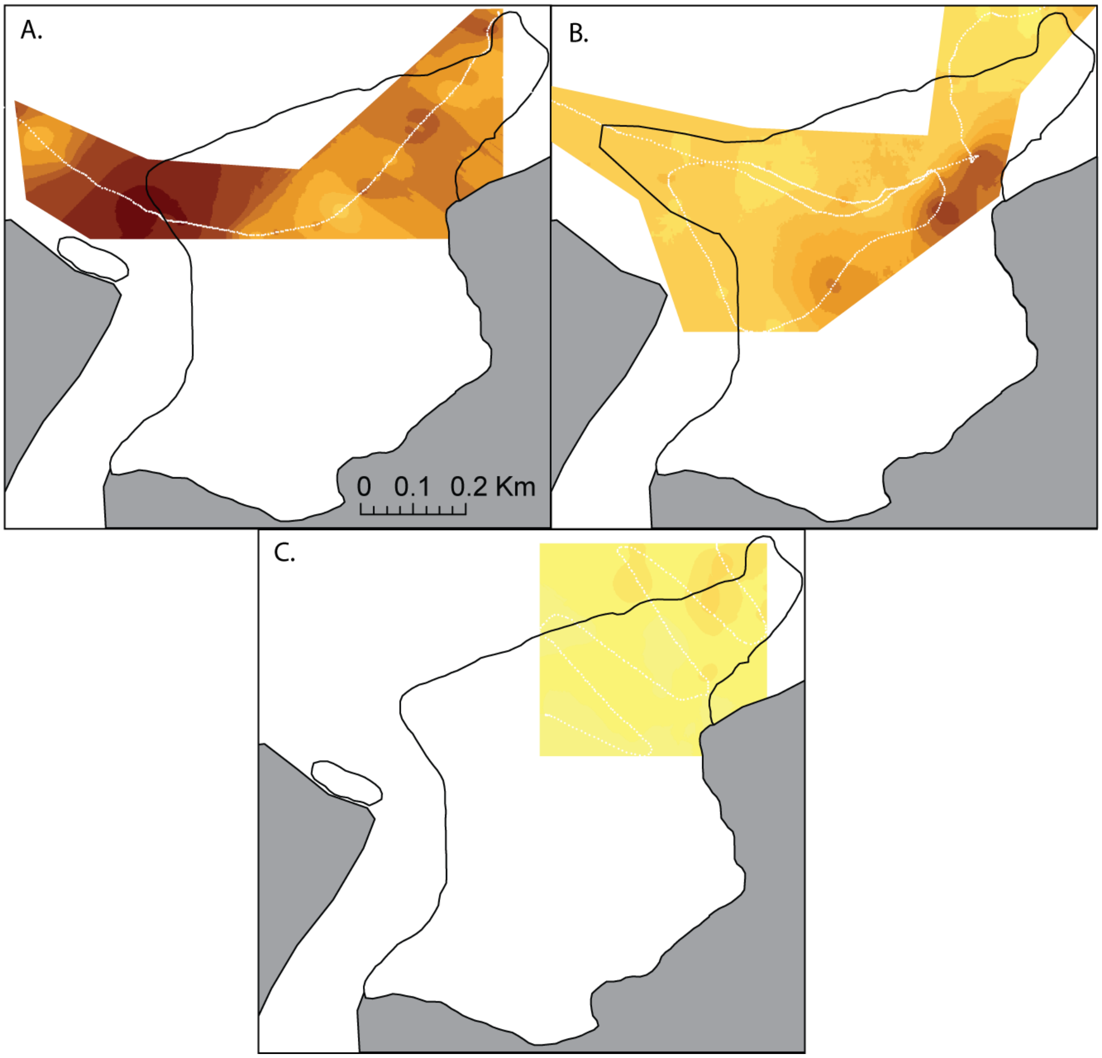
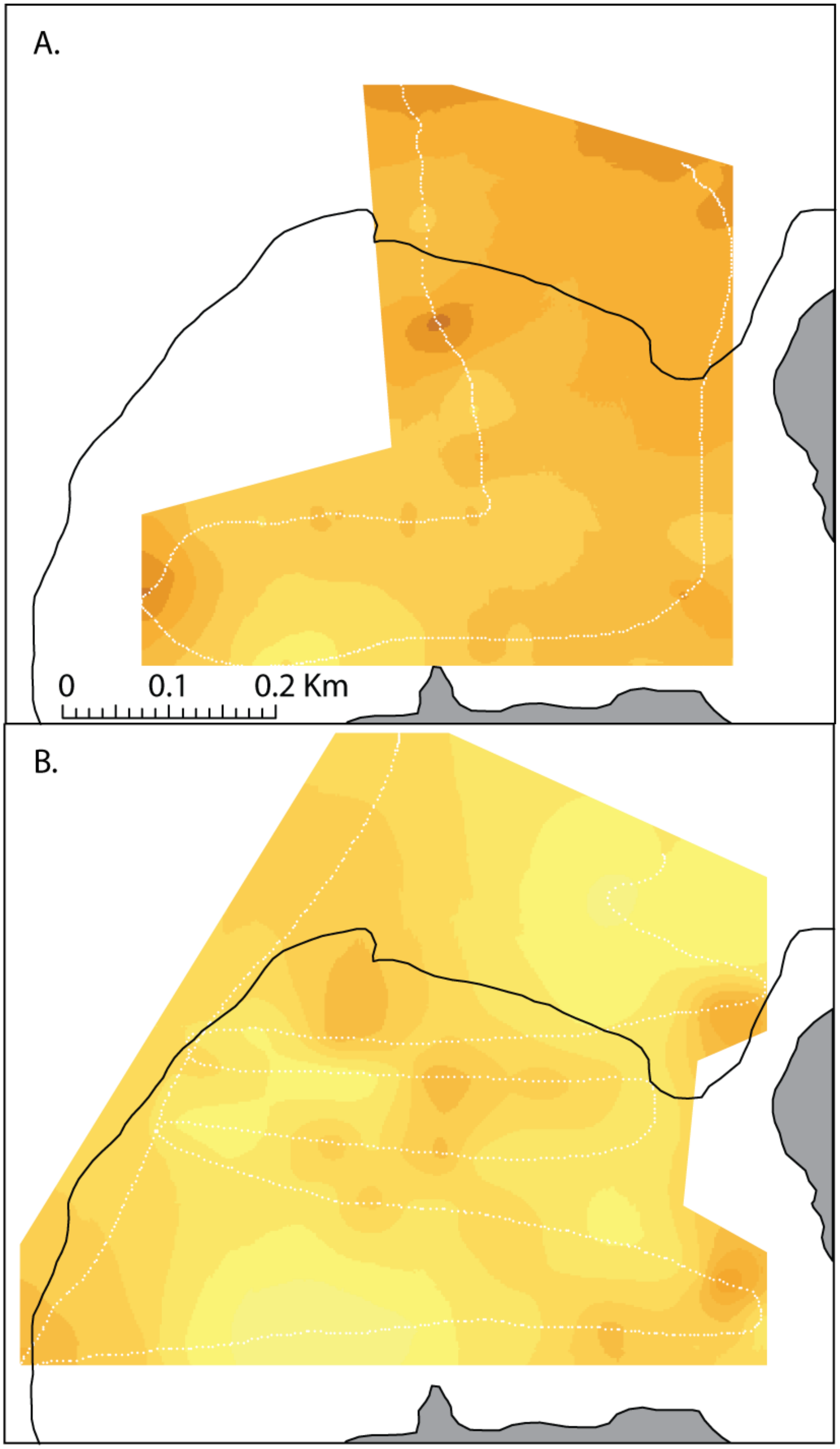


Figure AII.4: Chapel Creek on 7/24/2007 (A), 6/26/2008 (B), and 8/29/2007 (C).

Figure AII.5: Cooks Cove on 7/26/2007 (A) and 8/29/2007 (B).



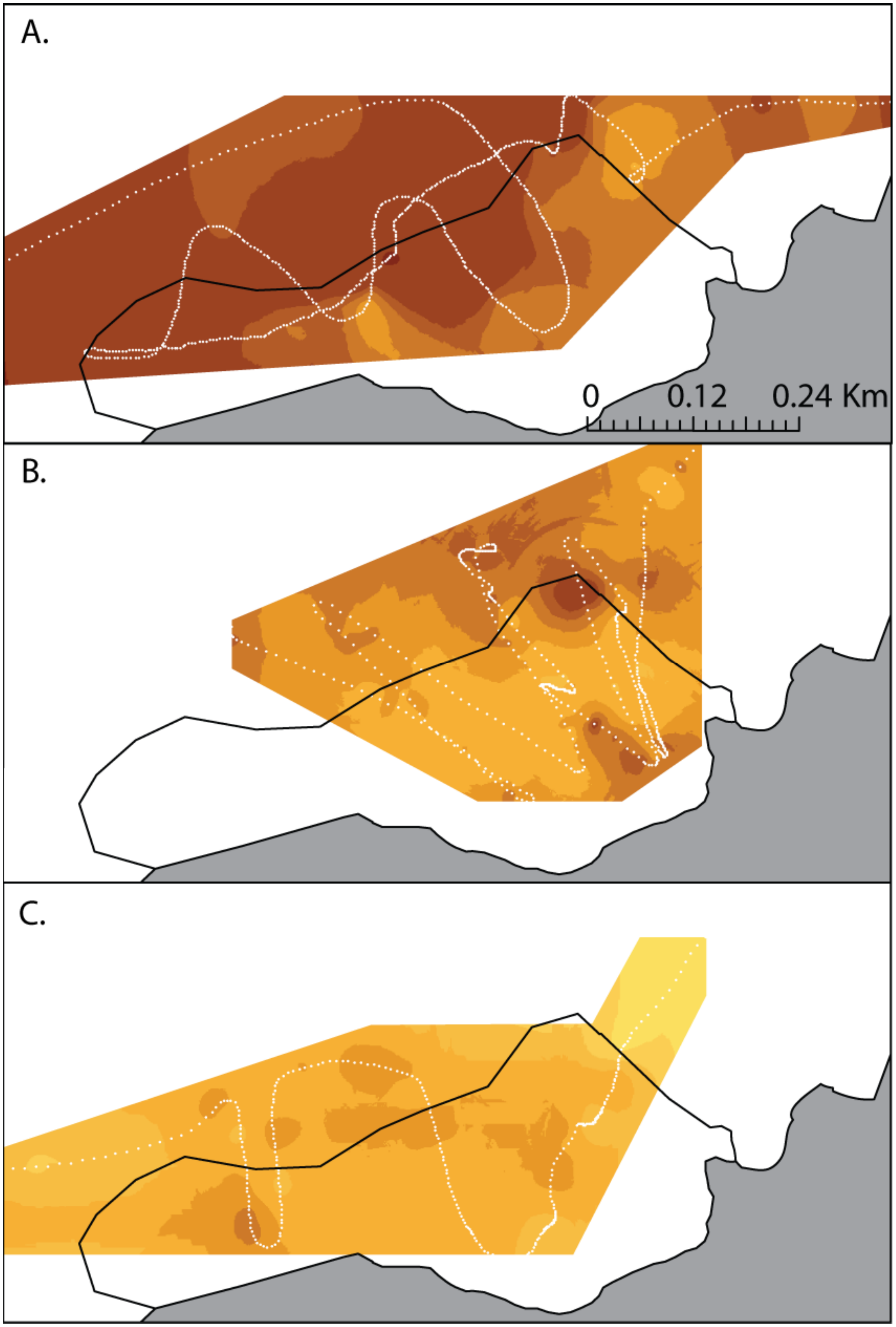


Figure AII.6: Deep Neck on 6/26/2008 (A), 7/01/2008 (B), and 9/11/2008 (C).

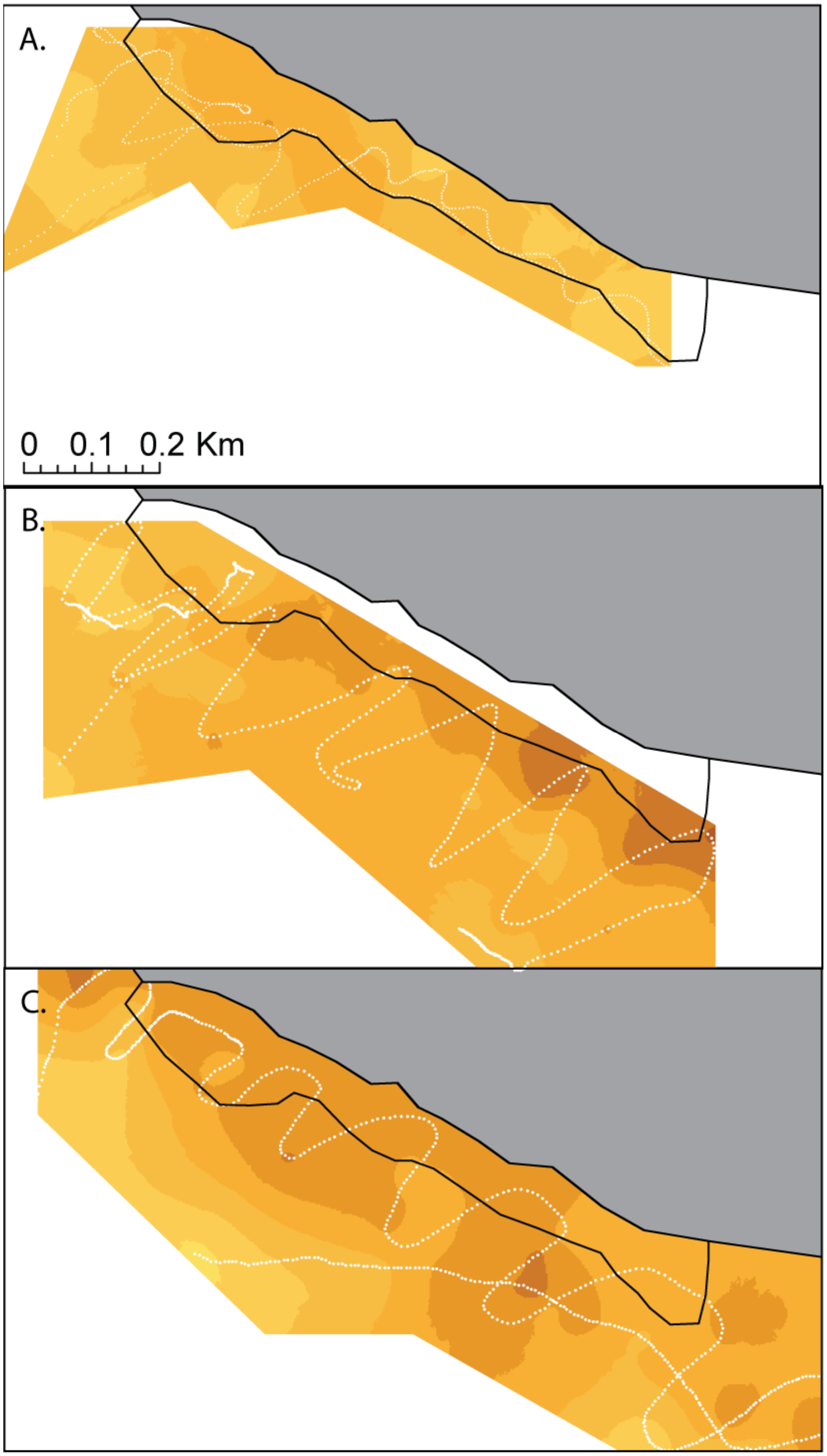


Figure AII.7: Drum Point on 6/26/2008 (A), 7/01/2008 (B), and 9/11/2008 (C).

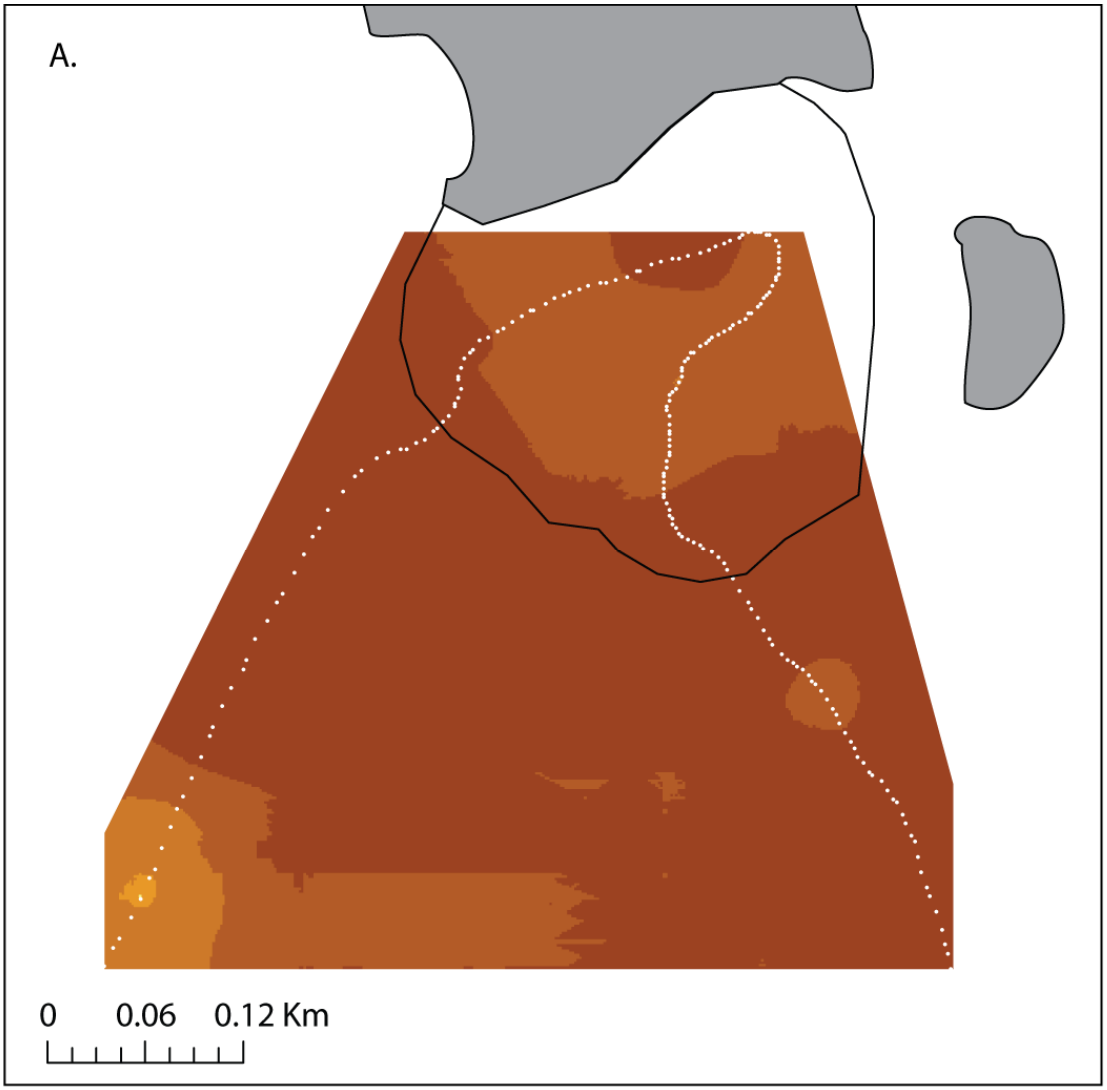


Figure AII.8: Hambleton Island on 7/24/2007 (A).

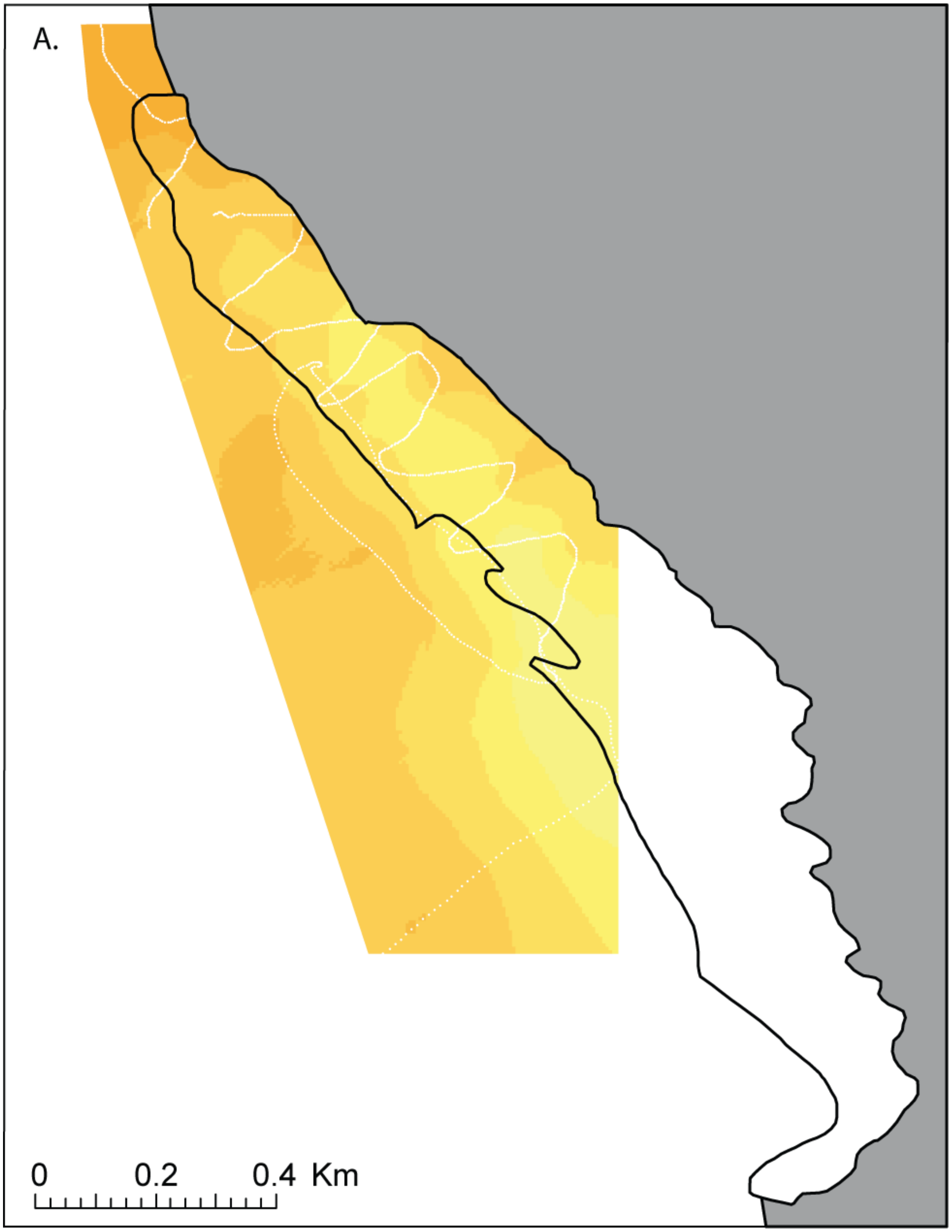


Figure AII.9: Kirwans Neck on 7/21/2008 (A).

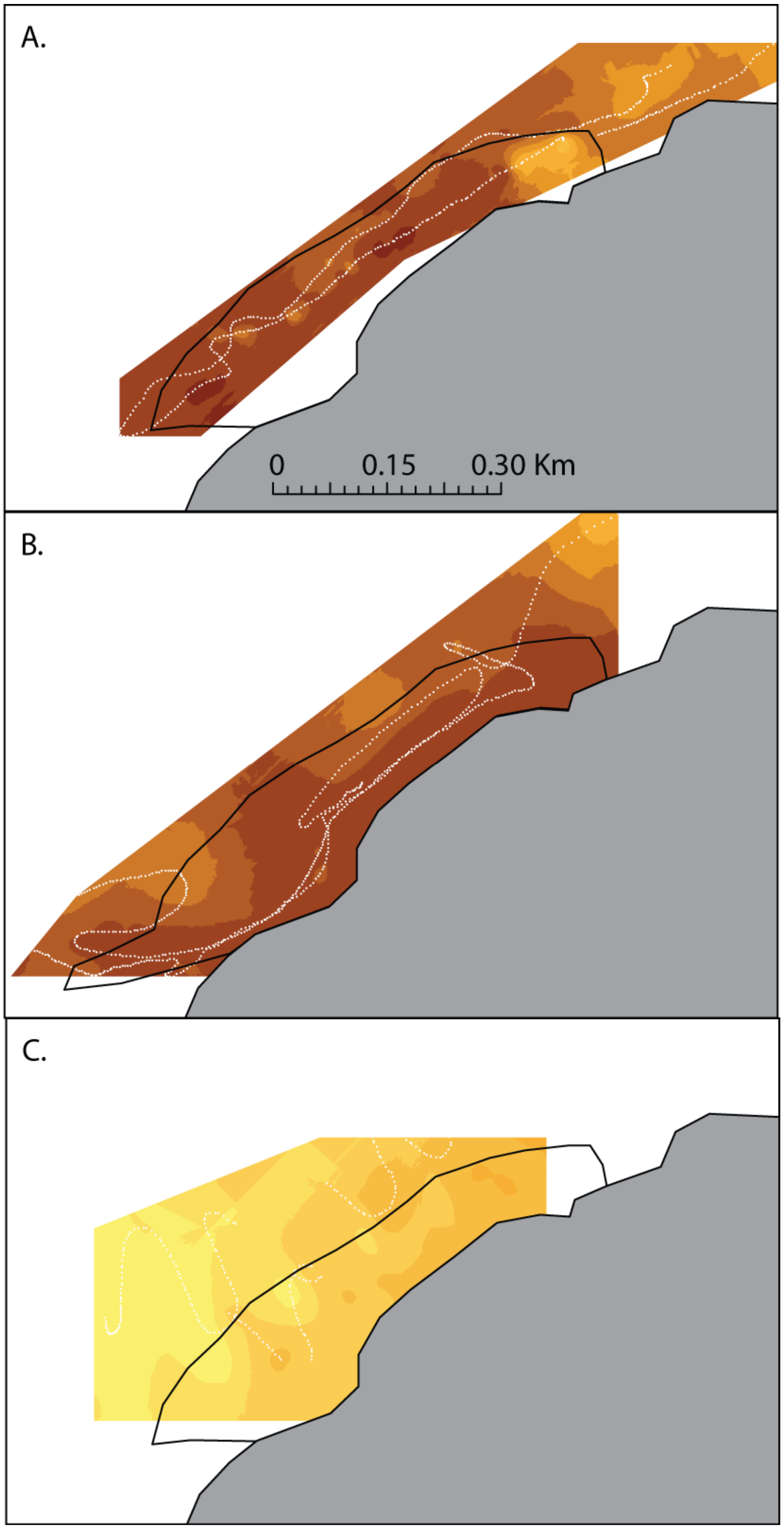


Figure AII.10: Leadenham Creek on 7/24/2007 (A), 6/26/2008 (B), and 8/29/2007 (C).

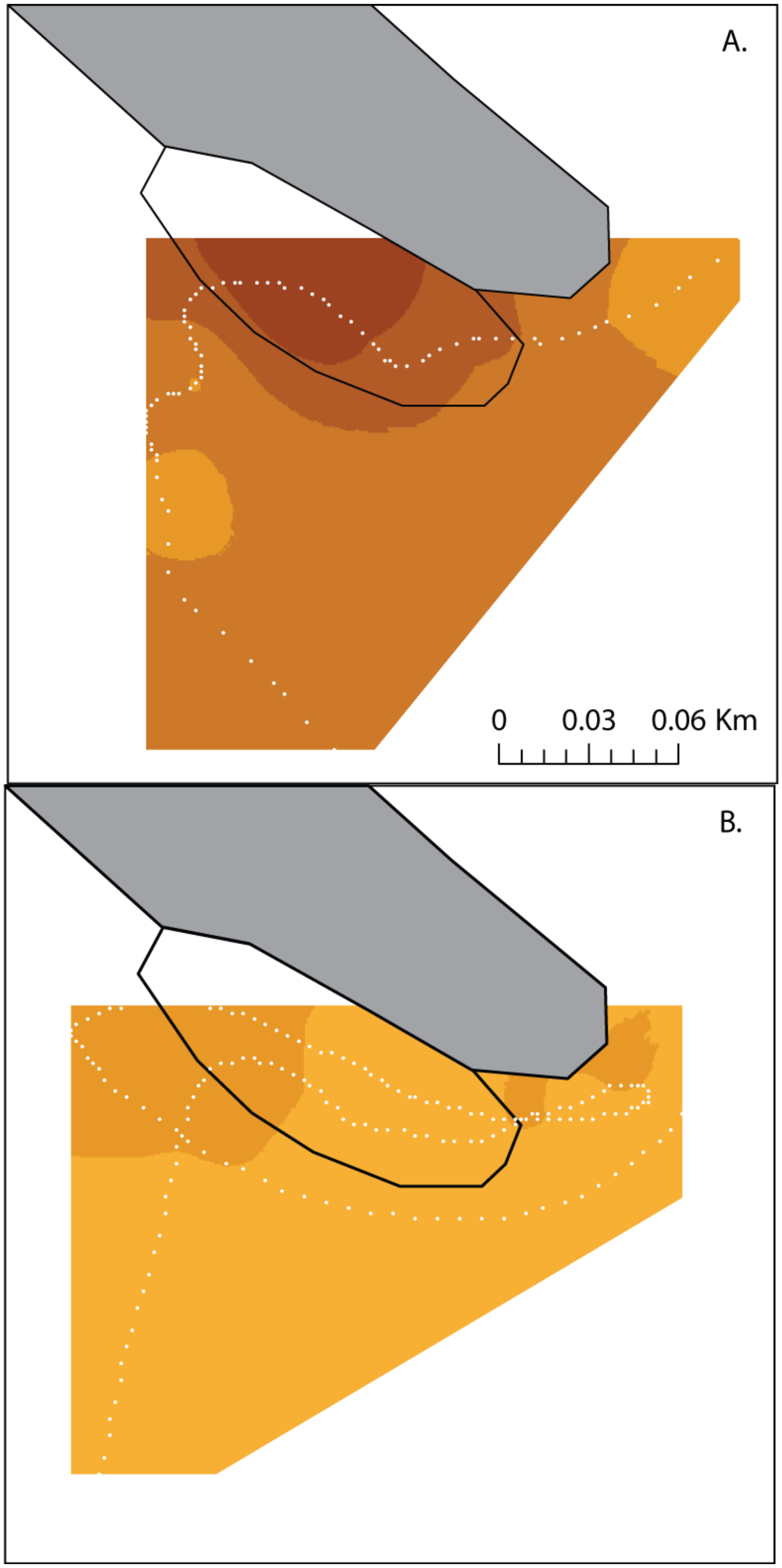


Figure AII.11: Mulberry Point on 7/24/2007 (A) and 6/26/2008 (B).

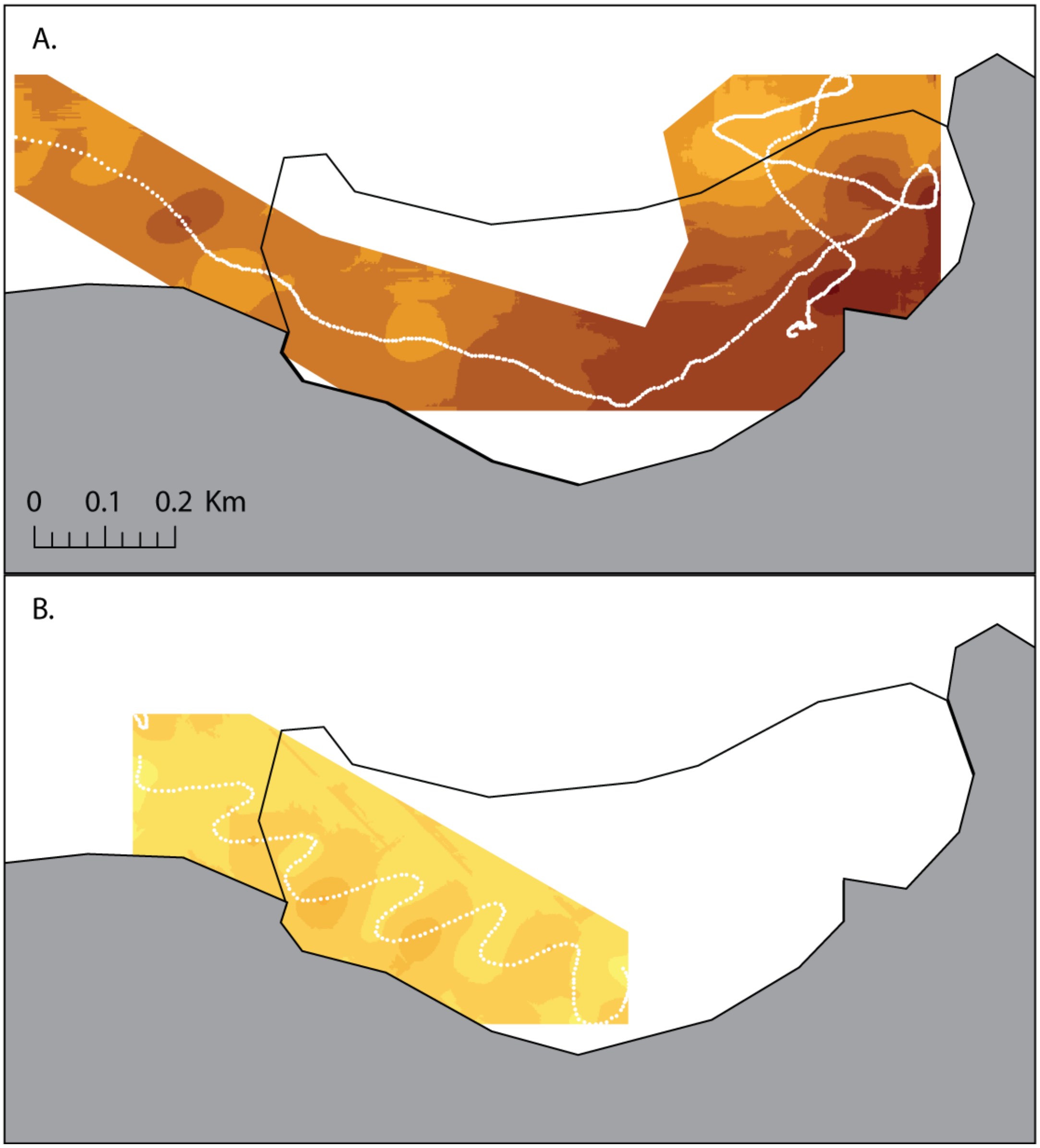


Figure AII.12: Smoke Point on 7/25/2008 (A) and 9/12/2008 (B).

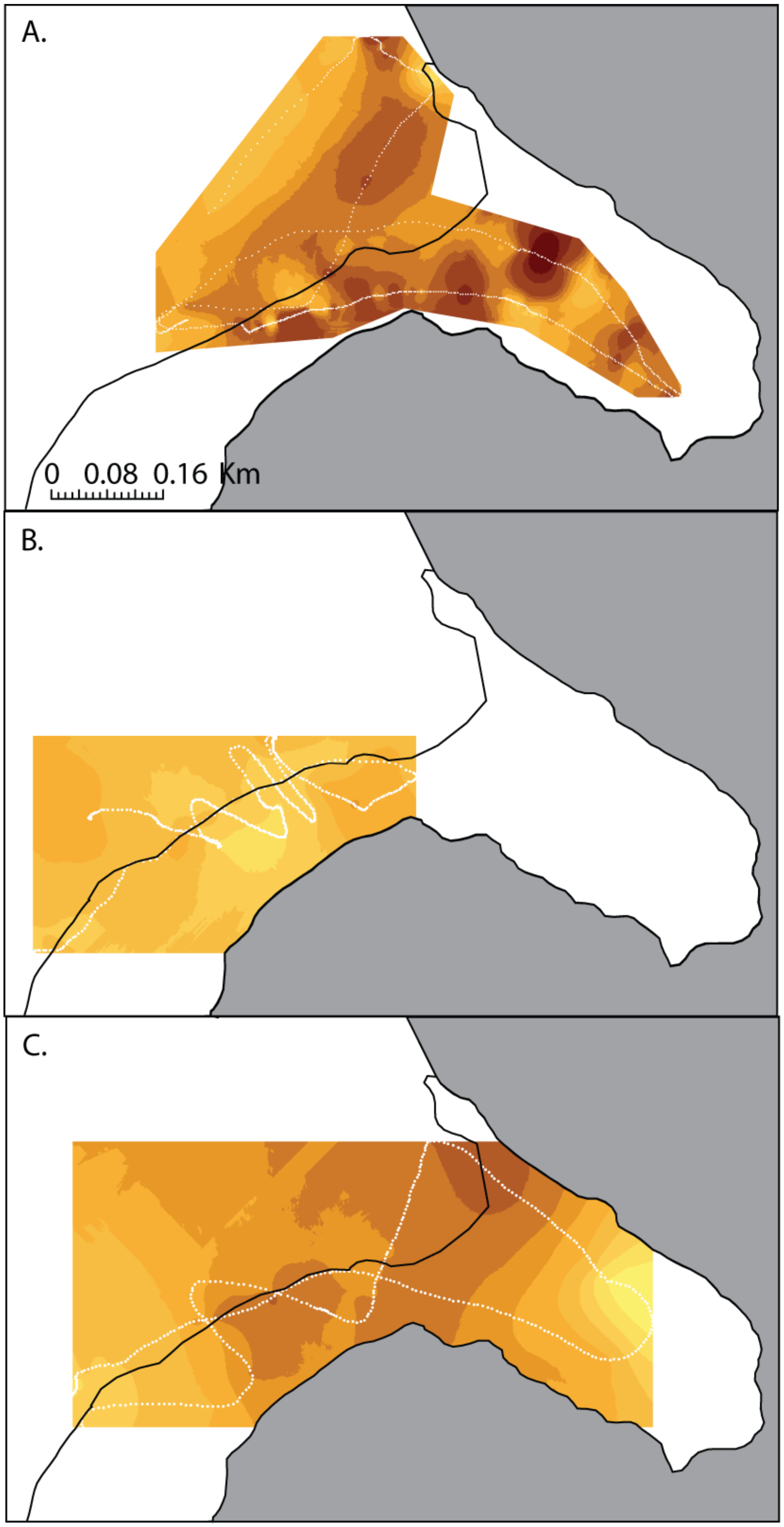


Figure AII.13: Transplant on 7/26/2007 (A), 7/21/2008 (B), and 9/11/2008 (C).

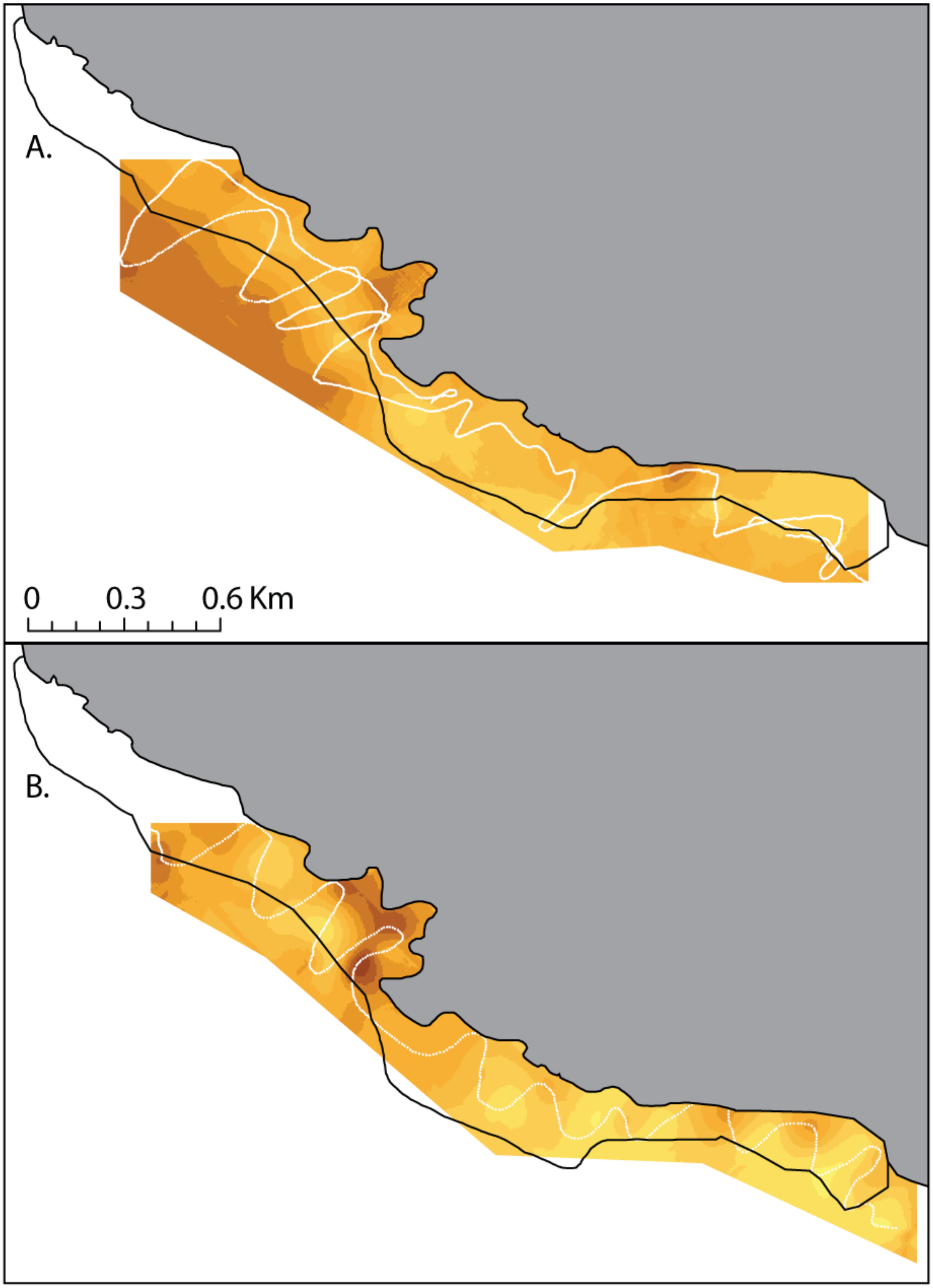


Figure AII.14: Wallace Creek on 7/21/2008 (A) and 9/12/2008 (B).

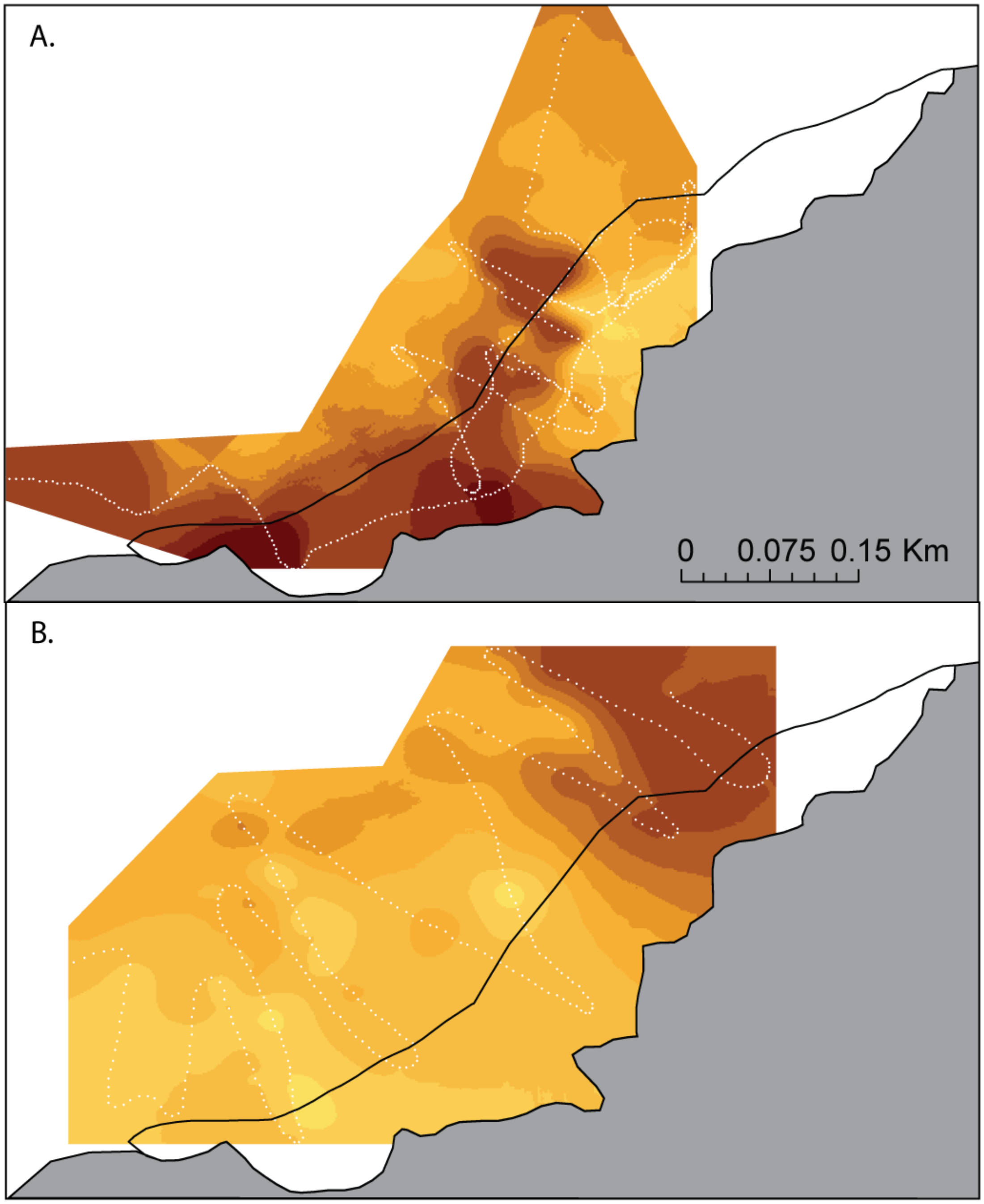


Figure AII.15: Wheatley Point on 7/21/2008 (A) and 9/12/2008 (B).

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