

ABSTRACT

Title of Document: WATER FLOW AND SEDIMENT GRAIN
SIZE AS CO-VARYING SUBMERSED
AQUATIC VEGETATION (SAV) HABITAT
REQUIREMENTS

Rebecca Swerida, Master of Science, 2013

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This study examined the importance of water flow and sediment texture as co-varying habitat parameters of submerged aquatic vegetation (SAV) in the Chesapeake Bay.

An outdoor mesocosm experiment was conducted to test the response of SAV (*Zostera marina* and *Ruppia maritima*) to combinations of water flows and sediment grain sizes characterized by sediment deposition, bedload transport and erosion.

Water flow, sediment and SAV characteristics were also determined at vegetated and adjacent unvegetated areas at 11 study sites and sediment motion conditions assessed.

Greater SAV biomass was developed by *Z. marina* and *R. maritima* experiencing sediment motion than sediment deposition. Although habitat parameter thresholds *in situ* were site-specific, overall SAV presence was limited to moderate ranges of both water flow and sediment grain size. All SAV habitat observed was characterized by sediment bedload transport. Consideration of both water flow and sediment habitat requirements will improve SAV restoration success.

WATER FLOW AND SEDIMENT GRAIN SIZE
AS CO-VARYING SAV HABITAT REQUIREMENTS

By

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Chapter 1: Water Flow and Sediment Texture in Submersed Aquatic Vegetation Beds

Introduction

Loss of submersed aquatic vegetation (SAV) is a serious problem world-wide. In particular, a review of 215 peer-reviewed studies has determined that seagrass (a group of marine SAV species) habitat has declined 29% since 1879. Seagrass habitat has been lost at rates that have increased from approximately $0.9\% \text{ yr}^{-1}$ before 1940 to $7\% \text{ yr}^{-1}$ since 1990 (Waycott et al. 2009). This rate of habitat loss exceeds even the rate of disappearance of tropical rainforests ($0.5\% \text{ yr}^{-1}$) and approximately matches that of mangroves ($1.8\% \text{ yr}^{-1}$) and coral reefs (1 to $9\% \text{ yr}^{-1}$) (Valiela et al. 2001; Achard et al. 2002; Gardner et al. 2003). Currently, one third of all seagrass species are believed to be in global decline, and one fifth of all seagrass species have been listed as “Endangered, Vulnerable or Near Threatened” under the IUCN-Red List Criteria as of 2011, although the status of many species requires more thorough investigation (Short et al. 2011).

Regional declines in SAV populations are more quantifiable than global losses, are often rapid, and can be quite severe (Orth 2002). More importantly, primary causes can often be pin pointed for these SAV die offs. Human activity is most often the cause of SAV decline, whether from anthropogenic inputs of nutrients and sediments, degrading water quality, from destructive fishing practices or other

activities such as direct removal through habitat conversion (Short and Wyllie-Echeverria 1996; Short et al. 2001). SeagrassNet, a world-wide seagrass monitoring network, has observed regional seagrass declines since 2001. In two out of five cases, eutrophication caused by agricultural and residential use was identified as the driver of SAV decline. In two other cases, increased storm frequency and increasing temperatures associated with global climate change were implicated, and, in one, human caused trophic shifts impacted SAV populations (Short et al. 2006). Preen and Marsh (1995) described how Hervey Bay, Australia suffered pulsed turbidity events following frequent storms resulting in 1000 km² of seagrass loss which in turn negatively impacted local dugong populations, demonstrating both regional seagrass decline and the importance of SAV as an ecological keystone species. Seagrass decline was successfully reversed in Mondego Bay, Portugal when anthropogenic stressors were mitigated. The highly eutrophic system was managed to significantly reduce nitrogen loading, increasing water quality and light availability within the seagrass habitat (Cardoso et al. 2004).

SAV populations in the Chesapeake Bay represent one of the most severe, overall declines in the USA. Only a small fraction of the historic Chesapeake Bay SAV distribution exists today, a loss both exacerbated by and contributing to growing benthic hypoxia (Fisher et al. 2006). The first known considerable decline in SAV population occurred in the 1930s when the ‘wasting disease’, presumably a slime mold infection, took hold in *Zostera marina* beds in the North Atlantic and the Chesapeake Bay (Orth and Moore 1984; Hartog 1987; Short et al. 1988). SAV began another precipitous decline in the 1970’s due to increased eutrophication and an

intense storm event in the estuary (Orth et al. 2002). Some re-growth in SAV population has occurred since, but much less than the Chesapeake Bay Program recovery goal of 185,000 acres of SAV coverage in the Chesapeake Bay and its tidal tributaries (CBP 2013).

Research on SAV restoration and conservation has increased worldwide due to this decline. Combating the loss of SAV is important as these plants are among the most valuable and productive ecosystems in the world (Costanza et al. 1997). Primary production rates have been measured as high as $1000 \text{ g dry wt m}^{-2} \text{ yr}^{-1}$, higher than that of mangrove ecosystem production measured in the Dominican Republic to be $197 \text{ g dry wt m}^{-2} \text{ yr}^{-1}$ (McRoy and McMillan 1977; Sherman et al. 2003). SAV also helps to cycle nutrients (Orth et al. 1984), provides a substantial carbon sink (Attrill et al. 2000), filters suspended materials from the water column (Madsen et al. 2001) and provides nursery habitat (Wigand et al. 1997) for a wide variety of fish and invertebrates such as the blue crab (*Callinectes sapidus*) and striped bass (*Morone saxatilis*) (Kenworthy et al. 1982; Wyda et al. 2002). Large scale, international restoration efforts have been launched in response to the loss of such valuable habitat (Thom et al. 2005). It is, in fact, considered imperative to mitigate SAV losses with restoration in order to maintain near shore and estuarine ecosystem health (Constanza et al. 1997; Duarte et al. 2008). From the 1940's until the 1980's, scientific interest in SAV restoration was inconsistent, sometimes very high, but not always a priority. The goal of SAV habitat recovery has remained a fairly high priority in the marine science community since then (Fonseca 2011). An estimated \$1 billion per year was

spent on river and estuarine restoration between 1990 and 2005 in the USA, and that level of effort has presumably continued (Bernhardt et al. 2005).

The most common method of SAV restoration is currently the transplantation of adult shoots and seedlings from healthy beds to unvegetated areas. Shoots can be transplanted as part of sod mats or as individual shoots (Fonseca et al. 1998). They can also be attached to a large metal planting frame which is thrown over the selected restoration site and holds the plants in place long enough for them to take root, and then the frames are collected for reuse (Short et al. 2002). Broadcasting of seeds, both by hand (Orth 2002) and through a mechanized buoy deployed seeding system that was developed for *Z. marina* but is being adapted to the needs of other species (Pickerell et al. 2006), is another method growing in popularity. Several other mechanized techniques (Fonseca et al 1998, Paling et al. 2001, Traber et al. 2003, Fishman et al. 2004, Bell et al. 2008, Orth et al. 2009, Uhrin et al. 2009) have been tested, but these applications remain largely experimental. An assessment of different restoration techniques was conducted in South Australia using several species of indigenous SAV (Irving et al. 2010). It was found that shoot transplantation success was very variable and appeared to be site dependent. Seed culturing and outplanting produced poor survival, but those seedlings that did survive grew well. The use of sand filled hessian, or burlap, bags in order to protect transplanted seedlings produced the best results (Irving et al. 2010). A somewhat similar technique using the hardier SAV species *Ruppia maritima* instead of hessian bags to create a protected site for seedling transplantation has also been explored (Hengst et al. 2010).

Although some success (i.e. vegetation persists interannually) has been achieved through these methods of SAV restoration, the improvements have not been proportional to the amount of effort expended. Despite the implementation of several large scale restoration projects in the Chesapeake Bay, only 10% of restoration has been successful, i.e. self-sustaining over time (Orth et al. 2006; Bell et al. 2008; Orth et al. 2009). Similarly, a survey of European restoration projects has found that none of the participant restoration projects over the past 10 years were entirely successful (Cunha et al. 2012). The variability in success of these projects within site was often related to habitat parameters such as depth (light availability), wave exposure and sediment characteristics among other factors (Fonseca et al. 1998; Bologna et al. 2001). Restoration projects also tend to be poorly monitored and do not always apply standards for site selection to their design (Fonseca et al. 1998; Bernhardt et al. 2005; Fonseca 2011). For example, restoration attempts in New Jersey have largely failed due to physical and biological disturbances, poor project planning and arbitrary site selection with no consideration for SAV habitat requirements (Bologna et al. 2001). A more recent study very specifically addressed these project design flaws and restored both *Z. marina* and *R. maritima* beds through transplantation with some success in Barnegat Bay (Bologna and Sinnema 2012). Restoration success has improved as methods are developed to implement a growing, but still small, knowledge base about SAV habitat requirements (Paling et al. 2009; Ailstock et al. 2010; Busch et al. 2010; Hengst et al. 2010; Koch et al. 2010; Leschen et al. 2010; Moore et al. 2010; Pan et al. 2011).

Recently, a greater emphasis has also been placed on the protection and conservation of existing beds as a priority instead of relying on SAV restoration after initial bed degradation. The Chesapeake Bay Agreements (five between 1983 and 2000), an SAV Management Policy and Implementation Plan for Chesapeake Bay and Tidal Tributaries (1989 and 1990), Chesapeake Bay Blue Crab Fishery Management Plan (1997) and additional state and federal guidelines for the protection of SAV have been put in place to reduce the deterioration of existing SAV beds (Orth et al. 2002). Mitigation of negative anthropogenic inputs such as agricultural and industrial run off and protection of existing beds from boater damage has effectively reversed SAV decline in Florida and Portugal among other sites (Waycott et al. 2009).

SAV conservation and if necessary, restoration is nonetheless an important tool for improving local and worldwide SAV health. SAV restoration may benefit most from improved site selection methods (Fonseca et al. 1998). The establishment of minimum SAV habitat criteria has been an area of research focus for the improvement of SAV restoration success (Koch 2001; Short et al. 2002; Kemp et al. 2004; Steward et al. 2005). The understanding that the biological and physical limits of SAV survival must be accounted for when selecting sites for restoration is not new; one of the seminal papers concerning *Z. marina* restoration in the Chesapeake Bay references the importance of selecting sites with attributes specifically similar to nearby successful SAV beds (Addy 1947). It has been clearly seen through a review of restoration projects that a greater degree of success can be achieved when site selection has been properly evaluated and implemented (Paling et al. 2009). However,

it also seems clear that mistakes in restoration site selection and ignorance of specific SAV habitat requirements “constitute the single greatest challenge in the restoration process” (Fonseca 2011).

When SAV habitat requirements are considered during restoration site selection and project planning, light availability criteria is usually the only habitat requirement considered (Orth et al. 2010; McGraw and Thom 2011; Fonseca 2011). Light is unquestionably a key limiting factor for SAV survival and the primary limitation to SAV distribution (Kemp 1984; Duarte 1991; Dennison et al. 1993; Livingston et al. 1998). A depth limit of where <1-4% of light is able to reach the plants has been proposed, and freshwater species of SAV have been observed mainly between 0 and 4 meters depth, although occasionally appearing as deep as 6 m (Sculthorpe 1967; Sheldon and Boylen 1977; Maemets and Freiberg 2007). In the Chesapeake Bay, marine SAV (i.e. seagrasses) tends to require more light than freshwater species, presumably as a result of general differences in their morphology (Dennison et al. 1993). The relationship between successful SAV restoration and increased light availability has also been noted in other places. For example, the recovery of nearly 30 km² of seagrasses due to a decades long effort to reduce nitrogen loading of Tampa Bay and the resulting doubling of water clarity exemplifies the dependence of SAV on light availability (Greening and Janicki 2006). Also, regrowth of SAV occurred in the Choptank River, located in the mesohaline region of the Chesapeake Bay, after a reduction of anthropogenic inputs reduced the mean light attenuation coefficient (K_d) to < 2 m⁻¹ (Staver et al. 1996).

However, the inconsistency in success of SAV restoration under conditions meeting light availability requirements indicates that other parameters also need to be considered (Koch 2001). An explanation remains elusive as to why SAV often occurs in one region with sufficient light while nearby areas with the same light availability are bare. It was estimated that only approximately 9% of restoration projects account for recommended sediment characteristics during site selection despite evidence of the importance of habitat parameters other than light (Fonseca et al. 1998).

Hydrodynamic and sedimentological SAV habitat requirements have both been researched and habitat criteria recommended (Koch 2001). The variability in seagrass distribution in the Indian River Lagoon in Florida was only explained to 50% by light availability. The other 50% of variability in distribution was attributed to wave activity, sediment characteristics and biological competition (Steward et al. 2005). Similarly, the success of *Z. marina* restoration in Boston Harbor was highly dependent on sediment characteristics. Restoration failed at sites where sediment silt and clay content exceeded 35% (Leschen et al. 2010).

Not only is it important to consider hydrodynamic and sedimentary habitat requirements individually in order to assess SAV habitat suitability, but it is also important to consider water flow and sediment characteristic requirements jointly. These habitat parameters are inherently linked to each other and both impact many of the same aspects of SAV growth in different, sometimes conflicting ways. Laboratory based flume experiments found that *Z. marina* and *R. maritima* grew successfully under several water flow conditions (Seeliger et al. 1984; Wicks et al. 2009). However, it was found that *Z. marina* could not tolerate finer grain size sediments due

to the drag of flow velocity on the shoots and leaves which grew a particularly large surface area in the sediment containing abundant nutrients (Wicks et al. 2009). This is an example of the importance of considering these habitat parameters together when establishing habitat requirement criteria.

Understanding the fluid dynamics driving sediment transport in and around seagrass canopies have been studied in detail from an engineering point of view and the significant relationship between the seagrass canopy, water flow and sediment grain size is well known. When water flows over a bed of sediment, bottom shear stress is generated in proportion to the flow speed and other characteristics and acts on the sediment surface. Sediment grains may be transported if the critical shear stress is met or exceeded, either in suspension within the water column or in bedload along the sediment surface. The critical shear stress for each grain is determined by its size, shape and density. If the shear stress generated by the water flow is excessively larger than the critical shear velocity necessary for the initiation of motion, erosion will occur. If the shear stress generated is less than the critical shear stress, deposition, or settling out of the water column, will occur in proportion to the deficit of shear stress below the critical value (van Rijn 1993). These principles of sediment motion are summarized in the Hjulstrom diagram (Figure 1.1) as it relates water flow velocity to sediment grain size (Hjulstrom 1935). This is a practical tool for understanding sediment motion under controlled conditions, however there are many assumptions associated with this diagram such as unidirectional flow, sediment density of quartz, homogeneous sediment grain size, constant temperature and fluid viscosity etc. that limit its applicability to natural SAV habitats. Also, shear stress, a

measure of the force of a flowing fluid against a surface area, is a more appropriate measure of hydrodynamic activity when applied to benthic ecology than the generic ‘water flow’ used in the Hjulstrom Diagram (Peterson 1999). The Shields diagram utilizes dimensionless parameters, Shields parameter derived from shear stress and boundary Reynolds number derived from sediment grain size, to account for many of those assumptions and allows for application under combined and oscillatory flows (*sensu* Miller et al. 1977, Figure 1.2). A modification of this diagram relates shear stress to sediment grain size. These diagrams provide accessible and accurate means of characterizing the sediment motion characteristics of vegetated and potential SAV habitats.

Despite the physical understanding of sediment, there has been little application of sediment motion assessment to SAV restoration studies. Sediment motion and antecedent flow velocity and sediment characteristics have been suggested (Koch et al. 2006) and then shown to limit the minimum depth of distribution of *Posidonia oceanica* (Infantes et al. 2009). Most research suggests that SAV thrive in quiescent depositional habitats (Barko and Smart 1983; Szmeja and Bazydlo 2005; Moore et al., 2010) as well as depositional habitats in terms of sediment transport (Gambi et al. 1990, Ackerman and Okubo 1993, Heiss et al. 2000). Seagrass beds are known to change the sediment motion within a bed by reducing wave orbital velocities and dissipating all but the longest period waves (Hansen and Reidenbach 2012). Sediment can be eroded outside seagrass beds, while deposited inside the bed (Hansen and Reidenbach 2012). Evidence exists indicating that depositional habitat could be as limiting to SAV as highly erosional habitat. SAV,

seedlings in particular, are vulnerable to being uprooted and dislodged under erosion conditions based on the capacity of the roots to remain anchored (Madson et al. 2001; Infantes et al. 2011). The ability of SAV to survive burial in depositional habitats is strongly dependent on the size and morphology of plants (Idestam-Almquist and Kautsky 1995, Mills and Fonseca 2003; Cabaco et al. 2008; Infantes 2011).

Water flow and sediment grain size are each limiting to SAV through different mechanisms, but these limitations are also affected by other habitat parameters. SAV can thrive in a wide range of hydrodynamic conditions and sediment grain sizes (Arts et al. 1990; Szymeja and Bazydlo 2005; Puijalon et al. 2005). Upper limits of water flow velocity ranging from 7 cm s⁻¹ to 180 cm s⁻¹ have been identified for different species of SAV (van Katwijk and Hermus 2000; Koch 2001; Cabaco et al. 2010; Infantes 2011). SAV can grow in very coarse, sometimes armored sediment with very little organic content as well as very fine sediment with high organic content (Barko and Smart 1983; De Falco et al. 2000; Puijalon et al. 2005).

Changes in SAV morphology have been associated with both water flow and sediment grain size individually and in combination. Exposure to high wave activity can change the size, shape and orientation of plants as they adapt to withstand increased drag (Blanchette 1997; Doyle 2001; Strand and Weisner 2001; Bal et al. 2011; Loher and Nepf 2011). Flower fertilization and seed and fragment dispersal are important benefits of water motion (Ackerman 1986; Johansson et al. 1996; Boedeltje et al. 2004). SAV in coarse sediment, often containing limited organic content (Berner 1977) can experience limited growth (Short 1987), and develop shorter, narrower leaves and longer roots (Lee and Dunton 2000; Wicks 2009). Conversely,

SAV in fine sediment containing higher organic content can develop greater above-ground biomass and lesser below-ground biomass (Short 1983; Lee and Dunton 2000). The development of reproductive structures can also be closely dependent on the organic content of sediments (Palinkas et al. 2010). The proportion of above and below ground biomass can also be dependent on the availability of nutrients in the water column as well as the sediment (Maitai and Newton 1982). Thus, both water flow and sediment grain size can impact SAV morphology. Water flow can exert drag forces on leaf tissue, impacting plants with greater leaf surface area more strongly (Wicks et al. 2009; Infantes et al. 2011) and potentially causing a limitation to plant stability.

Proportional levels of both water flow and sediment grain size in SAV habitat is important to the emergence and survival of seedlings. High water flow may erode the fine sediments associated with higher organic matter, or deposit large amounts of sediment causing the burial of the seed bank (Combroux and Bornette 2004; Koch et al. 2010), demonstrating the necessity of proportional moderate water motion and sediment grain size. Very fine sediment can be limiting to seed recruitment if very dense seeds sink until they reach a similar density in low cohesive strength sediment, burying themselves too deeply for adequate light access (Barrat-Segretain 1996). On the other hand, very high cohesive strength sediment may limit the ability of some species to root (for example *Naja marina*) and may be indicative of oxygen depletion resulting in accumulation of phytotoxic compounds (Pezeshki 2001; Handley and Davy 2002). The successful recruitment of *Z. marina* seedlings is much more dependent on physical sediment-seedling interactions than seed germination rates

(Marion and Orth 2012). An appropriate balance of both habitat parameters appears to be necessary for SAV seedling and adult survival.

In light of previous research and the present generally accepted hypothesis that SAV habitats are quiescent and depositional, the initial hypothesis of this study is that SAV will grow better in habitats characterized by water flow and sediment texture that promote sediment deposition. This hypothesis will be evaluated based on mesocosm studies in Chapter 2, the re-formulated if necessary for consideration based on field studies in Chapter 3.

Figures

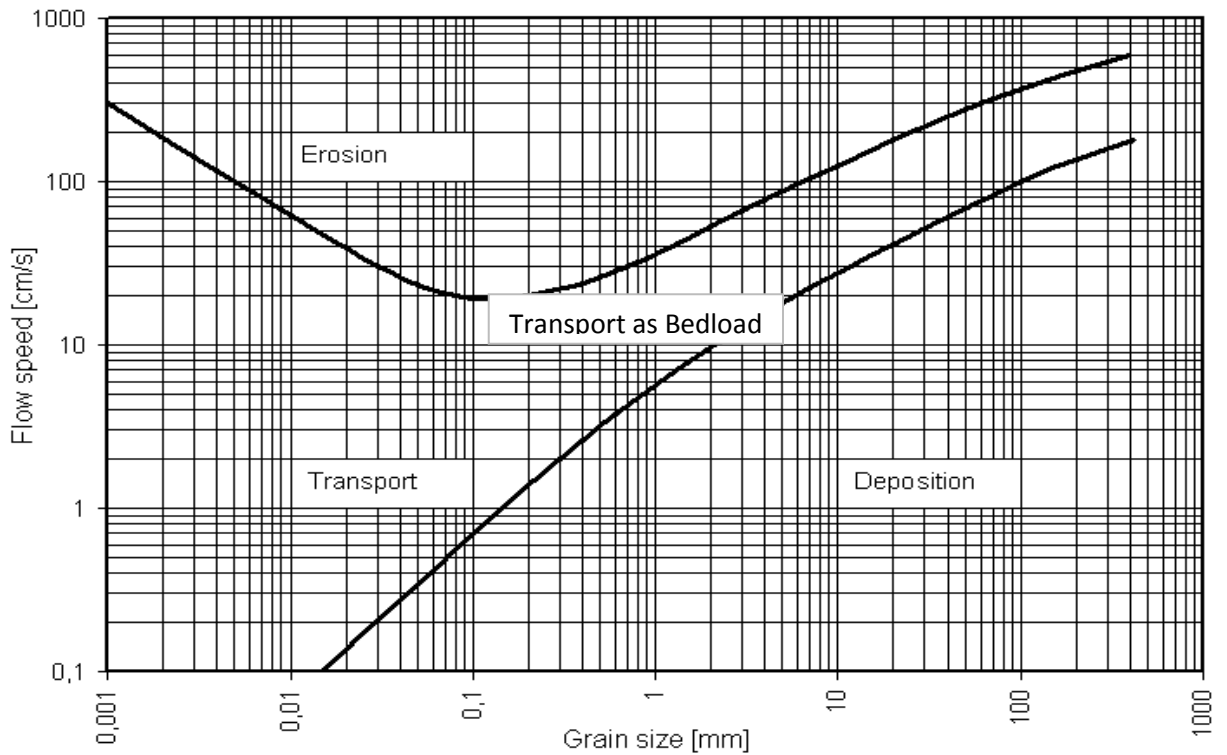


Figure 1.1 The Hjulstrom diagram describing the relationship between sediment grain size and water flow speed. The types of sediment motion initiated by different combinations of these factors are categorized.

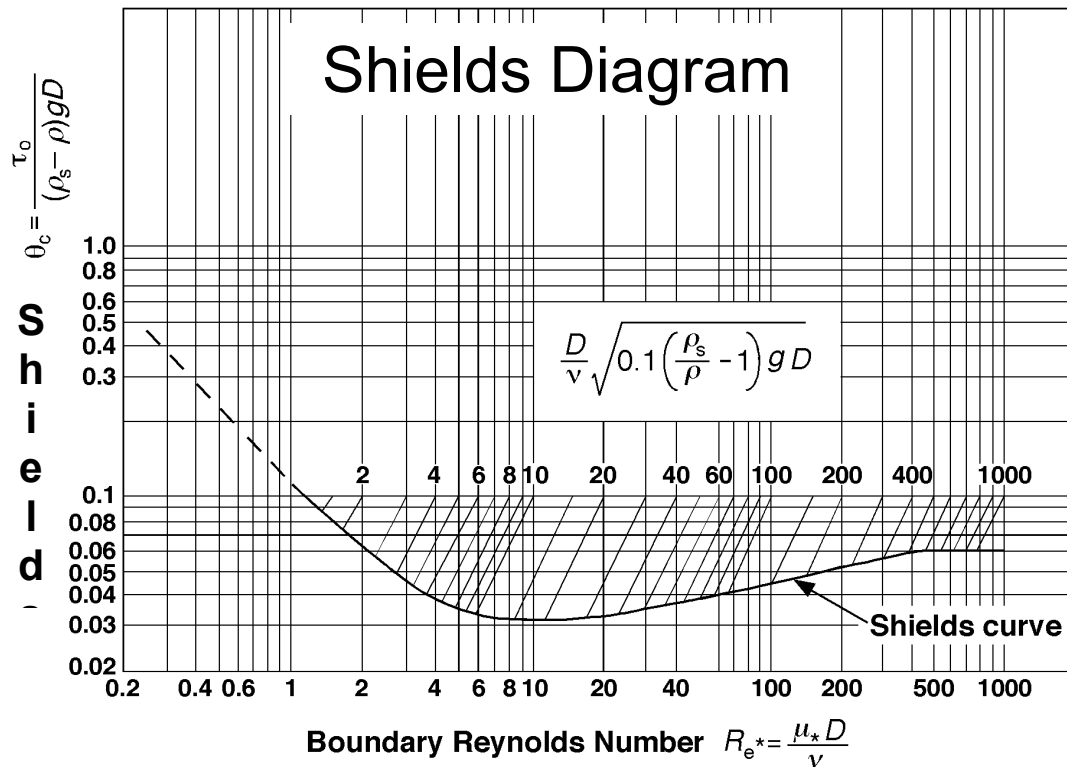


Figure 1.2 Shields diagram relating the non-dimensional parameters boundary Reynolds number, derived from sediment grain size, and Shields parameter, derived from shear stress, to describe sediment motion conditions. The Shields curve represents the threshold of initiation of sediment motion.

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Chapter 2: Effects of Water Flow and Sediment Grain Size on Submersed Aquatic Vegetation Biomass and Morphology

Abstract

Despite many efforts to restore submersed aquatic vegetation (SAV) in the Chesapeake Bay, including several large scale restoration projects, only a small percentage of restored SAV sites have survived for more than one season. Potential restoration sites are traditionally selected primarily based on light availability, i.e. depth and water clarity. Additional habitat parameters such as sediment composition may need to be taken into consideration in the SAV restoration site selection process. Although research has been conducted concerning the impact of sediment characteristics and water flows on SAV success, the interaction between water flow, sediments and SAV have not yet been considered. The size of sediment grains and the speed of water flow interact, resulting in bottom shear stress and, therefore, the type of sediment motion experienced by potential SAV habitat. In turn, these processes impact plant populations.

In order to assess the synergistic effect of sediment type and flow velocities on two species of SAV, *Zostera marina* and *Ruppia maritima*, an outdoor mesocosm experiment was conducted. Experimental treatments exposed the SAV species to 0, 4, and 24 cm s⁻¹ as they grew in very fine or medium sand for 6 weeks. SAV biomass, shoot density and, for *Z. marina*, morphology responded primarily to sediment type and secondarily to water flow. The two species responded to both factors similarly in

terms of biomass and shoot density, but varied in morphological response. The highest biomass and shoot density, was produced in very fine sand and the fastest water flow (24 cm s^{-1}), conditions predicted to induce low level sediment erosion. In contrast, leaf morphology response differed between *Z. marina* and *R. maritima*. *Z. marina* leaf area increased with water flow when grown in medium sand but not in very fine sand while *R. maritima* leaves and roots of both species did not significantly vary in length between sediment types or with water flow. Also, significantly higher densities of *R. maritima* reproductive shoots were developed in very fine sand, particularly under high water flow. These results suggest that these SAV species have a higher tolerance to substrate instability than anticipated and do not require depositional habitats. Future restoration projects informed by these conclusions may select more suitable potential SAV habitat and encounter greater success.

Key Words

SAV, seagrass, *Z. marina*, *R. maritima*, eelgrass, Widgeon grass, water flow, sediment, sediment grain size, sediment motion, restoration, habitat requirements, mesocosm experiment, deposition, erosion

Introduction

Although submersed aquatic restoration (SAV) restoration projects have been increasingly numerous in the Chesapeake Bay since the sharp decline in SAV in the 1930's, only 10% of efforts have resulted in colonization and growth for more than one season (Thom et al. 2005; Orth et al. 2008; Waycott 2009; Orth et al. 2010). The most traditional method of SAV restoration is transplanting adult shoots from a

successful SAV bed to an unvegetated area. This method tends to be cost, labor and time intensive and may harm the donor SAV bed, although recent progress has reduced this danger (Busch et al. 2010). Many newer methods, including seed collection and dispersal and the use of hessian, or sand filled burlap, bags and nursery beds have been developed and tested and found to be very efficient (Irving et al. 2010; Busch et al. 2010; Hengst et al. 2010). Despite improvement to restoration methods, most restoration site selection methods utilize only light availability habitat criteria if any criteria at all (Fonseca et al. 1998; Fonseca 2011). Light is the major habitat parameter limiting SAV distribution, however the importance of parameters other than light to SAV distribution is gaining increasing recognition (Koch 2001). SAV restoration failure is often attributed to site specific variations in habitat parameters or poor site selection. Restoration success for *Z. marina* and *R. maritima* in Barnegat Bay, NJ and the Patuxent and Potomac Rivers in the Chesapeake Bay has been dependent on site planning and assessment of both sediment characteristics and hydrodynamic activity in addition to light availability (Golden et al. 2010; Bologna and Sinnema 2012). It may be important to consider habitat parameters other than light and also how they relate to one another when selecting potential SAV restoration sites.

An important habitat parameter, exposure to waves and currents, may affect SAV growth and distribution through drag exerted on leaf surfaces and access to nutrients in the water column. Unidirectional water flow tends to impact SAV shoot morphology creating streamline shapes such as flat, strap like leaves (Idestam-Almquist and Kautsky 1995) while more complex hydrodynamic conditions

combining the effect of both currents and waves (Strand and Weisner 2001) may cause plants to develop smaller shoots and leaves with greater below-ground biomass and variations in density (Doyle 2001; Boeger and Poulson 2003). Submerged plants experience much more drag, approximately 25 times higher, than terrestrial plants in winds of similar speeds (Denny and Gaylord 2002). Wave activity resulting in 38 to 42 cm s⁻¹ near bottom orbital velocity limits the shallow water distribution depths of *Posidonia oceania* (Infantes et al. 2009), and an upper limit of 60 cm s⁻¹ has been proposed for *Z. marina* and *Cymodosea nodosa* (van Katwijk and Hermus 2000; Cabaco et al. 2010), among other observed limitations. *R. maritima* has been grown under weak or no water flow in the laboratory (Seeliger et al. 1984). Conversely, it is known that water flow is important for SAV growth and reproduction (Fonseca and Kenworthy 1987), enhancing photosynthesis and the rate of nutrient (Hurd 2000; Morris et al. 2008) and oxygen transfer into leaf material due to a thinning diffusive boundary layer (Koch 1994; Mass et al. 2010). Water flow also fertilizes SAV flowers and disperses seeds that can create new SAV populations (Ackerman 1986).

SAV may be affected by sediment characteristics including grain size and organic content (Kenworthy and Fonseca 1977; Short 1987; Silva et al. 2009). Grain size and organic content are usually closely related; sediment with high organic content tends also to contain finer grains (Wargo and Styles 2007). SAV has been described to colonize quiescent habitats with relatively fine and organic sediment (Koch 2001; Katwijk et al. 2010). In the Chesapeake Bay, healthy SAV beds were most often observed growing in sediment with 6-10% silt and clay and 1-5.3% organic content (Batiuk et al. 1992). Organic matter provides the nutrients and

sediment lacking in porewater nutrients can be limiting to SAV which acquires the majority of its nutrients through root tissue (Short and McRoy 1984). Low porewater nutrient levels and limiting rates of nutrient diffusion and exchange, such as when sand makes up 75% or more of the sediment dry weight, can degrade SAV growth (Barko and Smart 1986). Conversely, too much organic content in fine sediments can also limit SAV through the accumulation of toxic, soluble organic compounds formed during anaerobic processes (Barko and Smart 1983). Several upper thresholds of organic content and fine mud component percentages have been proposed ranging from 5 to 44% organic content and 10 to 57% mud (Barko and Smart 1983; Barko and Smart 1986; Batiuk et al. 1992; Kreiling et al. 2007; Makkay et al. 2008; Leschen et al. 2010; Moore et al. 2010; Krause-Jensen et al. 2011). In fact, a small sand component in sediments appears to be necessary for SAV colonization and growth in addition to some organic content (Palinkas and Koch 2012). However, sediment that is too coarse may still be limiting to SAV distribution as was observed during a restoration project in Ria de Aveiro, Portugal (Silva et al. 2009). The sediment grain size and organic content also impact SAV morphology, roots growing longer and shoots smaller in low organic content sediment (Cunha and Duarte 2007). Sediments with higher organic content usually resulted in larger plants with fewer roots than lower organic content sediments (Short 1983). When sediment nutrients are not limited in muddy organic rich sediments, *Z. marina* roots tend to increase in length with increasing water flow (Jordan 2008).

When determining SAV habitat requirements it may be important to also account for functional linkages, such as those between sediment grain size, and co-

varying organic content, and water flow velocity as described by Hjulstrom and Shields (Miller et al. 1977; Swerida 2013 Chapter 1). The importance of sediment characteristics to SAV growth has been referenced several times during studies of the effect of water flow on SAV and vice versa (*sensu* Bornette and Puijalon 2011; Bologna and Sinnema 2012). It was determined that sediment grain size, toxicity and wave activity, in addition to light availability and competition with algae, explained 50% of the variability in SAV distribution in the Indian River Lagoon, FL (Steward et al. 2005). Usually, sediment grain size increases with flow velocity while sediment organic content decreases (Hjulstrom 1936; Keddy 1983; Coops et al. 1991). In the Chesapeake Bay, some potential SAV habitat (i.e. shallower than 2 m) is an exception to this rule, fine sediment occurring under higher flow speed and coarser sediment occurring under lower flow speed due to local sediment sources (Palinkas et al. 2010). Sediment conditions that may not be limiting to SAV under some water flows do prevent colonization and growth under other water flows. *Z. marina* has not been able to grow in very fine sediments under stronger water flow when it has been able to flourish in such sediments under stagnant laboratory conditions (Wicks et al. 2009). *P. oceania* has not been able to colonize highly organic dredged sediment in a hydrodynamically energetic (due to boat activity) port both because of high leaf surface drag and because of light limitation from resuspended fine particles (De Falco et al. 2006).

The objective of this study was to investigate the combined water flow-sediment type habitat requirements of SAV in the Chesapeake Bay. Relatively little research has been conducted on the impact of these habitat parameters individually,

and almost none has considered them in conjunction with one another. It is hypothesized that suitable SAV habitat is characterized by sediment grain size and flow velocity resulting in moderate bedload transport of sediments. The sheltered, depositional areas that SAV are thought to commonly colonize have been found to stimulate growth (Gallegos et al. 1993) but may also cause seedling and plant burial or sulfide toxicity and death (de Boer 2007). Restoration efforts of *Halodule wrightii* in fine dredged material in Texas quickly failed due to poor site selection and no consideration for combined sediment-flow habitat parameters (Kaldy et al. 2004). The very fine sediment was exposed to high water flow and limited light access when resuspended and was severely eroded (30 cm in less than 1 year) limiting SAV stability through substrate loss in addition to stressing the plants with very high concentrations of porewater ammonium (600 μm). Although there is no substitute for field observations in terms of ecological accuracy, controlled lab experiments are quite useful for defining trends, limitations and understanding direct responses to habitat perturbations. Here, an outdoor mesocosm experiment was conducted to test the response of two common species of SAV in the Chesapeake Bay, *Z. marina* and *R. maritima*, to sediment-water flow combinations. The results of this experiment will help to explain the relationship between SAV and sediment-water flow conditions and provide important site selection guidance for future restoration efforts.

Materials and Methods

Combinations of sediment characteristics and flow speeds were chosen to create different types of sediment motion (Sanford and Halka 1993). The most

accurate way to test the response of SAV to sediment motion would be to create specific levels of shear stress to act upon different sized sediment grains. It was not possible to quantify either shear stress or the degree of sediment motion during this experiment. Instead, empirically-derived velocity thresholds of sediment motion developed by Hjølstrom, Shields and others as well as a series of standard open channel fluid dynamics equations (Daily and Harleman 1966) were used to predict the degree of motion experienced in the experimental treatments. First, the shear stress necessary to create the desired level of sediment motion for each sediment type in the specific mesocosm channels was calculated. Then the velocity of water flow necessary to create the prescribed levels of shear stress was determined.

Experimental Design

An outdoor mesocosm experiment was conducted to test the response of 2 species of SAV to combinations of sediment type and flow speed. The sediment types and flow velocities for each experimental treatment were chosen to represent the following predicted conditions: sediment deposition, bedload transport and moderate sediment erosion (Table 2.1). Medium sand (320 μm grain size and $0.35 \pm 0.07\%$ SE organic content) and very fine sand (85 μm grain size and $4.35 \pm 0.07\%$ SE organic content) (Figure 2.1) were collected from Mason Neck ($38^{\circ}37'49.17''\text{N}$, $77^{\circ}12'41.66''\text{W}$) on the Potomac River. The flow velocities necessary to generate the correct shear stress needed to create the desired levels of sediment transport were predicted using a series of open channel flow equations (Daily and Harleman 1966) (Table 2.2). High ($24 \pm 3 \text{ cm s}^{-1}$ SD) and low flow ($4 \pm 2 \text{ cm s}^{-1}$ SD) speeds were used and the resulting sediment motion visually assessed (Table 2.3, Figure 2.2).

Experimental Set Up

Nine outdoor mesocosm re-circulating tanks were used to replicate three water flows (n=3). Six tanks (3.0 x 0.7 x 0.6 m L x W x D) were converted into raceway flumes with a central PVC divider (Figure 2.3 and 2.4A). In half of these tanks, 4 cm s⁻¹, and in half, 24 cm s⁻¹ was generated by electric trolling motors (MinnKota C2 Endura 30, Sevylor 12V) (McKone 2009). Flow velocity was spatially homogenized using vertical lever flow correctors and collimeters. Three additional mesocosms (1.14 x 1.14 x 0.65 m L x W x D) served as control replicates with 0 cm s⁻¹ water flow (i.e. stagnant). These mesocosms were modified to create light conditions consistent with the raceway flumes by inserting PVC walls (Figure 2.4B).

Eighteen trays (20 x 15 x 10 cm L x W x D), nine containing medium sand and nine containing very fine sand, were planted with 5 *Z. marina* seeds each in the fall of 2011, germinated, and allowed to winterize in the mesocosm tanks until the early spring of 2012. The same number of trays containing the same types of sediment were planted with 5 *R. maritima* seedlings (8 days old) each during the early spring of 2012. The timing of germination and planting mimicked the natural life cycle of each species. Four trays were randomly arranged in each mesocosm on a line perpendicular to the water flow (Figure 2.3). Choptank River water was mixed with sea salt (Instant Ocean) to achieve a salinity of 28 and exchanged bi-weekly. When necessary, epiphytes were brushed away from the above ground plant material by hand.

Temperature and light at plant depth (0.6 m) were monitored using temperature loggers (Sensor HOBO, Water Temp Pro v2, data collected every 6 hours

for the duration of the growth period) and a light meter (Li-Cor, LI-1400 dataLogger, data collected once per week). The flow velocity was monitored with an electromagnetic flow meter (Flo-Mate, Marsh-McBirney Inc., data collected once per week).

Sample Processing

SAV was allowed to grow for six weeks after which the conditions of the rhizomes were characterized for each tray. Rhizome conditions were described as “buried” in the sediment, “exposed” at the surface of the sediment, or including “runners” growing out of the sediment. If more than one condition was observed in a single tray, a fractional score representing each was assigned, e.g. a tray including both exposed rhizomes and runners would be scored as 0.5 exposed and 0.5 runner. Then the experiment was terminated by gently sieving the sediment away from the roots and removing plants. All plant material was carefully cleaned and all epiphytes removed using water, a brush and razor when necessary. The number of roots, shoots and reproductive shoots were counted. The length of roots, rhizome internode length, and the length and width of leaves were measured using a metric ruler and calipers. Above- and below-ground material was separated, dried and weighed to determine biomass.

Data Analysis

Statistical analysis was completed using R version 2.12.2 (The R Foundation for Statistical Computing) statistical software. Data was tested for homogeneity of variance and normality with Anderson-Darling, Cramer-von Mises and Bartlett tests (Crawley 2007). A two way ANOVA was conducted for SAV biomass, density and

morphology grown in different sediment types and flow velocities (Table 2.4). Linear regressions were calculated to assess the relationship between SAV above- and below-ground biomass and density, morphology, flow velocity and sediment grain size.

Results

Biomass and Density

Both *Z. marina* and *R. maritima* biomass responded primarily to sediment type and secondarily to water flow (Figure 2.5). Above ground biomass did not exceed 1.25 ± 0.5 (g dry wt m⁻² ± SD) and 2.51 ± 0.77 (g dry wt m⁻² ± SD) in medium sand for *Z. marina* and *R. maritima* respectively. In very fine sand, *Z. marina* produced up to 23.91 ± 10.2 (g dry wt m⁻² ± SD) and *R. maritima* produced up to 53.15 ± 11.99 (g dry wt m⁻² ± SD), significantly higher values than in medium sand (p-values= $1.98e^{-4}$, $4.12e^{-5}$). Below ground biomass production was also significantly higher when grown in very fine sand than in medium sand (p-values= $5.89e^{-4}$, $6.64e^{-5}$), although the range of values was smaller than in above ground biomass.

In addition to a significantly higher biomass in very fine sand than in medium sand in nearly every case, a significant response of biomass to water flow can also be seen. Biomass of *Z. marina* was significantly higher in moving water than in stagnant water (p-value=0.047), exhibiting a threshold response to water flow in both sediment types (Table 2.4). Trends in shoot and root density of this species mirrored those of biomass. Root densities were generally higher than shoot densities (Figure 2.6), however, a different pattern appeared in *R. maritima* biomass. In medium sand, there

was no variability in biomass, shoot or root density. While grown in very fine sand, biomass was significantly higher in the fastest moving water (24 cm s^{-1}) than the slower or stagnant conditions (above-ground p-value= 0.012, below-ground p-value= < 0.0001). *R. maritima* leaf and root densities were significantly lower under 4 cm s^{-1} flow speed than 24 cm s^{-1} (p-value= 0.020, p-value= 0.047) while still water densities were not different from moving water densities (Figure 2.6).

For most SAV species-sediment type combinations, the ratio of above- to below-ground biomass tended to be higher under stagnant conditions than either 4 or 24 cm s^{-1} water flow, although the difference was only significant in the case of *Z. marina* grown in very fine sand (Figure 2.7, p-value= 0.049). The ratio showed a positive trend with increasing water flow for *Z. marina* grown in medium sand, the 24 cm s^{-1} condition significantly higher than 0 cm s^{-1} (p-value= 0.049). There was no difference in the ratio of above- to below-ground biomass for *R. maritima* grown in different sediment types or flow velocities (p-value= 0.656). Samples grown in stagnant water flow tended to have the highest ratio in both sediment types.

Morphology

The responses of leaf and root morphology to sediment type were less marked than the responses of biomass and density (Figure 2.8). Leaf length, leaf width and area were smaller for *Z. marina* when grown in medium sand than when grown in very fine sand (p-value= $5.63e^{-4}$, $1.01e^{-6}$, $5.53e^{-5}$). The larger *Z. marina* plants grown in very fine sand developed brighter green coloration and consistent leaf and root morphology despite variations in water flow: leaf length between 12.57 ± 8.02 and 15.43 ± 10.23 (cm \pm SD), leaf width between 2.05 ± 0.61 and 2.50 ± 0.69 (cm \pm SD),

and root length between 6.27 ± 4.26 and 7.50 ± 5.99 (cm \pm SD). The smaller *Z. marina* grown in medium sand appeared weak and discolored in addition to a smaller size. Water flow had a greater impact on shoot size in plants grown in medium sand. Leaf length and width were significantly smaller (p-value= 0.023, $1.60e^{-3}$) under stagnant conditions than under 24 cm s⁻¹ flow speed and tended to increase with water flow. The differences in leaf length and width, however, did not result in significantly different leaf area between water flows (p-value= 0.099). In contrast, root length remained unaffected by water flow even when grown in medium sand (p-value= 0.512).

There was no significant difference (Table 2.4) in leaf length, leaf width or leaf area for *R. maritima* (p-value= 0.455, 0.352, 0.280). Leaves measured between a mean of 5.35 ± 2.97 and 6.99 ± 2.54 (cm \pm SD) long when grown in medium sand and between 9.22 ± 3.17 and 10.60 ± 3.06 (cm \pm SD) long when grown in very fine sand under all water flows. Leaf width exhibited even less variation in this species, growing only from 0.51 ± 0.16 to 0.60 ± 0.15 (cm \pm SD) in medium sand and from 0.63 ± 0.11 to 0.66 ± 0.09 (cm \pm SD) in very fine sand. Consistently, *R. maritima* roots ranged from 5.43 ± 4.92 to 7.18 ± 5.03 (cm \pm SD) in medium sand and from 12.08 ± 10.08 to 14.34 ± 9.43 (cm \pm SD) in very fine sand. These very similar dimensions resulted in close to uniform mean leaf area measurements under all flow velocities and both sediment types between 0.31 ± 0.22 in 4 cm s⁻¹ water flow over medium sand and 0.71 ± 0.25 (cm \pm SD) in no flow, very fine sand conditions.

Correlations between leaf dimensions, leaf density and biomass help to further explain the source of variations in biomass across experimental treatments. Above

ground biomass in very fine sand relates to density and morphology measurements with much steeper slopes than those in medium sand. These correlations indicate that *Z. marina* above ground biomass is controlled by leaf morphology as well as density (r^2 values= 0.99, 0.99, 0.92). Higher biomass is associated with shorter, wider leaves and increasing leaf density. The variance in *R. maritima* above ground biomass grown in very fine sand is less clearly explained by morphology, and only 27% is explained by leaf density.

Reproduction and Dispersion

Reproductive structures developed only in *R. maritima* (Figure 2.9) because eelgrass does not reproduce until the second season. In medium sand, a very low density of *R. maritima* reproductive shoots (11.11 ± 10.0 to $22.22 \pm 11.11 \text{ m}^{-2} \pm \text{SD}$) grew under 0 and 4 cm s^{-1} while none grew under 24 cm s^{-1} . In contrast, in very fine sand, a significantly higher density (344.41 ± 184.91 to $366.63 \pm 134.70 \text{ m}^{-2} \pm \text{SD}$) grew under 0 and 4 cm s^{-1} (p-value= < 0.0001), while the reproductive shoot density in 24 cm s^{-1} water flow ($1249.86 \pm 50.0 \text{ m}^{-2} \pm \text{SD}$) was four times as large as that in 0 or 4 cm s^{-1} (p-value= < 0.0001).

Runners, or rhizomes extending out of the sediment into the water column, were observed in only *R. maritima* samples (Figure 2.10). All *Z. marina* rhizomes grown in medium sand remained buried at the end of the growth period, while 0.5 to 1 out of 3 samples grown in very fine sand contained exposed rhizomes. All three rhizome conditions were observed in *R. maritima* grown in each sediment type and flow velocity. In medium sand, exposed rhizomes were most common under 0 cm s^{-1} while runners were most common when flow velocity, grown under 24 cm s^{-1} . In

very fine sand, the occurrence of exposed rhizome and runners tended to increase with water flow.

Discussion

In the Chesapeake Bay, SAV has been found in a broad and variable range of water flows and sediment characteristics. Despite the apparent wide range of hydrodynamic and sedimentary habitat parameters tolerated by SAV, specific combinations of these parameters may be relatively narrow and an SAV habitat requirement. SAV grown in this study's mesocosm experiment displayed a primary response to sediment characteristics, a secondary response to water flow and a possible preference for habitat conditions predicted to create sediment motion.

Sediment type, as a primary controlling factor, was shown to suppress or inflate some responses of SAV to water flow because sediment type and water flow are related through sediment transport (Miller 1977). Sediment size distribution is also often related to sediment organic content, which can affect requirements for water column nutrients and therefore sensitivity to water flow (Kautsky 1987; Silva et al. 2009). Sediment nutrient limitation is the likely cause for the lower biomass of both species grown in medium sand (Barko and Smart 1986) as represented by stunted growth and discolored leaves (Powell et al. 1989). Water chemistry in each mesocosm tank was uniform, therefore porewater nutrient content was most likely limiting nutrient supply to the plants. Medium sand contained only 0.35 ± 0.07 % organic content while very fine sand contained 4.25 ± 0.07 %. SAV has been observed growing in sediment with as little as 0.3% organic content, however

mechanisms of growth limitation for many species of SAV in unfavorable sediments have been attributed to multiple nutrient (N, P, Fe etc.) deficiencies (Barko and Smart 1986; Moore et al. 2010). The organic content of sediments determines the level of nutrients available for SAV roots to utilize, finer sediments normally containing high percentages of organic content than coarse sediments (Keddy 1983). Poor growth has been observed when sand makes up 75% or more of the sediment dry weight and several species have been seen to grow better in finer sediments with higher organic levels (Barko and Smart 1986; Silva et al. 2009; Ye et al. 2009; Barth et al. 2010). The significant biomass development limitation observed in SAV grown in medium sand may have reduced the ability of the plants to respond to the impacts of water flow.

Although both species responded similarly to sediment type in terms of biomass and shoot and root density, the response in terms of morphology was species-specific. *Z. marina* not only developed fewer shoots, but those leaves were shorter and thinner in medium sand, particularly under low water flow. *R. maritima* is a fast growing, ephemeral, opportunistic species (Bird et al. 1994) while *Z. marina* tends to be more stable and slow growing (Orth et al. 1984). The particular growth strategies of these two species are the most likely explanations for the difference in above ground morphological response to sediment type (Moore and Short 2006). The ratio of above- (shoots and leaves) to below-ground (roots and rhizomes) biomass has been observed to be greater in fine sediments, where fewer, shorter roots are able to access abundant nutrients for the production of large shoots and leaves, than in medium sediments, where longer roots are necessary for nutrient access, limiting the

energy that may be allocated to above-ground production (Cunha and Duarte 2007; Wicks et al. 2009). Root length can be increased in sandy and gravelly sediments in response to physical challenges of anchoring the plant among very coarse grains usually found in strong water flow habitats (Silva et al. 2009; Bornette and Puijalon 2011). Neither root length nor the ratio of above- to below-ground biomass (Figure 2.7) varied with sediment type in this experiment, likely due to water flow.

SAV differs from terrestrial plants in its ability to utilize nutrients both from the sediment through root tissue and from the water column through leaf tissue (Thursby and Harlin 1984). The form of carbon, nitrogen and phosphorous that can be used and the mechanism by which nutrients can be absorbed by leaf tissue often differs between species (Maberly and Madsen 1998; Beer et al. 2002; Bornette and Puijalon 2011). Photosynthesis, oxygen and nutrient uptake from the water column are all clearly enhanced by water flow (Enrique and Rodriguez-Roman 2006; Larkum et al. 2006; Mass et al. 2010). Faster water flow leads to thinner diffusive boundary layers at the leaf surface and allows for more efficient nutrient uptake and oxygen transfer, particularly for species that do not benefit from catalyzed carbon absorption mechanisms (Koch 1994; Hurd 2000). Here, both species of SAV responded to water flow in terms of biomass, shoot and root density as well as to sediment type (Figure 2.5, 2.6). A threshold response to water flow was clear in both species when grown in very fine sand and for *Z. marina* in medium sand. Oscillatory flow has been suggested to enhance nutrient acquisition even more than unidirectional flow (Weitzman et al. 2013), therefore, to study the importance of water motion to SAV growth may be even more significant under field conditions with wave exposure.

Sediment organic matter has been shown to be the primary source of nutrients to SAV roots, however when sediment organic matter is limiting to roots, increases in water column nutrient uptake have been observed (Thursby and Harlin 1984). Leaf area of *Z. marina* grown in medium sediment increased with water flow while root length did not change, suggesting leaf morphology changes increased access to water column nutrients, benefiting the plants and increasing growth potential. Leaves of *Z. marina* exposed to a variety of water flow speeds in flumes have increased in length with flow speed, possibly also reacting to increased nutrient access (Fonseca and Kenworthy 1987; Jordan 2008). Root biomass has been observed to decrease with increasing water column nutrient concentrations when the pelagic nutrient availability has been high enough to satisfy the plants' demands through foliar uptake (Maitai and Newton 1982). The increase in above-ground over below-ground material development in medium sand was also displayed by the increasing trend of the above-to below- ground biomass ratio (Figure 2.7). Primary access to water column nutrients was less important when sediment organic content was not limiting, although biomass and density continued to increase with flow speed in very fine sand.

The relatively high shoot density and biomass of *R. maritima* growing under stagnant conditions was surprising. This species may have a mechanism for carbon, nitrogen and/or phosphorous acquisition under such circumstances that is independent of diffusion. The expected results of diffusive boundary layers limiting growth are seen in the significantly lower *R. maritima* shoot density in water flow of 4 cm s^{-1} when compared to 24 cm s^{-1} (Table 2.4). It suggests that 4 cm s^{-1} did not saturate the flux of carbon to the plant surface to maximize photosynthesis. A water flow

requirement of approximately 5 cm s^{-1} (friction velocity) has been previously suggested for *Thalassia testudinum* (Koch 1994).

Water flow impacts SAV physically as well as chemically. Waves and currents can determine both the morphology and distribution of SAV (Haslam 1978; Koehl 1984; van Katwijk and Hermus 2000; Schutten et al. 2005; Infantes et al. 2011; Bal et al. 2011; Loher and Nepf 2011). Water flow across leaf surfaces creates a drag force that can impact growth and development reducing the size and changing the shape of above ground material and increasing the length and density of roots (Bal et al. 2011). Roots must be of adequate length to anchor plants in flowing water. When root material insufficiently anchors SAV, drag induced by water flow can uproot plants and prevent colonization, limiting SAV distribution (Wicks et al. 2009; Infantes et al. 2009). The anchorage capacity of roots generally increases with size; *P. oceania* and the smaller leafed *C. nodosa* in the Mediterranean Sea require 0.35 and 1.6 times the square root of the total leaf area in order to avoid being uprooted (Schutten et al. 2005; Infantes et al. 2011). Kelp also develops smaller holdfasts under lower flow than when under higher flow (Roberson and Coyer 2004).

In this experiment, no difference in shoot or root morphology was observed except for *Z. marina* grown in medium sand (Table 2.4). Instead, *Z. marina* roots appear to have responded through increasing their density with water flow. The morphology of *R. maritima* shoots and roots did not vary with flow speed, however a trend for higher above- to below- ground biomass ratio grown under stagnant conditions in both sediment types suggests a decreased need for root biomass

allocation when there is no water movement. This trend was also observed in *Z. marina*, but only in fine sediment.

SAV responses to different habitat parameters may represent a balance between competing influences. SAV shoots, for example, may grow large in order to maximize photosynthesis and nutrient uptake from faster water flow, but not so large that the available root material cannot anchor the plant. Roots can grow longer in response to drag stress or in nutrient poor sediments where a larger area of sediment coverage is necessary to access nutrients (Cabaco et al. 2008; Infantes et al. 2009). For *Z. marina*, the development of both above- and below- ground material is determined by the water flow-sediment type combinations of its habitat. *Z. marina* roots have been found to be longer growing in sandy sediment than in muddy sediment where roots also increased in length as a function of water flow (Jordan 2008). Here, leaf area of *Z. marina* significantly increased with flow speed in sandy sediment, accessing pelagic nutrients, and presumably avoided dislodgement due to proportionally increased root density. When grown in fine sediment, *Z. marina* leaf length and area did not change with increasing flow speed, however as water flow and potentially the drag on the constant leaf surface area increased, root density significantly increased. In Chincoteague Bay, this species has been limited from colonizing very fine sediment but hydrodynamically active areas because this balance of leaf area, drag force and sufficient root anchorage could not be achieved (Wicks et al. 2009). The length of shoots and roots did not vary in *R. maritima* grown in response to either sediment type or water flow, but the above- to below- ground biomass ratio was markedly higher in stagnant water. This could be not only a

response to nutrient availability, but also to water flow. Usually, less root material is necessary to anchor plants when there is no water motion to create drag forces (Schutten et al. 2005).

Sediment type and water flow are important to SAV reproduction and dispersal in addition to growth and morphology (Johansson et al. 1996). Reproductive strategies vary between the species studied. *R. maritima* produces reproductive shoots throughout the summer while *Z. marina* reproduces earlier in the summer, but not until the second season of growth (Orth et al. 1984). Thus, reproductive shoots contributed to the biomass of *R. maritima* but not *Z. marina* in our experiments (Figure 2.9). Sediment had a significant effect on the production of reproductive shoots of *R. maritima* with nearly sixty times the number of reproductive shoots growing in very fine sand as in medium sand (Table 2.4). This is possibly due to the nutrient limitation associated with medium sediments (*sensu* Jordan 2008). Additionally, the number of reproductive shoots grown in very fine sand under high water flow (24 cm s^{-1}) was an order of magnitude greater than the number grown in very fine sand under stagnant (0 cm s^{-1}) or low water flow (4 cm s^{-1}). High water flow is advantageous to SAV reproduction by fertilizing flowers and dispersing seeds and shoot fragments (Ackerman 1986; Fonseca and Kensworthy 1987; Bornette and Puijalon 2011). A high enough flow speed could trigger a physiological cue to increase reproduction when nutrients are plentiful in some species. Seedling recruitment can be dependent on both sediment and water flow. Extremely cohesive, dense, fine sediment can prevent some species, such as *Naja marina*, from taking root, and very low density muddy substrate may cause high density seeds to sink to

deeply out of the reach of sunlight (Barrat-Segretain 1996; Handley and Davy 2002). Seedling recruitment of *Z. marina* is suggested to be more dependent on physical sediment-seedling interactions than by seed germination rates (Marion and Orth 2012).

The production of aerial runners (branches of rhizomes which grow out of the sediment into the water column) in *R. maritima* in both sediment types suggests that this species may use fragmentation of the rhizome to colonize new areas (Figure 2.10). The number of trays containing runners in *R. maritima* increased significantly with water flow, but only in the very fine sand. When nutrients from both the sediment and water column are plentiful, it may be that more energy is used for reproduction and dispersal.

Although shear stress and sediment motion were not directly measured in this experiment, sediment grain sizes and flow velocities were chosen based on calculations predicting deposition, bedload transport and erosion (Table 2.3). Biomass and shoot density were highest for both species in treatments combining very fine sand and 24 cm s^{-1} water flow where sediment transport in the form of low levels of erosion or bedload transport occurs and resources from sediment and water column are maximized. This result did not directly support the general hypothesis that suitable SAV habitat is characterized by bedload transport, or the more specific hypotheses that SAV morphology would respond to grain size and water flow as in Wicks et al. (2009). It was anticipated that high water flow would cause the sediment to become too unstable (i.e. erode) for SAV, and stagnant water would not provide necessary flux of materials. Extremely coarse sediment can be limiting physically and

nutritionally to SAV while extremely fine sediment can accumulate phytotoxic compounds (Pezeshki 2001; Handley and Davy 2002). Levels of permeability and water flow may determine the amount of organic particle entrainment and porewater advection that can occur in sediments, in turn impacting nutrient and chemical fluxes. Bedload transport or low level erosion, such as that experienced by very fine sand in the mesocosm experiment, may prevent sediment from becoming densely packed with particles while supplying enough organic material to support plant growth. This combination of water flow and sediment characteristics may benefit SAV the most, providing enough benthic and pelagic nutrients and seed dispersal without dislodging or burying plants.

Conclusions

Growth of *Z. marina* and *R. maritima* in the mesocosm experiment was strongly impacted by sediment type and water flow, respectively. Although this trend was evident in both species considered, particular responses varied between species. *Z. marina* biomass, density and leaf morphology were dependent both on sediment type and flow velocity while *R. maritima* biomass and density of shoots, roots and reproduction and dispersion structures were dependent on sediment type and, particularly for the last, water flow. Morphology of *R. maritima* leaves and roots was independent of either habitat parameter. Biomass and shoot and root density, and in one case leaf area, were usually largest under water flow conditions that were predicted to induce bedload transport and low level erosion of either sediment type. This information is valuable in understanding the importance of interrelated habitat

requirements. Most importantly, the results of this study are different than the indication of most research that SAV habitat is quiescent and characterized by depositional environments (de Boer 2007). Habitat requirements of SAV should include water flow in proportion to sediment grain size, and potentially a degree of sediment motion. Improvements in understanding of SAV habitat requirements and the establishment of detailed criteria may help to improve the success of SAV conservation and restoration efforts in the Chesapeake Bay.

Tables

Table 2.1 Sediment grain sizes, flow velocities and the predicted sediment motion of experimental treatments. Critical velocities were calculated based on Hjulstrom, Shields and open channel flow equations (Hjulstrom 1935; Shields 1936; Daily and Harleman 1966).

Sediment Type	Grain Size (μm)	Organic Content (% \pm SE)	Flow Speed ($\text{cm s}^{-1} \pm \text{SE}$)	Sediment Motion
Medium Sand	320	0.35 \pm 0.07	0	Deposition
Medium Sand	320	0.35 \pm 0.07	4 (\pm 1)	Bedload Transport
Medium Sand	320	0.35 \pm 0.07	24 (\pm 3)	Erosion
Very Fine Sand	85	4.35 \pm 0.07	0	Deposition
Very Fine Sand	85	4.35 \pm 0.07	4 (\pm 1)	Bedload Transport
Very Fine Sand	85	4.35 \pm 0.07	24 (\pm 3)	Erosion

Table 2.2 Equations used to calculate the water flow necessary to initiate sediment motion. Re^* = boundary Reynolds number, U_* = particle velocity, D = particle diameter, ν = kinematic viscosity, P = wetted perimeter, H = height of water column, W = width of channel, A = cross sectional area, D_h = hydraulic diameter, ρ = density of liquid, ρ_s = density of water, g = acceleration due to gravity, f = friction factor, τ_c = critical shear stress.

Equations
Wetted Perimeter: $P=H+W+H$
Cross Sectional Area: $A=HW$
Hydraulic Diameter: $D_h=4A/P$
Relative Roughness= D/D_h
$D/\gamma\{0.1[(\rho_s/\rho)-1]gD\}^{-2}$
Boundary Reynolds #: $Re^*=(U*D)/\gamma$
Critical Shear Stress: $\tau_c=\rho(f/8)U^2$
Shear Velocity: $U_*=(\tau_b/\rho)^{0.5}$

Table 2.3 Results of calculation process used to define the water flow necessary to initiate bedload transport or erosion of sediments in the mesocosm experiment.

Sediment Motion	Grain Size (cm)	Relative Roughness	Boundary Reynolds #	Critical Shear Stress (dynes cm ⁻²)	Threshold Flow (cm s ⁻¹)	Experiment Water Flow (cm s ⁻¹)
Deposition	0.032	6.56e ⁻⁴	0	0	0	0
Bedload Transport	0.032	6.56e ⁻⁴	831.015	1.806	3.376	4
Erosion	0.032	6.56e ⁻⁴	5547.815	98.951	22.538	24
Deposition	0.0085	1.74e ⁻⁴	0	0	0	0
Bedload Transport	0.0085	1.74e ⁻⁴	45.9	0.702	0.6	4
Erosion	0.0085	1.74e ⁻⁴	144.565	2.211	18	24

Table 2.4 2-way ANOVA results for mesocosm experiment testing for significant differences in SAV biomass, density and morphology. The * denotes a significant difference.

SAV Response	Effects	Degree of Freedom	F-value	P-value
<i>Zostera marina</i>				
Above-ground Biomass	Grain Size	1	23.844	1.988e ⁻⁴ *
	Water Flow	1	4.651	0.047*
	Grain Size*Water Flow	1	4.113	0.062
Below-ground Biomass	Grain Size	1	18.791	5.89e ⁻⁴ *
	Water Flow	1	4.672	0.047*
	Grain Size*Water Flow	1	4.032	0.064

Above- to Below-ground Biomass Ratio	Grain Size	1	3.661	0.074
	Water Flow	1	0.104	0.752
	Grain Size*Water Flow	1	4.611	0.049*
Leaf Length	Grain Size	1	18.989	5.63e ⁻⁴ *
	Water Flow	1	2.206	0.158
	Grain Size*Water Flow	1	6.527	0.023*
Leaf Width	Grain Size	1	62.325	1.01e ⁻⁶ *
	Water Flow	1	14.760	1.60e ⁻³ *
	Grain Size*Water Flow	1	2.668	0.124
Leaf Area	Grain Size	1	30.838	5.53e ⁻⁵ *
	Water Flow	1	3.092	0.099
	Grain Size*Water Flow	1	2.078	0.171
Root Length	Grain Size	1	8.450	0.011*
	Water Flow	1	0.449	0.512
	Grain Size*Water Flow	1	3.552	0.080
Shoot Density	Grain Size	1	16.601	9.96e ⁻⁴ *
	Water Flow	1	4.517	0.049*
	Grain Size*Water Flow	1	4.091	0.062
Root Density	Grain Size	1	21.508	3.22e ⁻⁴ *
	Water Flow	1	6.012	0.027*
	Grain Size*Water Flow	1	4.777	0.046*
<i>Ruppia maritima</i>				
AG Biomass	Grain Size	1	32.627	4.12e ⁻⁵ *
	Water Flow	1	8.194	0.012*
	Grain Size*Water Flow	1	18.839	6.78e ⁻⁴ *
BG Biomass	Grain Size	1	29.752	6.64e ⁻⁵ *
	Water Flow	1	5.930	0.028*
	Grain Size*Water Flow	1	10.082	6.75e ⁻³ *
Above- to Below-ground Biomass Ratio	Grain Size	1	0.068	0.798
	Water Flow	1	0.467	0.505
	Grain Size*Water Flow	1	0.207	0.656
Leaf Length	Grain Size	1	0.548	2.201
	Water Flow	1	0.779	0.391
	Grain Size*Water Flow	1	0.590	0.455
Leaf Width	Grain Size	1	2.83	0.113
	Water Flow	1	0.918	0.353
	Grain Size*Water Flow	1	0.929	0.352
Leaf Area	Grain Size	1	1.826	2.730
	Water Flow	1	1.180	0.295
	Grain Size*Water Flow	1	1.261	0.280
Root Length	Grain Size	1	0.822	1.791
	Water Flow	1	0.647	0.434
	Grain Size*Water Flow	1	3.562	0.080

Shoot Density	Grain Size	1	34.087	$3.26e^{-5}$ *
	Water Flow	1	1.767	0.020*
	Grain Size*Water Flow	1	1.819	0.199
Root Density	Grain Size	1	32.824	$3.99e^{-5}$ *
	Water Flow	1	3.353	0.047*
	Grain Size*Water Flow	1	3.867	0.069
Reproductive Shoot Density	Grain Size	1	23.660	$2.06e^{-4}$ *
	Water Flow	1	9.475	$7.65e^{-3}$ *
	Grain Size*Water Flow	1	30.496	$7.51e^{-5}$ *

Figures

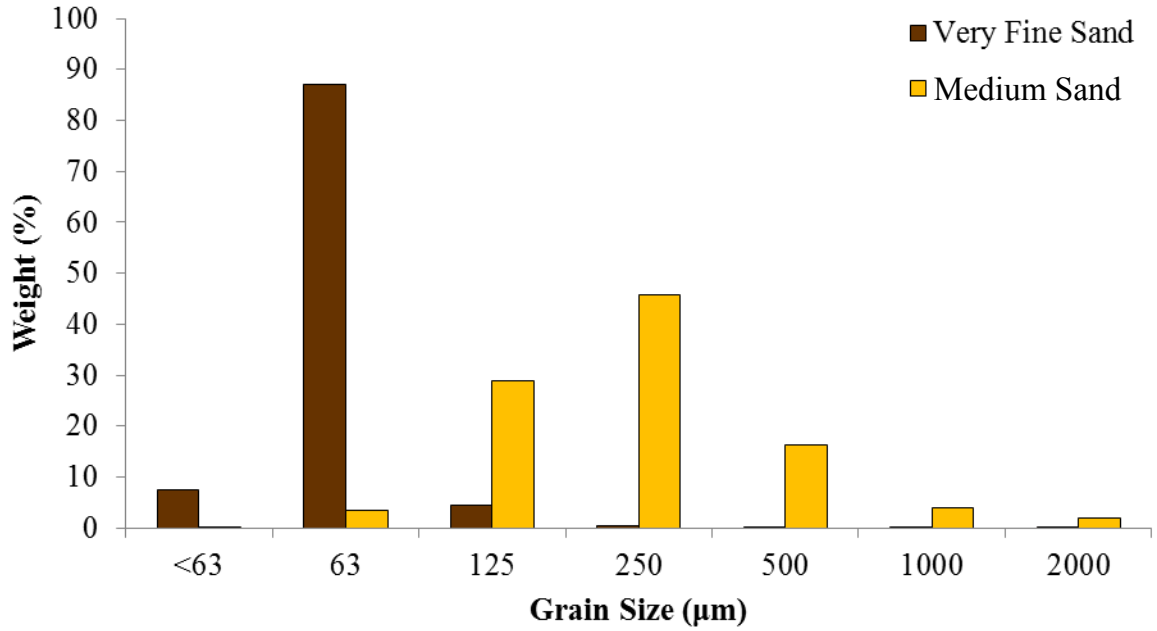


Figure 2.1 Grain size distribution of the very fine sand (median grain size 83 µm) and medium sand (median grain size 325 µm) used in the outdoor mesocosm experiment.

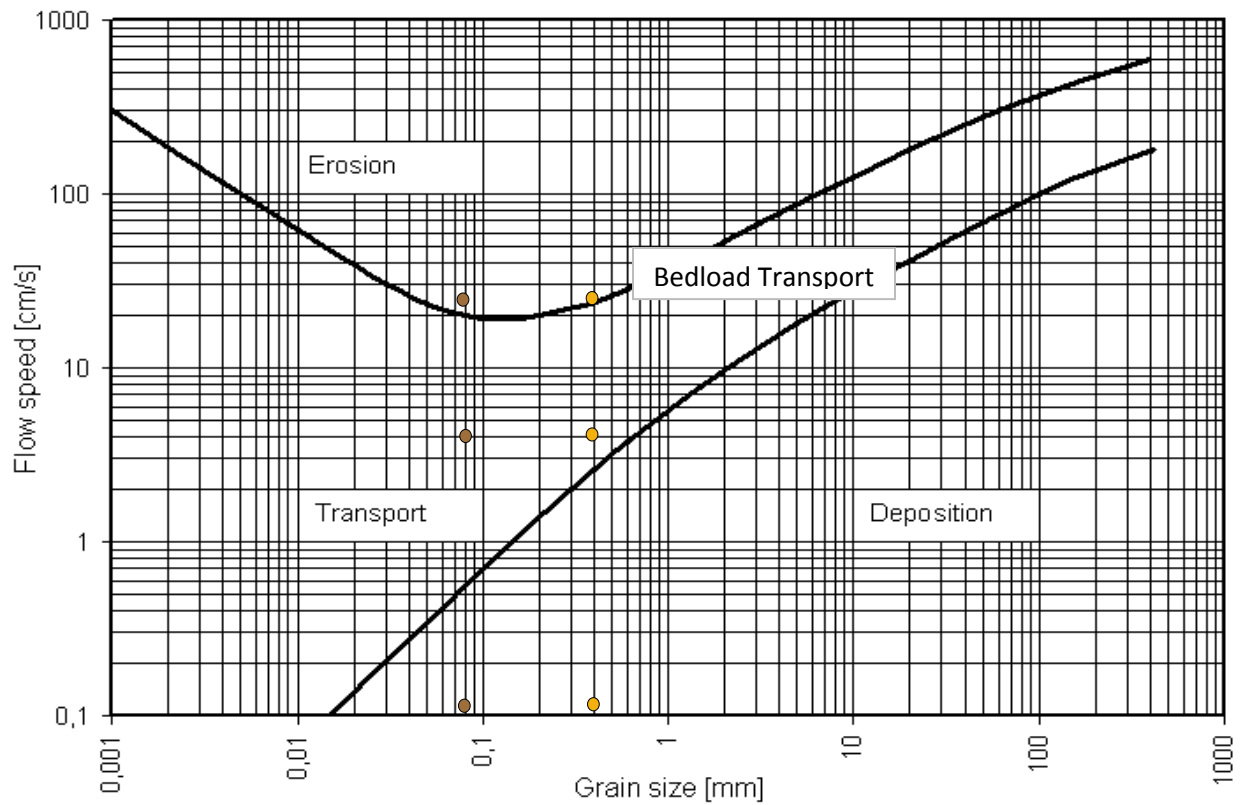


Figure 2.2 The Hjulstrom diagram showing flow velocities at which sediment motion is initiated for specific grain sizes. Experimental conditions are identified with dark brown (very fine sand) and light brown (medium sand) points.

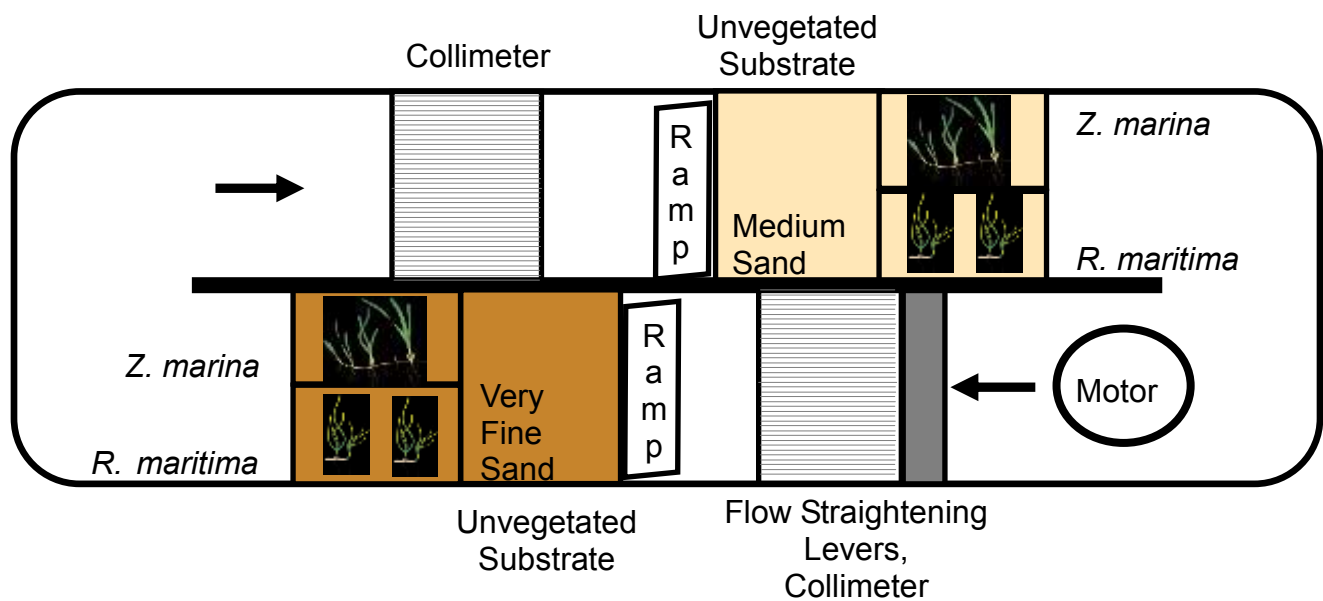


Figure 2.3 Diagram of outdoor mesocosm raceway flume including: central divider, trolling motor, flow straightening levers, collimeters, sediment filled flow adjustment trays and seagrass trays.



A.)



B.)

Figure 2.4A Photograph of long mesocosm tank converted to an outdoor flume.

Figure 2.4B Photograph of stagnant treatment mesocosm tanks without flume modifications.

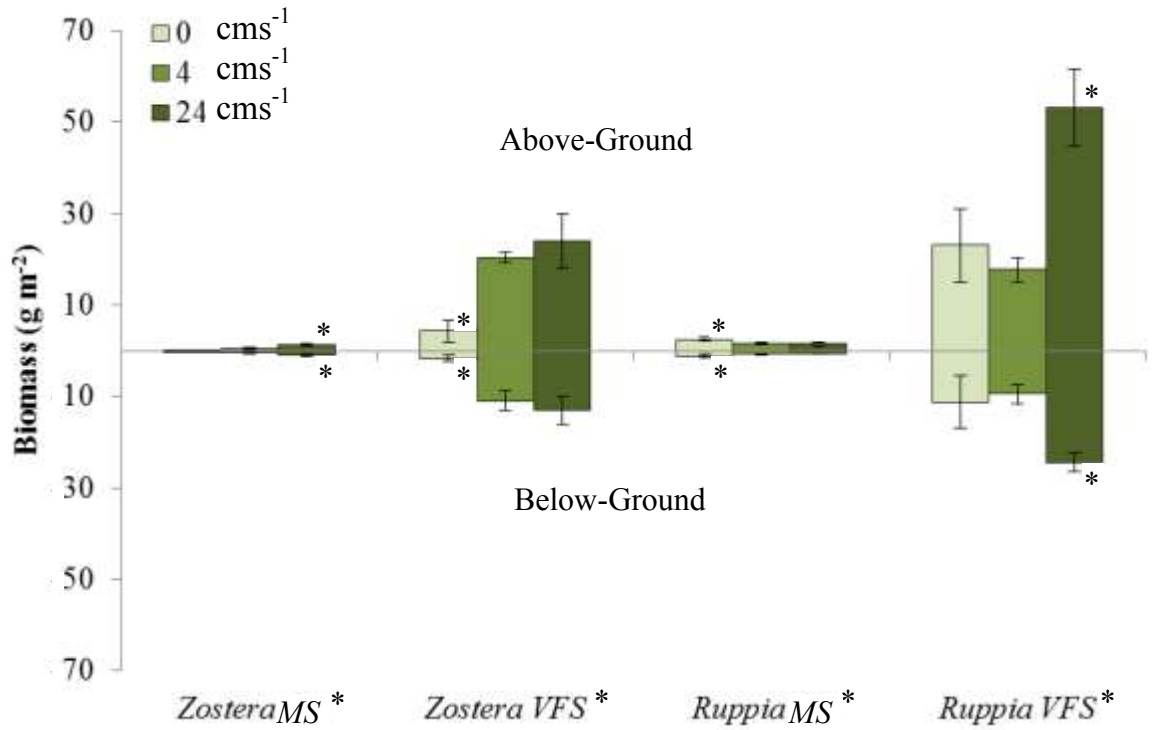


Figure 2.5 Above and below ground biomass (g dry wt m⁻² ± SD) of *Z. marina* and *R. maritima* grown in combinations of sediment grain size (VFS – very fine sand; MS – medium sand) and water flow. Asterisks indicate a significant difference in biomass between water flows (next to bars) or sediment type (next to sediment type label).

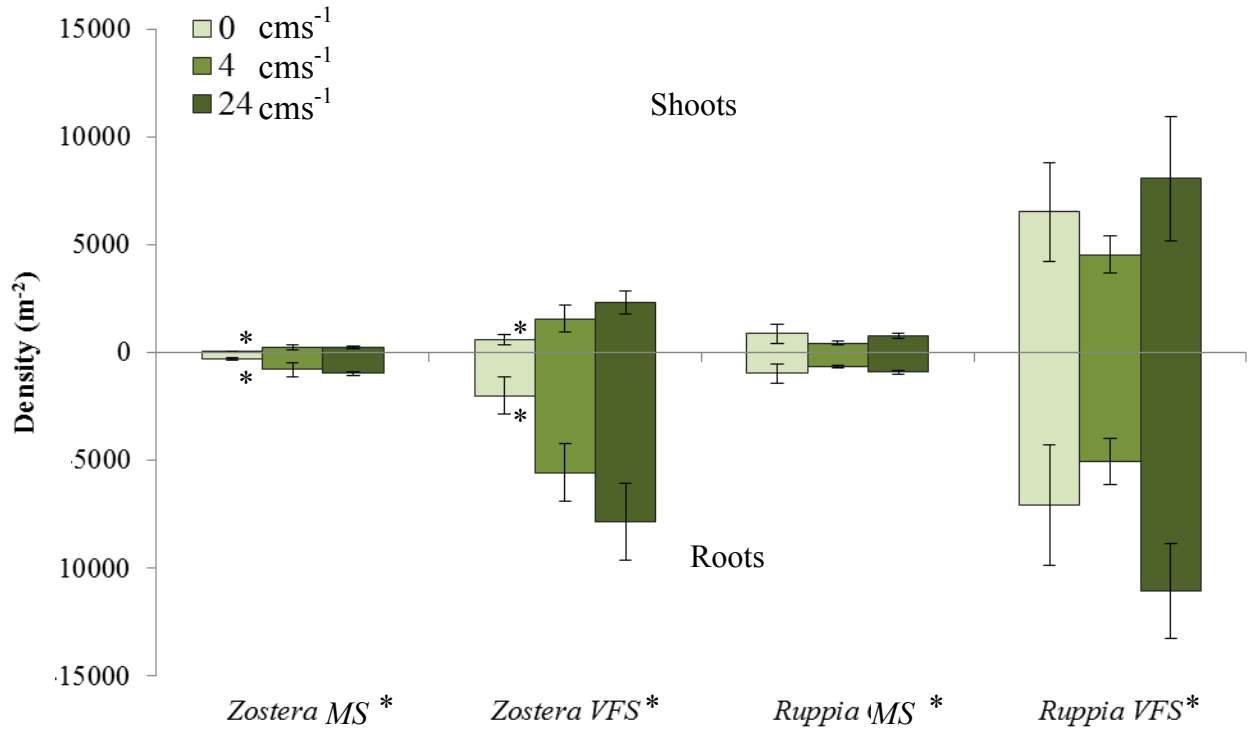


Figure 2.6 The density of leaves and roots (m⁻² ± SD) of *Z. marina* and *R. maritima* grown in combinations of sediment grain size (VFS – very fine sand; MS – medium sand) and water flow (0, 4, 24 cm s⁻¹). No reproductive shoots were included here. Asterisks indicate a significant difference in density between water flows (next to bars) or sediment type (next to sediment type label).

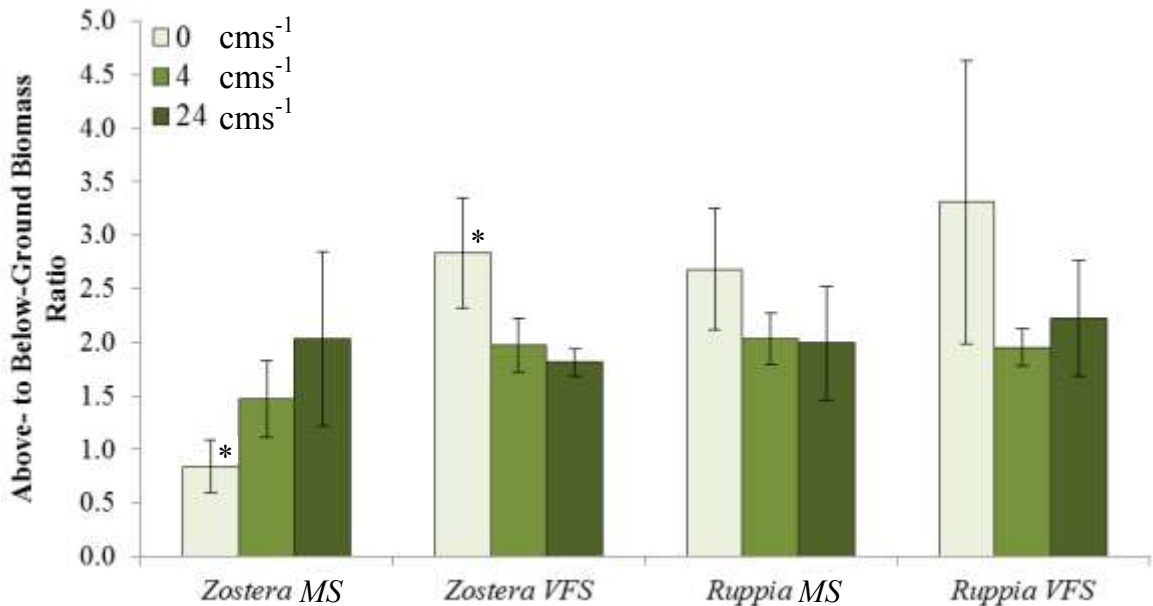


Figure 2.7 Ratio of mean above- to below-ground biomass of *Z. marina* and *R. maritima* grown in medium and very fine sand in outdoor mesocosms. Asterisks indicate a significant difference in ratio of above- to below-ground biomass between water flows (next to bars).

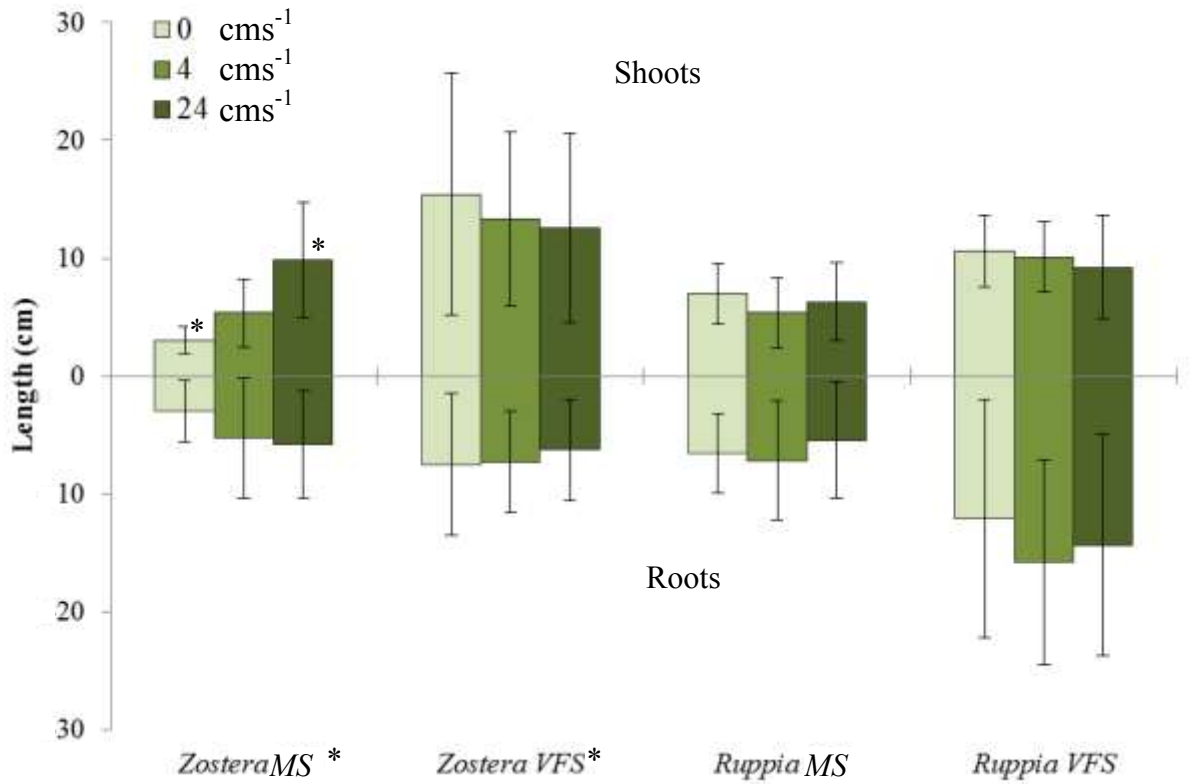


Figure 2.8 Mean leaf and root length (cm \pm SD) of *Z. marina* and *R. maritima* grown in medium and very fine sand in outdoor mesocosms. Asterisks indicate a significant difference in leaf or root length between water flows (next to bars).

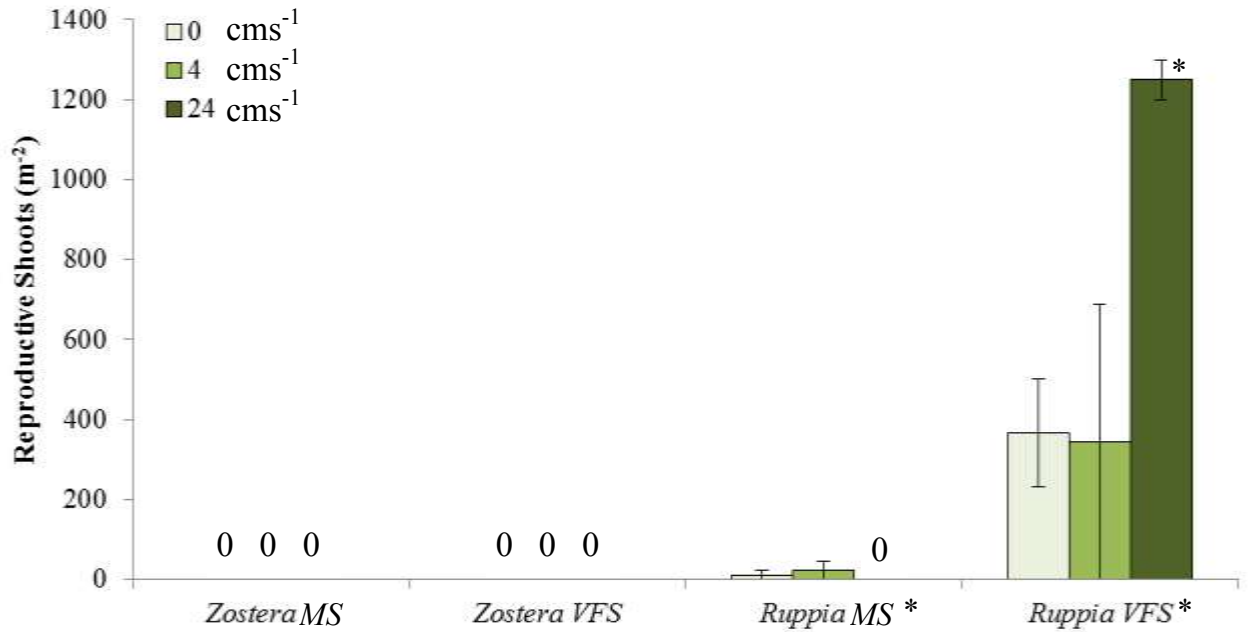


Figure 2.9 Density of reproductive shoots ($m^{-2} \pm SD$) of *Z. marina* and *R. maritima* grown in outdoor mesocosms under different combinations of sediment (MS- medium sand, VFS-very fine sand) and water flow (0, 4, 24 $cm s^{-1}$). Asterisks indicate a significant difference in reproductive shoot density between water flows (next to bars) or sediment type (next to sediment type label).

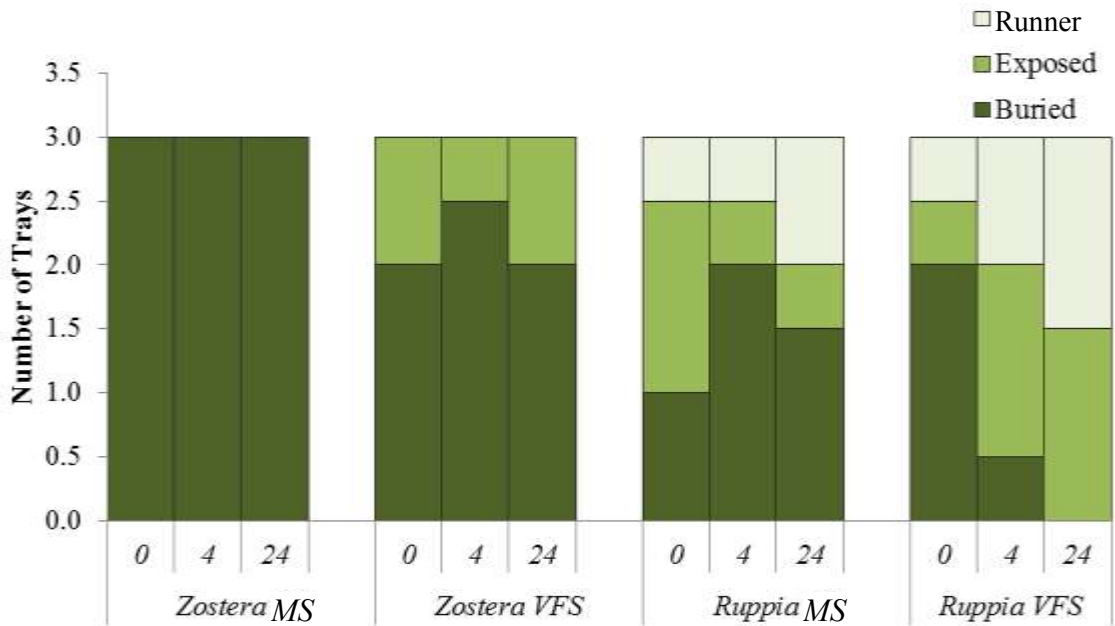


Figure 2.10 The occurrence of buried, exposed and aerial runner rhizomes in *Z. marina* and *R. maritima* grown in combinations of medium sand (MS) and very fine sand (VFS) and 0, 4, 24 cm s⁻¹. When more than condition was observed in one tray the score was assigned a fractional value.

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Chapter 3: Sediment Motion in Potential Submersed Aquatic Vegetation Habitat

Abstract

Submersed aquatic vegetation (SAV) restoration is extremely important in the Chesapeake Bay because of large scale population declines and the ecological value of SAV ecosystems. Despite great efforts to restore SAV populations, very few restoration projects have been successful, i.e. SAV establishment and sustained growth for more than 1 season. Currently, most restoration projects only consider SAV light requirements, the most important habitat requirements, when selecting restoration sites. This study investigated sediment motion as an additional SAV habitat requirement, considering wave-generated orbital velocity and sediment characteristics in concert as described by the Hjulstrom and Shields diagrams. Wave orbital velocity, sediment and SAV characteristics were determined at 11 study sites, encompassing a vegetated and adjacent unvegetated area, geographically distributed across the Chesapeake Bay.

Despite the common belief that suitable SAV habitats are wave-protected and depositional, the hypothesis that suitable SAV habitats are those characterized by orbital velocity and sediment grain size predicted to experience moderate bedload transport was supported. Nearly all vegetated sites were predicted to experience sediment transport, however, so were all unvegetated sites, indicating that further SAV habitat requirements should be investigated. SAV biomass tended to decrease and root length increase with increasing orbital velocity and increasing sediment

grain size. SAV was also limited to poorly sorted sediment, a sediment characteristic rarely considered and warranting further investigation. The results of this study will improve restoration site selection and increase awareness of the importance of SAV habitat requirement criteria beyond and in addition to light.

Keywords

Sediment Motion, Erosion, Bedload Transport, Submersed Aquatic Vegetation, SAV, Seagrass, Restoration, WEMo, Orbital Velocity, *Zostera marina*, *Ruppia maritima*, Chesapeake Bay

Introduction

World-wide populations of SAV have declined over 30% over the past several decades, including in the Chesapeake Bay (Orth 2002; Orth et al. 2006; Waycott et al. 2009; Orth et al. 2010). This loss is significant due to the high economic and ecological value of SAV habitats and the functions they perform. SAV beds increase nutrient cycling, act as a carbon sink, protect the shoreline and provide habitat for animals such as striped bass (*Morone saxatilis*) and blue crab (*Callinectes sapidus*) (Costanza et al. 1997; Madsen et al. 2001; Gross et al. 2001; Martin et al. 2005; Lazzari and Stone 2006; Rybicki and Landwehr 2007; Ma et al. 2010). SAV restoration projects have been conducted extensively in response to the loss in abundance, but have only been effective 10% of the time never succeeding for more than 1 to 2 years of growth in the Chesapeake Bay (Fonseca et al. 1998; Orth et al. 2006; Bell et al. 2008; Orth et al. 2009; Orth et al. 2010).

Restoration efforts of submersed aquatic vegetation (SAV) have often failed due to habitat parameters not considered during the site-selection process. Light is the main habitat requirement of SAV, so the majority of restoration sites have been

selected based on water clarity, depth and light availability (Kemp et al. 1984; Dennison 1987; Duarte 1991; Short et al. 2002; Orth 2007). Despite improvements to the traditional restoration methods, transplant and seed out-planting, that include the use of planting frames, mechanized seed distribution, nursery bags and Hessian bags, restoration success has been limited (Orth et al. 2002; Busch et al. 2010; Golden et al. 2010; Irving et al. 2010; Leschen et al. 2010). SAV light requirements are not always considered during restoration site selection, and habitat requirements other than light are almost never considered (Fonseca 2011). Restoration studies in New Jersey and South Australia have been significantly more successful when multiple habitat requirements are considered during site selection (Short 2002; Irving et al. 2010; Bologna and Sinnema 2012), suggesting that further consideration of SAV habitat requirements may improve SAV restoration success.

Recent research has shown that SAV is clearly impacted by habitat parameters beyond light such as sediment grain size and water flow (Koch 2001). Both *Zostera marina* and *Ruppia maritima* displayed selection for sediments containing <35% of silt and clay (<63 μm grain size) in Chincoteague Bay (Koch et al. in prep). Additionally, the distribution of several species, including *Posidonia oceanica*, *Cymodocea nodosa*, and *Z. marina*, appears to be limited by exposure to water flow between 30 and 60 cm s^{-1} (van Katwijk and Hermus 2000; Infantes et al. 2009, 2011). Habitat requirements other than light, including wave exposure, sediment grain size and toxicity and biological interactions, explained 50% of the variability in SAV distribution in the India River Lagoon while the remainder was attributed to light availability (Steward et al. 2005). Also, restoration success varied

by river despite identical light conditions when *Z. marina* seeds were broadcast in the Potomac and Patuxent Rivers, leaving habitat parameters other than light to explain the different results (Golden et al. 2010).

Clear impacts of sediment type and water flow on *Z. marina* and *R. maritima* biomass, density and morphology were observed in a mesocosm experiment conducted earlier in this study (Chapter 2). Natural complexities and synergies are not always represented in controlled laboratory settings. Therefore, studies of SAV responses to current velocity in flumes are not always supported by natural observations. For example, laboratory flume studies concluded that *Z. marina* leaf length increased with increasing water flow, while some field studies have found leaf length to decrease with increasing water flow (Fonseca and Kenworthy 1987; Schaz and Asmus 2003; Jordan 2008) When grown under stagnant controlled conditions, SAV may not develop the root mass needed for anchoring under wave exposed conditions *in situ* (Wicks et al. 2009). The effect of water flow was similarly significant when *Z. marina* was grown in different sediment type-water flow combinations: shoot size increased in response to increased water flow in coarse, but did not when grown in fine sediment where porewater nutrients were likely plentiful. Root biomass increased with water flow in both cases even when greater root mass was not necessary for nutrient access (Chapter 2).

While sediment and water flow affect SAV, SAV also affect sediments and water flow. SAV attenuates currents and waves (Fonseca et al. 1981; Gambi et al. 1990; Fonseca and Cahalan 1992) creating relatively quiescent conditions that promote sediment deposition (Gacia and Duarte 2001; Koch 2001; Widdows et al.

2008). SAV presence not only reduces flow speeds and increases sediment deposition, but the specific leaf area index has been significantly correlated with particle trapping, causing sediment retention to be as much as 15 times greater inside SAV beds than outside (Gacia et al. 1999). The ability of four species of SAV to prevent sediment motion and to encourage particle trapping has been tested in a wide range of flow speed and depth conditions, and all species were found to perform these functions, *Thalassia testudinum* to the greatest extent followed by *Z. marina* and *Halodule wrightii* (Fonseca and Fisher 1986). High wave exposure can limit SAV distribution, limit seedling recruitment and erode seed banks (Combroux and Bornette 2004; Infantes et al. 2009, 2011; Marion and Orth 2012). Therefore, SAV beds are usually described as depositional environments (Koch 2001).

The hypothesis that suitable SAV habitats are those characterized by sediment grain sizes and water flow resulting in moderate sediment transport conditions is tested here. Although it is tempting to determine one sediment-water flow threshold, the different SAV species found in estuaries and coastal waters are likely to differ in their habitat requirements. To address this hypothesis, SAV distribution, sediment grain size, and orbital velocities were compared in vegetated and unvegetated areas at 11 study sites in the Chesapeake Bay.

Materials and Methods

Study Sites

Eleven study sites were selected in the Chesapeake Bay (Figure 3.1). Each site encompassed a vegetated area and a nearby unvegetated area, both approximately 1 meter in depth. The Chesapeake Bay is an estuary approximately 300 km long, 50 km

wide at its widest point, varying spatially in salinity. Study sites represent the 3 salinity zones in the Bay: oligohaline, mesohaline and polyhaline (Table 3.1). Several study sites were selected to take advantage of previously collected wave climate data.

Wave Climate

Wave climate observations (wave height, period and depth) were collected at 1 m depth in the vegetated and unvegetated areas of each study site using shallow water pressure transducers (Macro Wave, Coastal USA) deployed for at least 2 week periods. At several sites, wave climate observations had previously been collected during past studies. Observations were collected during the summers of 2010 and 2011 for the remaining study sites. Only summer wave data was used for all sites. Water pressure was recorded at a 5 Hz frequency for approximately 13.5 minutes. After instrument retrieval, the data were downloaded and Fast-Fourier analyzed to obtain wave height, period and depth (Nielsen 1989). These data were used to determine near-bottom wave velocity fluctuations, as in Wiberg and Sherwood (2008) and wave-induced near-bottom orbital velocity and bottom stress were estimated based on wave height, wave period and water depth as in Sanford (1994) and Infantes et al. (2009) (Table 3.2, 3.3).

Sediment Characteristics

Four push cores (5-cm diameter) were used to collect surface sediment (10 cm) at each vegetated and unvegetated site during the summers of 2010 and 2011. The cores were collected at the corners of a 4.24 m by 4.24 m square oriented parallel to the shoreline and the specific locations recorded using a hand held GPS (eTrex Garmin) (Figure 3.2). Samples were homogenized and transported to Horn Point

Laboratory in plastic bags and stored in a refrigerator until processed. For sandy samples, grain size was analyzed by dry sieving samples through a series of six mesh sieves from 63 to 2000 μm . When a mud component was present in samples, grain size was analyzed by wet sieving through a 63 μm mesh sieve to separate the sand and mud fractions. The mud fraction ($<63\text{-}\mu\text{m}$) was then dried in pre weighed beakers and weighed while the sand fraction was dried and dry-sieved as described earlier. Sand and mud data were combined to form a complete grain size distribution for each sample. The mass median diameter (d50), silt and clay percentage were calculated for each sample using Matlab as in (Palinkas et al. 2010). The following equation was used to calculate a sediment sorting index for each vegetated and unvegetated area:

$$\text{Sorting Index} = ((D84-D16)/4) + ((D95-D5)/6.6) \text{ (Folk and Ward 1957)}$$

Where D84, D16, D95 and D5 values are the grain size at which 84, 16, 95 and 5% of the sediment dry weight is coarser.

SAV Characteristics

Vegetative biomass was sampled at all of the 11 sites between August and November in 2010 and between April and July in 2011, representing different portions of the growing season. SAV shoot and root density and leaf and root morphology at each vegetated study site was assessed by collecting 4 push cores (15-cm diameter and 20-cm long, encompassing the full rhizosphere) in the same 3-m by 3-m square arrangement as the sediment push cores. A 1-mm mesh sieve was used to rinse sediments and detritus from the plant matter *in situ*. The remaining plant matter was transported to the lab in plastic bags and frozen (-17°C) until processing. Care was taken throughout to keep the plants as intact as possible.

At the lab, samples were thawed and carefully cleaned of sediment and epiphytes with a brush and razor blade. Samples were separated by species and then into above (shoots and leaves) and below (roots and rhizomes) biomass. The length of all intact leaves and roots were measured with a metric ruler and the density of all shoots and roots in a core determined and then extrapolated to 1 m^2 . The above- and below-ground biomass of each sample was measured in grams by drying the separated material in pre-weighed foil packets at 60°C until constant weight was reached.

Sediment Motion

The type of sediment motion occurring at vegetated and unvegetated study sites was estimated based on a modified Shields diagram relating sediment grain size (cm) and bottom shear stress (dynes cm^{-2}) (Miller et al. 1977; van Rijn 1993). The mean wave-induced bottom shear stress was calculated for each vegetated and unvegetated site based on field-collected time series of wave height, period and water depth accounting for the dispersion relationship and wave friction factor using Matlab (Jonsson 1966; Jonsson and Carlesen 1976; Dyer 1986; Wright 1999; Sanford personal communication 2011). Certain variables were assumed to be constant including water viscosity, water density and sediment particle density ($1.2 \times 10^{-6} \text{ m}^2 \text{ s}^{-2}$ and 1000 kg m^{-3} , 2.65 g cm^{-3} respectively). The critical threshold for the initiation of sediment motion based on the empirically established Shields parameter and a critical threshold for sediment erosion based on a Rouse number calculation were included (van Rijn 1993). The percentage of time that sediment remained in motion during field observation was calculated based on the frequency of shear stress events over

the period of wave data collection. Data were also gathered from the literature to assess sediment motion conditions in additional areas. Shear stress estimates were not always possible, so water flow velocity was related to sediment grain size on the Hjulstrom diagram instead.

Data Analysis

Normality and homogeneity of variance were assessed using Anderson-Darling, Cramer-von Mises and Bartlett tests (Crawley 2007). Both assumptions were broken and could not be rectified through data transformation. Non parametric statistical analyses were conducted for the field data using R version 2.12.2 (The R Foundation for Statistical Computing) statistical software. A paired Spearman rank test, the non-parametric equivalent to a paired t-test, was conducted for sediment characteristics and wave climate in vegetated and unvegetated areas. A one-way Kruskal Wallace analysis of variance was conducted for sediment characteristics, wave climate and SAV biomass, density and morphology across sites.

Results

Wave and Sediment Characteristics

The wave climate in SAV habitats in the shallow, near shore Chesapeake Bay was described in terms of the component of flow with greatest impact on the plant populations and sediment surface: the maximum near bottom orbital velocity. The velocity ranged from $0.019 \pm 0.008 \text{ m s}^{-1}$ (Hungars Creek Vegetated) to $0.304 \pm 0.006 \text{ m s}^{-1}$ (Trippe Bay Unvegetated) (Figure 3.3). The sites with the highest orbital velocity (0.171 to 0.304 m s^{-1}) were found in the mid bay, from Irish Creek to Fleets Bay. Significantly lower orbital velocities (0.019 to 0.139 m s^{-1}) occurred in the

upper Bay, from Susquehanna Flats to Severn River, and lower bay, from Piankatank River to Hungars Creek ($p\text{-value}= 7.87e^{-3}$ (Table 3.5)). At study sites in the mid bay region, unvegetated areas tended to experience significantly higher orbital velocities than vegetated areas ($p\text{-value}=0.014$). Study sites in the upper bay did not significantly vary in orbital velocity between vegetated and unvegetated areas. In the lower bay region, orbital velocity was significantly higher when SAV was present in the Piankatank River and when SAV was not present in Hungars Creek.

The field-collected wave data represents conditions at each site including bathymetry, slope of shore and sediment roughness. However, limits of the dataset need to be noted. Each mean maximum near bottom orbital velocity estimate is based on approximately two weeks of data. This short observation period represents a limited snapshot within long term wave climate trends and does not capture large events such as winter storms or hurricanes. The data were collected during the SAV growing season (May to November) when winds ranged from 2.28 ± 1.17 to $5.85 \pm 2.45 \text{ m s}^{-1}$ out of the south south west (Table 3.4). There was no significant difference in wind speed between sites ($p\text{-value}=0.44$). Therefore, orbital velocities are an underrepresentation of what SAV experience throughout the year.

Sediment Characteristics

The mass median sediment grain size (D50) from both sampling seasons ranged from $42.75 \mu\text{m}$ at the Bishops Head Unvegetated site, located along a retreating marsh shoreline, to $318.46 \mu\text{m}$ at the Piankatank River Vegetated site and varied significantly between study sites ($p\text{-value}= 3.31e^{-4}$) (Figure 3.4). During the 2011 sampling season the Susquehanna Flats Vegetated site sediment contained a

large cobble component layered with a sand component forming an armored, bimodal grain size distribution (Figure 3.5). The cobble component of the sediment sample skewed the D50 grain size (934.62 μm) to be significantly higher than any other site ($p\text{-value} = <0.0001$), making it a statistical outlier. The grain size including only the sand, silt and clay components of the armored sediment is 231.77 μm , which is more representative of the below ground environment for the SAV.

Sediment grain size was significantly lower in the mid-Bay than in the upper- and lower-Bay regions ($p\text{-value} = < 0.0001$). The majority of study sites contained sediment classified as fine sand on the Wentworth scale. Exceptions include Irish Creek Unvegetated and Bishops Head Vegetated, which were very fine sand, Bishops Head Unvegetated which was coarse silt and Sassafras River Vegetated, Fleets Bay Vegetated and Piankatank River Vegetated which contained medium sand. Sediment texture in vegetated and unvegetated areas were often significantly different at individual study sites. Limiting levels of sediment grain size to SAV appeared to vary greatly between study sites.

There was little variability in grain size between 2010 and 2011 (Figure 3.6). Sediment grain size increased between 2010 and 2011 for nine out of eleven sites in vegetated areas and decreased for seven out of eleven sites in unvegetated areas. Few sites changed in grain size enough to alter the Wentworth classification of the sediment. The most notable increase in grain size occurred at Piankatank River Vegetated which increased from 228.99 ± 5.48 to 407.93 ± 13.08 μm , or from fine to medium sand, and the most notable decrease occurred at Fleets Bay Unvegetated which decreased from 375.12 ± 30.40 to 206.991 ± 3.51 μm , or from medium to fine

sand. Susquehanna Flats Vegetated experienced the largest shift in grain size, from 236.14 ± 8.64 to 1512.24 ± 124.86 μm , with the addition of cobbles and transition to armored sediment in 2011, however, no change over time was observed in the sand, silt and clay sediment grain size component.

The percentage of silt and clay was significantly highest (65.2 and 72.1%) in the unvegetated area of Bishops Head for both sampling seasons while the majority of other sites contained less than 10% silt and clay (Figure 3.7). The unvegetated area of Bishops Head also contained the most poorly sorted sediment, followed by the vegetated area of Sassafra River (Figure 3.8). With the exception of Bishops Head unvegetated, the vegetated areas were significantly more poorly sorted than unvegetated areas ($p\text{-value}=1.814e^{-4}$).

Orbital Velocity and Sediment Characteristics

Local sediment characteristics do not appear to be determined by wave-generated near-bottom orbital velocity in the shallow, near-shore Chesapeake Bay (Figure 3.9). Although orbital velocity is significantly correlated to sediment grain size ($p\text{-value}=0.024$), very little variability was explained ($r^2=0.067$). The direction of the relationship was unexpected. No difference was found in the relationship of maximum near bottom orbital velocity and sediment grain size at vegetated or unvegetated sites.

SAV Observations

A total of eight species of SAV was observed over the course of this study (Table 3.1). Two of those species, *Elodea canadensis* and *Potamogeton crispus*, only occurred as negligible fragments. *Ruppia maritima* and *Zostera marina* grew at the

most sites, five for the former and four for the latter. These two species co-occurred at Fleets Bay and Hungars Creek. Severn River and Susquehanna Flats were the only other sites that contained more than one species of SAV.

The distributions of SAV biomass, shoot density and root density were geographically very variable and significantly different between the 2010 and 2011 sampling seasons (p-value= 0.009, 0.039, 0.042). Shoot length and root length did not vary significantly within species between sites (p-value= 0.334; 0.834; 0.399; 0.437). See appendix for further details.

SAV and Water Flow

Vegetated areas were most often characterized by orbital velocity between 0.1 and 0.15 cm s^{-1} (Figure 3.10). SAV appears to be limited by orbital velocities larger than $0.26 \pm 0.009 \text{ m s}^{-1}$. There was no significant relationship between orbital velocity and SAV biomass, strap bladed species density or *Z. marina* and *R. maritima* shoot length or root length (Table 3.6).

SAV and Sediment Characteristics

SAV grew at sites with a relatively narrow range of sediment grain sizes: very fine ($97.966 \pm 0.648 \mu\text{m}$) to medium sand ($407.92 \pm 13.079 \mu\text{m}$) (Figure 3.11). The majority of vegetated sites were characterized by fine sand, specifically sediment grain size between 150 and 200 μm in both 2010 and 2011. SAV was also able to grow in the unique armored sediment of Susquehanna Flats ($1512 \pm 128.863 \mu\text{m}$). *R. maritima* was the only species to grow in sediment below $177 \pm 10.171 \mu\text{m}$ grain size (at Bishop's Head). The sediment at the majority of vegetated sites contained between 0 and 2% silt and clay, only one vegetated site containing more than 14% silt and clay

(Figure 3.12). The sorting index of the majority of vegetated sites was between 1.5 and 2 signifying moderately sorted sediment (Figure 3.8, 3.13). Neither sediment grain size, the percentage of silt and clay nor sediment sorting index were significantly related to SAV biomass, density or morphology (Table 3.6).

Sediment Motion

Nearly all study sites were characterized by sediment motion, most often bedload transport, according to a modified Shields diagram (Figure 3.14). Two vegetated sites, armored Susquehanna Flats and sand bar protected Hungars Creek, fell just below the threshold of sediment motion. The sand, silt and clay components of sediment at Susquehanna Flats was characterized by bedload transport. Two vegetated sites, Bishops Head and Irish Creek, experienced moderate sediment erosion. This assessment of sediment motion may be an underestimation because the wave generated shear stress used represents summer conditions which tend to be very quiescent in comparison to other seasons. Although the study sites that experienced the highest level of sediment erosion were unvegetated, there was no difference in the sediment motion predicted for vegetated and unvegetated sites.

Sediment motion was estimated to have occurred during some percentage of the period of field wave observation at every study site, usually for at least 70% of the time (Figure 3.15). The mid-Bay region tended to experience sediment motion more often than the upper- and lower-bay regions. Over half of sites experienced more sediment motion at unvegetated than vegetated areas.

Data gathered from other studies both in the Chesapeake Bay and exterior systems such as Long Island Sound and the North Sea were plotted on the Hjulstrom

diagram because shear stress was not available (Figure 3.16). All sites with very few exceptions fell within a similar narrow range of grain sizes and orbital velocities characterized by bedload transport and moderate erosion.

Discussion

Both hydrodynamic and sedimentary characteristics SAV is exposed to in the Chesapeake Bay are complex, variable and geographically diverse (Sanford 1994). Wave-generated orbital velocity was significantly different between individual study sites ($p\text{-value} = <0.0001$) and between the regions of the Bay ($p\text{-value} = <0.0001$). Sites in the mid-bay study tended to be more exposed to open water than upper- and lower-bay sites which are often more sheltered by complex shorelines. The significantly higher wave-generated orbital velocities observed in the mid-bay than in the upper- and lower-bay could be attributed to higher fetch.

Wave generated orbital velocity was significantly related to sediment grain size ($p\text{-value} = 0.024$) in an unexpected way. The opposing regional trends resulted in a negative relationship, sediment grain size decreasing with increasing orbital velocity. Reciprocally, the percentage of silt and clay in sediments significantly increased with orbital velocity ($p\text{-value} = 0.005$). It is well known in the field of fluid dynamics that water flow strongly impacts sediment characteristics and that with increasing current velocity and wave exposure, sediments tend to become coarser and contain a smaller percentage of silt and clay and less organic content (Christiansen et al. 1981; Keddy 1982; Koch 1999; Wargo and Styles 2007). The negative correlation between orbital velocity and sediment grain size indicates that orbital velocity may not alone determine local sediment characteristics.

Sediment sources, both local and regional, may be an important determining factor of local sediment characteristics in addition to wave conditions in determining in near-shore Chesapeake Bay habitats. Nearly all sediments in the Chesapeake Bay are terrigenous, consisting mainly of quartz (Brush 1984). Sedimentary inputs into the Bay have also grown increasingly fine over recent years mainly due to human activity and run off (Sanford et al. 2001). As of 2005, approximately one third of the Chesapeake Bay shoreline is classified as eroding (Chesapeake Bay Program 2005). In the upper- and lower-bay regions, much of the eroding shoreline consists of sand cliffs and ancient dunes which provide sources of coarse sandy sediment. In the mid-bay, marshes characterized by compacted silt and clay are being eroded, contributing fine sediment to near shore areas (Wray et al. 1995). The study site at Bishops Head is a good example of this.

On a larger regional scale, the two largest sources of sediment to the Bay are the Atlantic Ocean, contributing 40% of the total net inputs (mostly sand), and the Susquehanna River, contributing a mixture of sands, silts and clays (Hobbs et al. 1992). Sediment may travel many 10s of kilometers from either of these sources, larger grains settling out of the water column sooner than fine grains. By the time sediment inputs from these sources at the top and bottom of the Bay reach the middle region, only fine sediments may remain to be deposited. Dams on the Susquehanna River sometimes retain coarse sediment components. Several large, though unnamed, storms caused doors to be opened and flood waters to overflow the Conowingo Dam in 2010 and 2011. These events may have impacted the sediment in large portions of the Bay and the Susquehanna Flats Vegetated sampling site in particular.

Waves and currents are known to impact SAV distribution (Fonseca et al. 1983; van Katwijk and Hermus 2000; Frederiksen et al. 2004; Infantes et al. 2009; Rivers et al. 2011). In particular, the minimum water depth inhabitable by SAV is determined by wave orbital velocity (van Katwijk and Hermus 2000; Koch 2001; de Boer 2007). For example, 86% of the variability in *Z. marina* coverage was explained by wave energy in Puget Sound, WA, making water flow a primary factor controlling SAV distribution (Stevens and Lacy 2012). In the Mediterranean Sea, *Posidonia oceanica* and *Cymodosea nodosa* appear to be limited by orbital velocities greater than 30 cm s⁻¹ (Infantes et al. 2009; Infantes et al. 2011). This limitation is consistent with the results of this study for SAV in the Chesapeake Bay where the threshold appears to be 26 cm s⁻¹. SAV appeared most often in orbital velocities ranging from 10 to 20 cm s⁻¹, freshwater species only occurring in orbital velocities ranging from 10 to 15 cm s⁻¹. SAV presence was neither observed under completely stagnant condition nor very high wave exposure (>26 cm s⁻¹), although observations were limited to the summer season, under-representing annual mean conditions.

SAV distribution was limited to a fairly small range of sediment grain size in this study. Sediments in SAV beds were usually sandy. More than half of sites were fine sand, but were also at times armored (Figure 3.12). It has been suggested that SAV colonization is limited by very coarse sediment due to low levels of organic content and physical constraints (Silva et al. 2009). Poor growth has been observed when sand makes up 75% or higher of sediment dry weight and the greatest seedling emergence has been observed in finer sediments for *R. maritima* (Barko and Smart 1986; Ailstock et al. 2010). Here, fresh water species of SAV were able to colonize

coarse sediment in the upper-bay when fine and medium sand were armored by cobble.

Sediment in the vegetated areas also contained a smaller percentage of silt and clay than the threshold of 35% suggested during a restoration study in the Boston Harbor where sediment characteristics played a major role in *Z. marina* restoration (Leschen et al. 2010). The finest sediment, observed at Bishops Head, was limiting to SAV colonization. Extremely fine, high clay silt and organic content percentage sediment can challenge seed burial and recruitment and have a negative effect on several species (Barko and Smart 1983; Barrat-Segratain 1996; Handley and Davy 2002). It has been suggested that SAV need a sufficiently thick (>2 cm) surficial sand layer for successful colonization and growth (Palinkas and Koch 2012). Well sorted sediments were also limiting SAV in this study, as in the Wadden Sea where *Z. marina* grew only in poorly sorted sand (Schaz and Asmus 2003). Sediment sorting may be an indicator of porewater advection and fine particle entrainment, impacting oxygen and nutrient fluxes within SAV root zones.

Although limiting thresholds appeared for SAV across all study sites in the Chesapeake Bay (26 cm s⁻¹ orbital velocity and medium sand), study site specific thresholds exhibited some variance. At more exposed sites in the mesohaline region of the Bay, SAV distribution was limited by high orbital velocity, but that was not the case at the more sheltered sites in the upper- and lower-bay. This trend reflects recent work on the impact of breakwaters on SAV habitat (Koch et al. in prep). Breakwaters in hydrodynamically active areas (fetch > 10 km) tend to increase SAV colonization by sheltering the plants while those constructed in quiescent areas (fetch < 3 km)

increase SAV colonization with higher fluxes (Koch et al. in prep). High wave activity may be physically limiting to SAV, but it is also well documented that water flow can enhance nutrient access, oxygen transfer and photosynthesis (Enrique and Rodriquez-Roman 2006; Larkum et al. 2006; Mass et al. 2010).

Surprisingly, considering much previous research, water flow-sediment conditions in SAV beds were not depositional, but sediment was usually transported as bedload. The two sites that fell just below the threshold for sediment motion on the Shields diagram most likely experienced some sediment motion as well. The threshold represents the mean of extensive experimental results, and so these sites most likely experience some sediment motion. Furthermore, this assessment was made based on field wave data collected during the calmest time of year and can be considered a minimum sediment motion status. Two vegetated sites, Bishops Head and Irish Creek, even experienced moderate sediment erosion. Although the study sites that experienced the highest level of sediment erosion were unvegetated, particularly in the mid-bay, there was no difference in the sediment motion experienced in vegetated and unvegetated sites (Figure 3.13, 3.14).

Data collected from other systems such as Long Island Sound and the Wadden Sea and from addition areas of the Chesapeake Bay fall into the same region of the less precise Hjulstrom diagram. SAV beds are often categorized as depositional (Koch 2001), however SAV bed sites that accumulate fine sediments over the growing season often also experience increased sediment erosion during the winter (Bos et al. 2007), indicating the need for some sediment motion. The majority of vegetated study sites contained coarser sediments in 2011, when sites were sampled

early in the summer, than 2010, when sites were sampled late in the summer after fine particles could be accumulated. Recent work has also found that mangrove seedlings benefit from moderate sediment accretion and erosion when growth rates exceed the temporal distribution of large sediment motion events (Balke et al. 2013).

The limitations from physical and geological habitat parameters can be explained ecologically. Light, the most important habitat requirement of SAV, can be limited when very fine sediments are transported in suspension. When sediment, particularly fine sediment, is deposited, the accumulating organic content can contain phyto-toxic compounds and seeds and shoots may be buried preventing germination or growth (Cabaco et al. 2008). It has been recommended not to out-plant seeds in areas with sediment accretion rates greater than 1 cm during the period of initial seedling establishment (Ailstock et al. 2010). Water flow, which would be extremely low in depositional or fine suspension environments, is necessary for SAV reproduction. Flowers are pollinated and seeds and reproductive fragments are dispersed through waves and currents (Ackerman 1986; Fonseca and Kenworthy 1987). Faster water flow also enhances photosynthesis, oxygen transfer, and nutrient access to the leaf tissue (Koch et al. 1994; Mass et al. 2010; Hurd 2000).

Very high water flow can exert high drag forces on above ground plant material, potentially dislodging the plant. It has been suggested that *Z. marina* seedling recruitment is more dependent on physical sediment-seedling interactions than seed germination rates. Although 90% of seeds germinated in one study, a ten-fold increase in seedling establishment was observed when seeds were protected through 2 cm burial than when seeds were eroded on the sediment surface (Marion

and Orth 2012). Rapid sediment erosion can further limit plant stability through constant substrate transport and loss. *Halodule wrightii* transplanted onto very fine dredge material in Texas died quickly because suspended fine sediment limited light access, high ammonium porewater concentrations (600uM and up) became toxic and rapid substrate loss limited plant stability (Kaldy et al. 2004). Very coarse sediment with low organic content can nutritionally limit SAV growth and challenge some species in taking root. Moderate bedload transport or low level erosion may provide shallow seed burial, organic particle flux, reproductive distribution and stable substrate without limiting light access (Figure 3.16).

Future studies would benefit from considering long term wave datasets, currents and an investigation of sediment permeability. Biofilms, or microphytobenthos, may interact with sediment motion, increasing the shear stress necessary to initiation sediment motion (Widdows and Brinsley 2002), and should be investigated further.

Conclusions

The investigation of SAV habitat requirements other than light is vital for the success of SAV restoration in the Chesapeake Bay. Beyond the consideration of individual SAV habitat requirements, the importance of related habitat parameters such as water flow and sediment characteristics must be recognized. This study assessed the sediment motion conditions within established SAV beds in comparison to adjacent unvegetated areas and supported the hypothesis that suitable SAV habitats are those characterized by water flow and sediment characteristics predicted to result in moderate bedload transport. SAV beds in other ecosystems and areas of the

Chesapeake Bay were also characterized by bedload transport according to the Hjulsrom diagram, supporting the hypothesis that SAV is found, and biomass production is high, in habitats characterized by moderate sediment transport. SAV was also only found in moderately and poorly sorted sediments in this study. Traditionally, only light requirements of SAV are considered during restoration site selection. The results of this study highlight the importance of weighing other habitat requirements, in addition to light availability, during site selection and to assess them in terms of moderate bedload transport, not depositional conditions.

Tables

Table 3.1 Sampling site location coordinates in each region of the Chesapeake Bay and SAV species observed there.

Region	Site	Vegetated Coordinates	Unvegetated Coordinates	Observed SAV Species
Oligohaline	Susquehanna River	39° 23' 06" N 76° 01' 18" W	39° 24' 24" N 76° 01' 22" W	<i>Myriophyllum spicatum</i> <i>Vallisneria americana</i>
	Sassafras River	39° 23' 20" N 76° 02' 27" W	39° 24' 24" N 76° 01' 22" W	<i>Vallisneria americana</i>
	Severn River	39° 01' 51" N 76° 31' 28" W	39° 02' 08" N 76° 31' 10" W	<i>Potamogeton perfoliatus</i> <i>Stuckenia pectinata</i>
Mesohaline	Irish Creek	38° 41' 33" N 76° 13' 1" W	38° 41' 42" N 76° 13' 17" W	<i>Ruppia maritima</i>
	Trippe Bay	38° 36' 33" N 76° 16' 37" W	38° 37' 17" N 76° 17' 02" W	<i>Ruppia maritima</i>
	Solomon's Island	38° 19' 27" N 76° 26' 39" W	38° 19' 06" N 76° 27' 06" W	<i>Ruppia maritima</i>

	Bishop's Head	38° 13' 9" N 76° 2' 19" W	38° 13' 18" N 76° 2' 27" W	<i>Ruppia maritima</i>
Polyhaline	Tangier Island	37° 50' 37" N 75° 59' 18" W	37° 50' 58" N 75° 59' 35" W	<i>Ruppia maritima</i> <i>Zostera marina</i>
	Fleets Bay	37° 38' 33" N 76° 18' 36" W	37° 37' 28" N 76° 16' 59" W	<i>Ruppia maritima</i> <i>Zostera marina</i>
	Piankatank River	37° 30' 51" N 76° 18' 12" W	37° 30' 7" N 76° 19' 45" W	<i>Zostera marina</i>
	Hungars Creek	37° 24' 59" N 75° 59' 25" W	37° 25' 01" N 75° 59' 23" W	<i>Ruppia maritima</i> <i>Zostera marina</i>

Table 3.2A Equations for converting wave height and period into orbital velocity. A_b = bottom particle excursion length, T_p = peak period, U_b = max near-bottom orbital velocity.

Equations
$A_b = (H_s) / 2 \sinh(2\pi D / \lambda)$
$T_p = \text{Measured Value}$
$U_b = 2\pi A_b / T_p$

Table 3.2B Wave particle excursion length, wave period and wave orbital velocity of each vegetated and unvegetated site based on summer field observations.

Site	Type	Particle Excursion Length (m±SD)	Wave Period (s ±SD)	Orbital Velocity (m s ⁻¹ ±SD)
Susquehanna	Veg	0.29 ± 0.18	1.72 ± 0.63	0.11 ± 0.07
Susquehanna	Unveg	0.29 ± 0.21	1.80 ± 0.72	0.11 ± 0.08
Sassafras	Veg	0.31 ± 0.21	1.89 ± 0.92	0.13 ± 0.09
Sassafras	Unveg	0.28 ± 0.21	1.80 ± 0.72	0.11 ± 0.08
Severn	Veg	NA	NA	NA
Severn	Unveg	0.14 ± 0.23	0.96 ± 0.49	0.04 ± 0.07
Irish	Veg	0.51 ± 0.24	2.33 ± 0.57	0.22 ± 0.11
Irish	Unveg	0.51 ± 0.23	2.44 ± 0.62	0.23 ± 0.11
Trippe	Veg	0.59 ± 0.29	2.30 ± 0.70	0.25 ± 0.11
Trippe	Unveg	0.75 ± 0.38	2.26 ± 0.73	0.30 ± 0.15
Solomons	Veg	0.29 ± 0.18	1.79 ± 0.80	0.11 ± 0.07

Solomons	Unveg	0.37 ± 0.31	2.03 ± 1.25	0.17 ± 0.15
Bishops	Veg	0.45 ± 0.23	2.11 ± 0.78	0.19 ± 0.10
Bishops	Unveg	0.71 ± 0.39	2.31 ± 0.55	0.28 ± 0.13
Tangier	Veg	0.41 ± 0.28	2.38 ± 0.91	0.18 ± 0.11
Tangier	Unveg	0.55 ± 0.31	2.61 ± 0.69	0.24 ± 0.12
Fleets	Veg	0.57 ± 0.35	2.53 ± 1.11	0.26 ± 0.15
Fleets	Unveg	0.55 ± 0.30	3.11 ± 0.85	0.27 ± 0.12
Piankatank	Veg	0.28 ± 0.21	2.36 ± 1.14	0.14 ± 0.10
Piankatank	Unveg	0.20 ± 0.24	1.52 ± 0.93	0.09 ± 0.11
Hungars	Veg	0.05 ± 0.08	0.96 ± 0.69	0.02 ± 0.04
Hungars	Unveg	0.20 ± 0.18	2.34 ± 1.25	0.11 ± 0.10

Table 3.3 Wind data recorded by the National Data Buoy Center for representative upper, mid and lower bay sites with reference to field collected wave statistics. (\pm SD).

Site	Start Date	Wind Speed (m s^{-1})	Wind Direction	Hs (m)	T (s)	Ub (m/s)
Susquehanna	7/20/2011	3.97 (± 1.97)	185.66 (± 87.51)	0.11 (± 0.04)	1.73 (± 0.63)	0.11 (± 0.08)
Sassafras	7/20/2011	3.97 (± 1.97)	185.66 (± 87.51)	0.09 (± 0.03)	1.89 (± 0.92)	0.13 (± 0.09)
Severn	11/21/2011	5.14 (± 2.94)	198.98 (± 96.76)	0.07 (± 0.02)	0.96 (± 0.49)	0.04 (± 0.07)
Irish	10/19/2010	4.57 (± 4.11)	219.42 (± 87.54)	0.20 (± 0.07)	2.33 (± 0.57)	0.22 (± 0.11)
Trippe	6/29/2006	3.56 (± 1.90)	212.46 (± 85.10)	0.17 (± 0.06)	2.30 (± 0.70)	0.25 (± 0.11)
Solomon	6/30/2006	3.74 (± 1.88)	215.31 (± 81.76)	0.13 (± 0.05)	1.80 (± 0.80)	0.11 (± 0.08)
Bishop	6/5/2000	3.79 (± 1.64)	143.05 (± 104.65)	0.12 (± 0.05)	2.11 (± 0.78)	0.19 (± 0.10)
Tangier	10/6/2010	2.28 (± 1.17)	226.48 (± 86.74)	0.12 (± 0.05)	2.38 (± 0.91)	0.18 (± 0.11)
Fleets	5/17/2006	5.85 (± 2.45)	213.07 (± 106.3)	0.20 (± 0.07)	2.53 (± 1.11)	0.26 (± 0.15)
Piankatank	8/16/2005	2.90 (± 1.56)	156.73 (± 100.37)	0.13 (± 0.05)	2.36 (± 1.15)	0.14 (± 0.10)
Hungars	7/21/2005	3.06 (± 1.56)	176.28 (± 105.55)	0.09 (± 0.02)	0.96 (± 0.69)	0.02 (± 0.4)

Table 3.4 *In situ* habitat parameter non parametric paired Wilcoxon test results.

Dataset	Factor	V-value	P-value
Orbital Velocity	SAV Presence	154	0.719
Orbital Velocity	Mid, SAV Presence	0	0.014
Grain Size	SAV Presence	158	0.321
Grain Size	Year	95	0.487
Total Biomass	Year	9	0.009
Above-ground Biomass	Year	9	0.008
Below-ground Biomass	Year	9	0.033
Shoot Density	Year	11	0.039
Root Density	Year	10	0.042
<i>Z. marina</i> Shoot Length	Year	3	0.334
<i>Z. marina</i> Root Length	Year	3	0.834
<i>R. maritima</i> Shoot Length	Year	5	0.399
<i>R. maritima</i> Root Length	Year	5	0.437

Table 3.5 *In situ* one way Kruskal-Wallis test results.

Response	Effect	Degree of Freedom	Chi-Squared Value	P-value
Orbital Velocity	Region	2	9.69	7.87e ⁻³ *
Orbital Velocity	Site	10	36.778	6.184e ⁻⁵ *
Grain Size	Region	2	19.609	5.519e ⁻⁵ *
Grain Size	Site	10	32.492	3.31e ⁻⁴ *
Grain Size	Orbital Velocity	19	37.766	6.355e ⁻³ *
Total Biomass	Region	2	0.798	0.671
Total Biomass	Site	10	2.119	0.995

Total Biomass	Orbital Velocity	19	33.487	0.021*
Total Biomass	Grain Size	36	38	0.378
Above-ground Biomass	Region	2	0.578	0.749
Above-ground Biomass	Site	10	2.268	0.994
Above-ground Biomass	Orbital Velocity	19	33.474	0.021*
Above-ground Biomass	Grain Size	36	38	0.378
Below-ground Biomass	Region	2	0.798	0.671
Below-ground Biomass	Site	10	2.101	0.996
Below-ground Biomass	Orbital Velocity	19	33.240	0.023*
Below-ground Biomass	Grain Size	36	38	0.378
Above- to Below-ground Biomass Ratio	Region	2	1.023	0.599
Above- to Below-ground Biomass Ratio	Site	10	2.166	0.995
Above- to Below-ground Biomass Ratio	Orbital Velocity	9	11.575	0.238
Above- to Below-ground Biomass Ratio	Grain Size	36	38	0.378
<i>Zostera marina</i>				
Total Biomass	Site	3	2.143	0.543
Total Biomass	Orbital Velocity	3	2.143	0.543
Total Biomass	Grain Size	5	5	0.416
Above-ground Biomass	Site	3	1.286	0.733
Above-ground Biomass	Orbital Velocity	3	1.286	0.733
Above-ground Biomass	Grain Size	5	5	0.416
Below-ground Biomass	Site	3	3.143	0.370
Below-ground Biomass	Orbital Velocity	3	3.143	0.370
Below-ground Biomass	Grain Size	5	5	0.416

Shoot Length	Site	3	2.143	0.543
Shoot Length	Orbital Velocity	3	2.143	0.543
Shoot Length	Grain Size	5	5	0.416
Root Length	Site	3	3.571	0.312
Root Length	Orbital Velocity	3	3.571	0.312
Root Length	Grain Size	5	5	0.416
<i>Ruppia maritima</i>				
Total Biomass	Site	6	6.8	0.339
Total Biomass	Orbital Velocity	6	6.8	0.339
Total Biomass	Grain Size	8	8	0.434
Above-ground Biomass	Site	6	7.333	0.291
Above-ground Biomass	Orbital Velocity	6	7.333	0.291
Above-ground Biomass	Grain Size	8	8	0.434
Below-ground Biomass	Site	6	7.133	0.309
Below-ground Biomass	Orbital Velocity	6	7.133	0.309
Below-ground Biomass	Grain Size	8	8	0.434
Shoot Length	Site	6	7.467	0.279
Shoot Length	Orbital Velocity	6	7.467	0.279
Shoot Length	Grain Size	8	8	0.434
Root Length	Site	6	6.867	0.333
Root Length	Orbital Velocity	6	6.867	0.333
Root Length	Grain Size	8	8	0.434

Table 3.6 *In situ* non parametric Spearman rank correlation results.

SAV/Parameter	Effects	Rho	S-value	P-value
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Response				
Total Biomass	Orbital Velocity	-0.059	7558.10	0.738
Total Biomass	Grain Size	-0.032	10196.83	0.846
Total Biomass	Silt and Clay %	0.249	7416.04	0.126
Above-ground Biomass	Orbital Velocity	-0.057	7544.24	0.747
Above-ground Biomass	Grain Size	-0.052	10388.91	0.756
Above-ground Biomass	Silt and Clay %	0.282	7093.69	0.082
Below-ground Biomass	Orbital Velocity	-0.055	7533.85	0.735
Below-ground Biomass	Grain Size	-0.016	10042	0.921
Below-ground Biomass	Silt and Clay %	0.235	7557.35	0.149
Above- to Below-ground Biomass Ratio	Orbital Velocity	-0.321	739.805	0.243
Above- to Below-ground Biomass Ratio	Grain Size	-0.015	828	0.959
Shoot Density	Orbital Velocity	-0.083	8413.97	0.631
Shoot Density	Grain Size	-0.106	10111.38	0.525
Root Density	Orbital Velocity	-0.103	9309.15	0.542
Root Density	Grain Size	-0.035	10221.11	0.8347
<i>R. maritima</i> Above-ground Biomass	Orbital Velocity	0.046	209.93	0.894
<i>R. maritima</i> Below-ground Biomass	Orbital Velocity	0.352	142.47	0.288
<i>Z. marina</i> Above-ground Biomass	Orbital Velocity	0.088	31.91	0.868
<i>Z. marina</i> Below-ground Biomass	Orbital Velocity	0.177	28.82	0.738
Above- to Below- ground Biomass Ratio	Orbital Velocity	-0.321	739.80	0.243
Silt Clay %	Orbital Velocity	0.431	6527.526	0.005*

Grain Size	Orbital Velocity	-0.351	15512.27	0.024*
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Figures



Figure 3.1. Locations of eleven sampling sites at vegetated and unvegetated areas in the Chesapeake Bay.

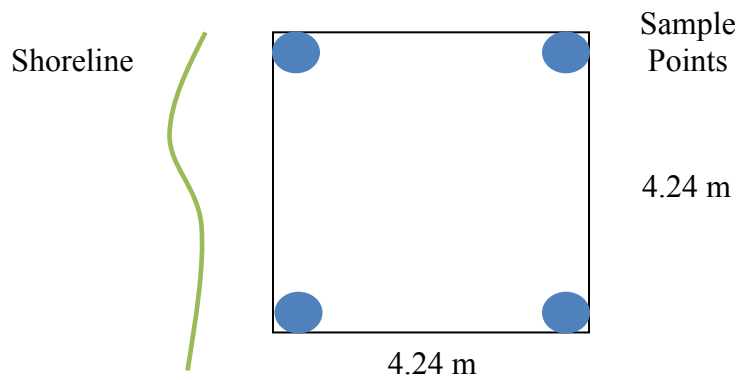


Figure 3.2. Sampling design for SAV biomass and sediment push cores. (figure not to scale)

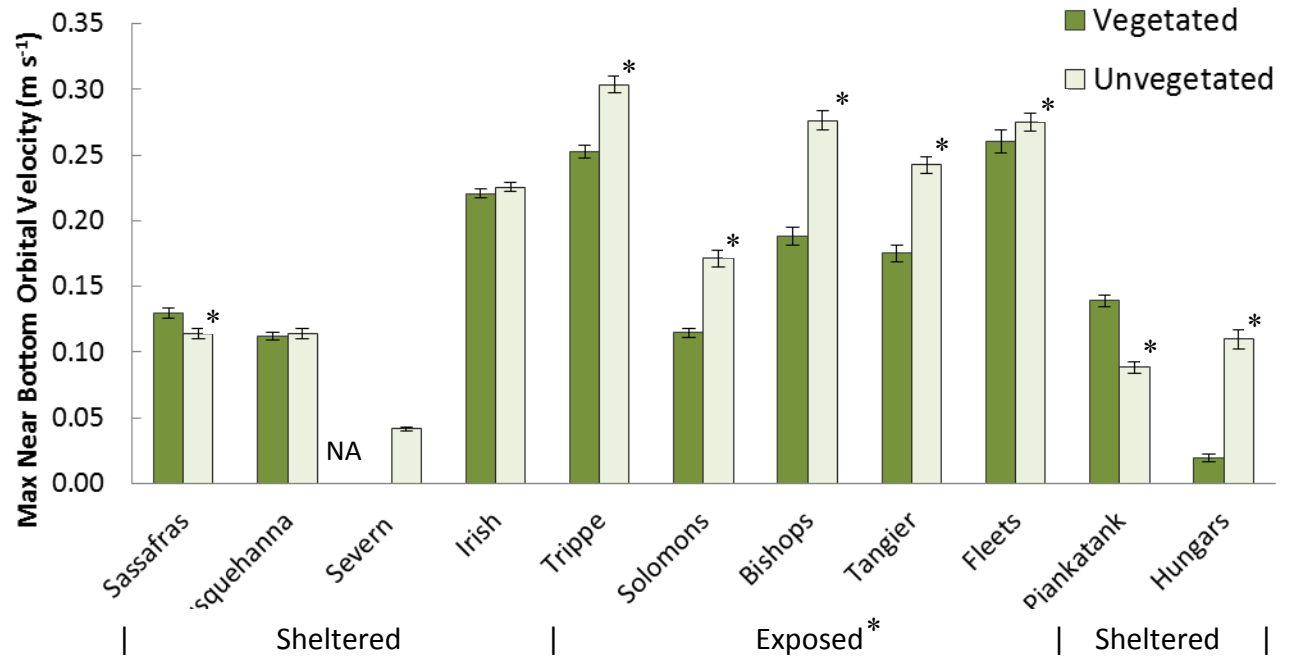


Figure 3.3 The maximum near bottom orbital velocity ($\text{m s}^{-1} \pm \text{SE}$) measured at each vegetated and unvegetated site (from north to south) in the Chesapeake Bay. Asterisks represent significant difference.

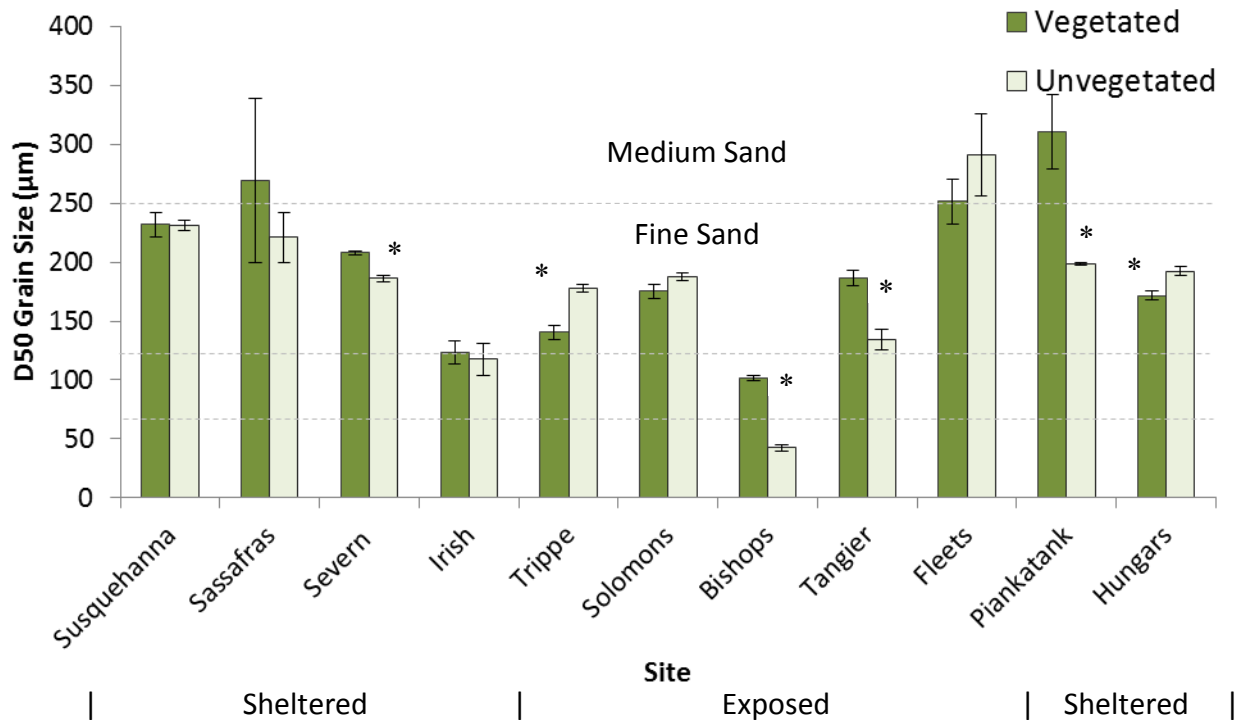


Figure 3.4. The D50 grain size ($\mu\text{m} \pm \text{SE}$) of vegetated and unvegetated sites (from north to south) in the Chesapeake Bay including only the sand component of vegetated Susquehanna. Grey dashed lines represent Wentworth grain size classifications. Asterisks represent significantly different vegetated and unvegetated sites.

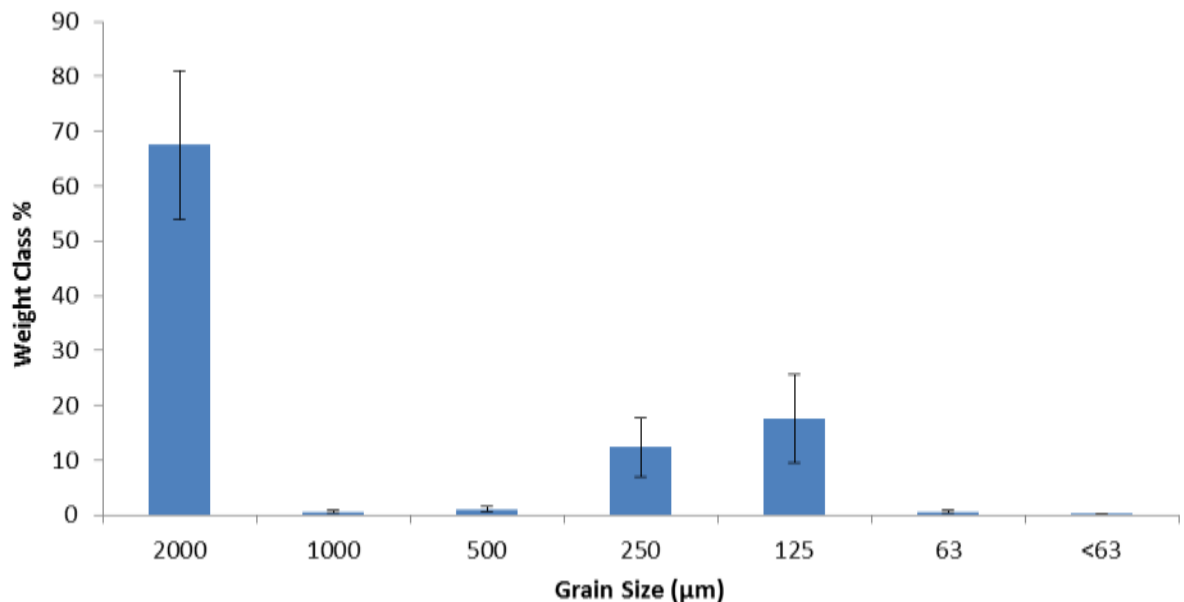


Figure 3.5. Sediment grain size distribution of the Susquehanna Flats Vegetated site in 2011 after a large cobble input creating a bimodal distribution.

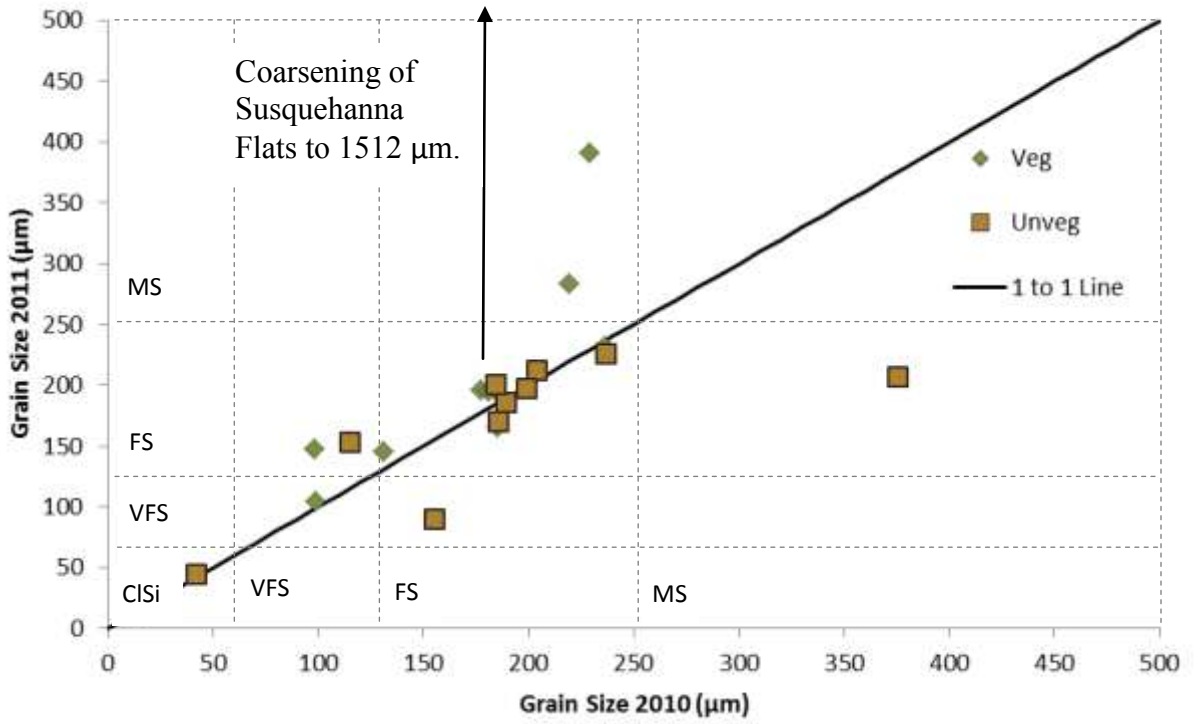


Figure 3.6. Inter-annual (2010-2011) variability in SAV-vegetated and adjacent unvegetated sites. The black line represents the line of ideal fit (1:1) where all grain sizes are the same over both years.

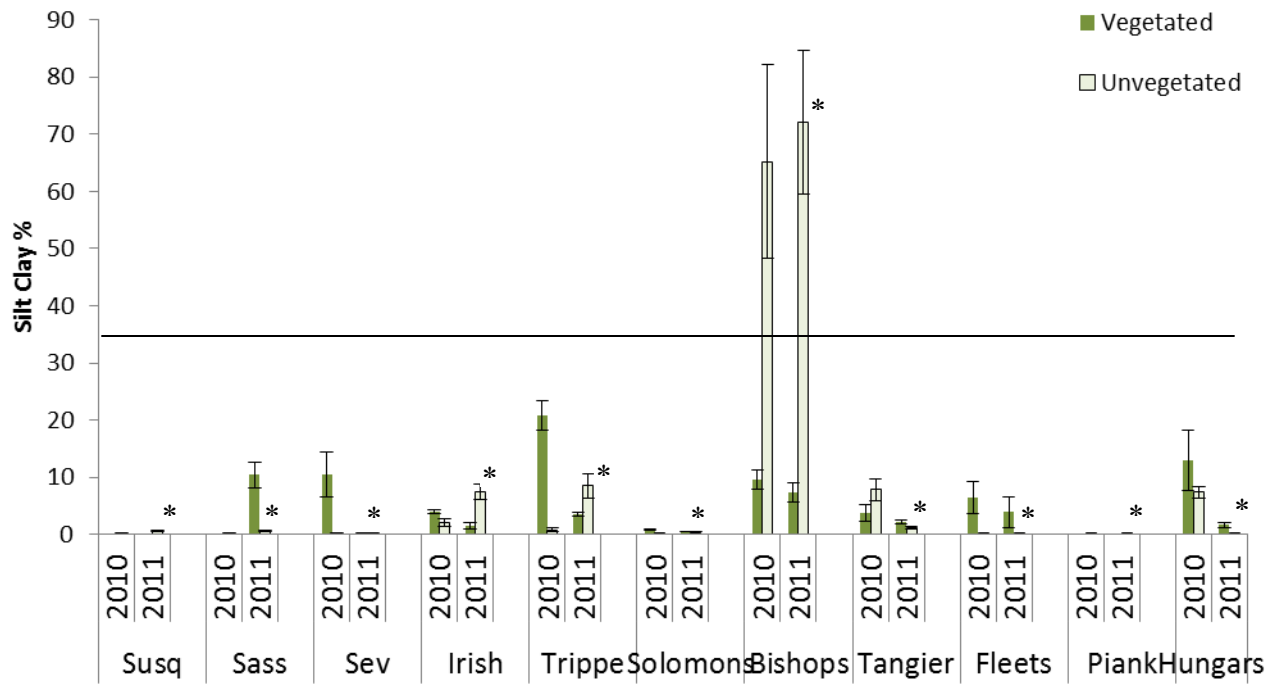


Figure 3.7. The percentage of silt and clay (% ± SE) in the sediment at vegetated and unvegetated sites. Black horizontal line represents a suggested threshold of 35% silt and clay for SAV.

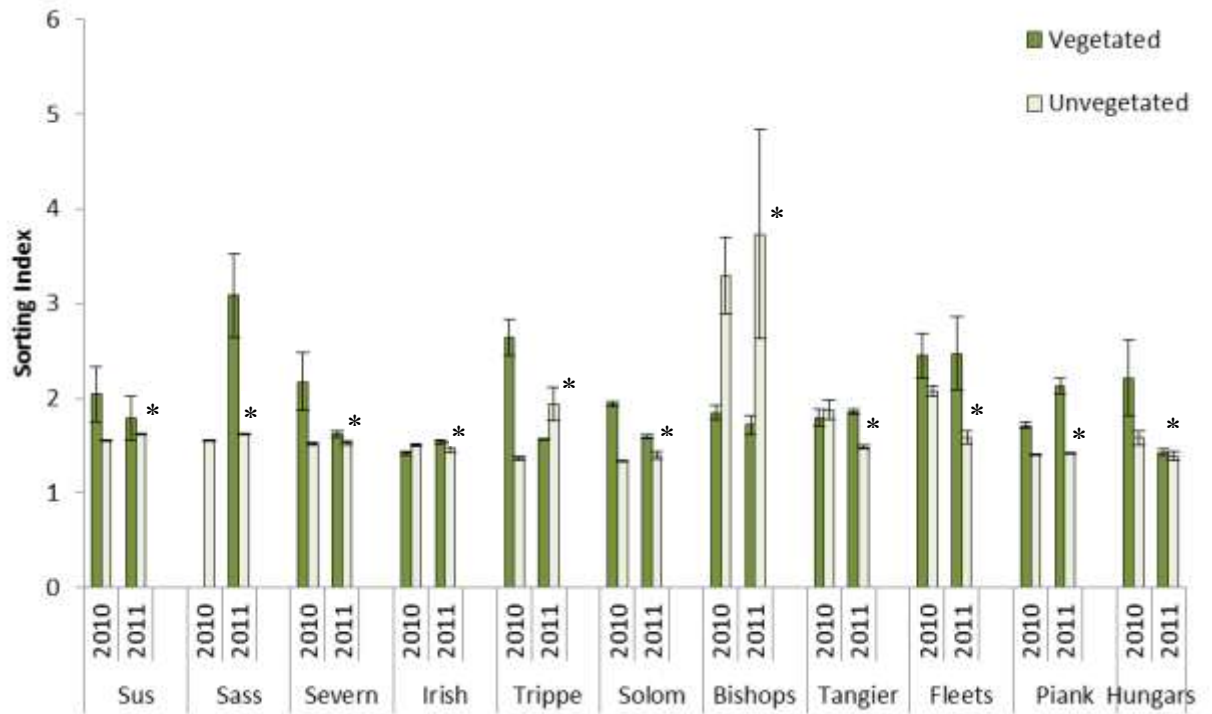


Figure 3.8 The sorting index of sediment at vegetated and unvegetated sites. Higher sorting index indicates a more poorly sorted grain size distribution.

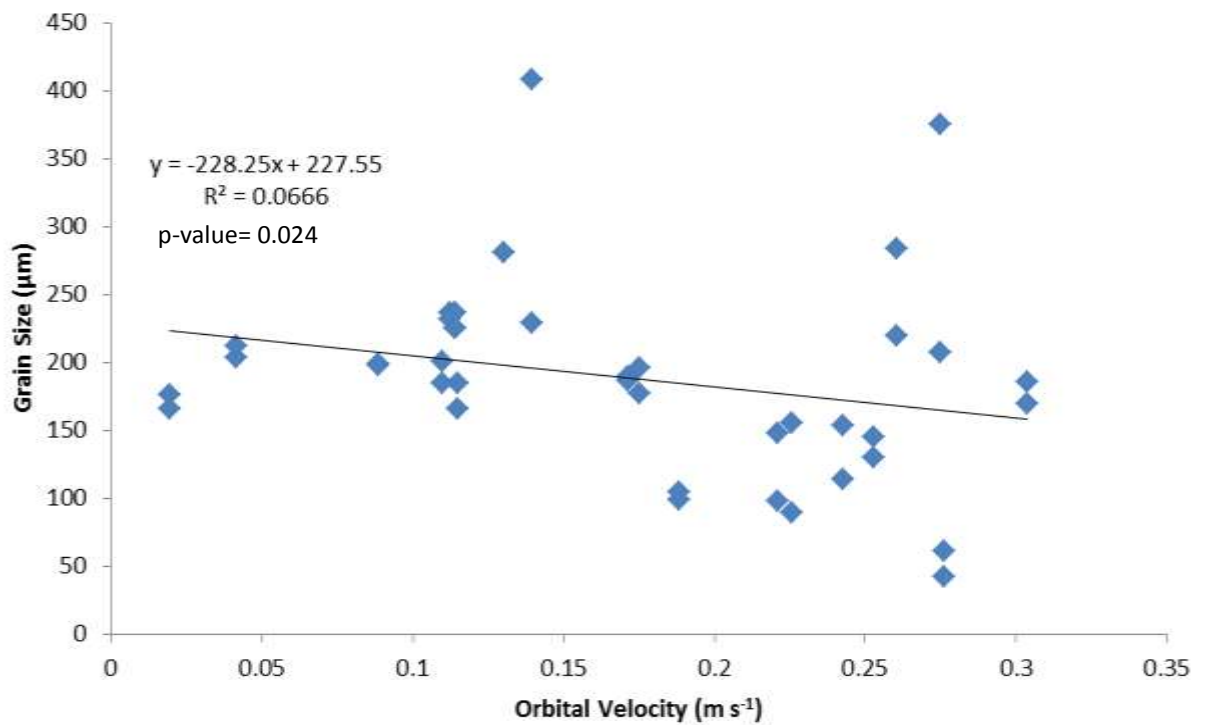


Figure 3.9 The maximum near bottom orbital velocity (m s^{-1}) of each vegetated and unvegetated site correlated to the D50 grain size (μm) sampled in 2010 and 2011.

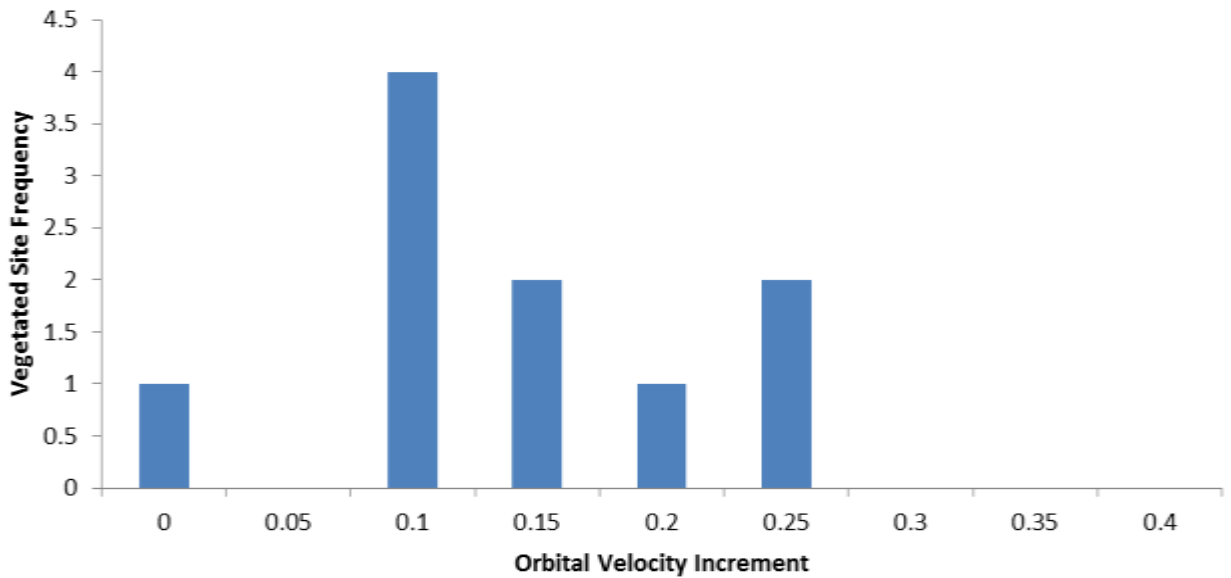


Figure 3.10 The distribution of vegetated sites over increments of maximum near bottom orbital velocity observed at sampling sites.

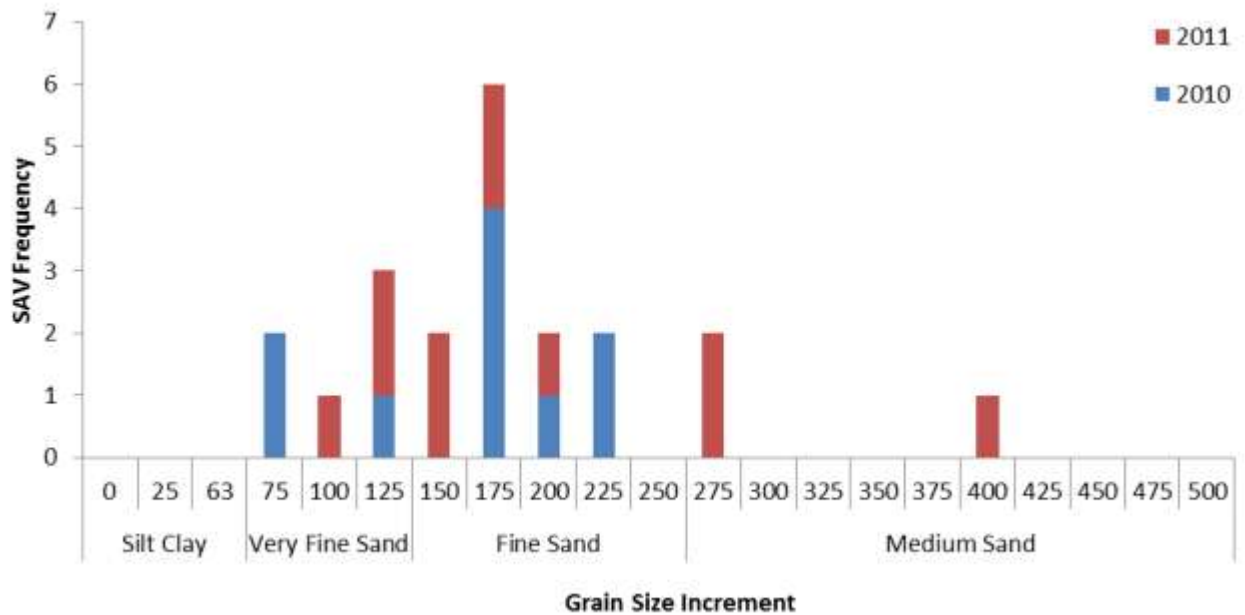


Figure 3.11 The frequency of vegetated sites growing in increments of sediment grain size (μm).

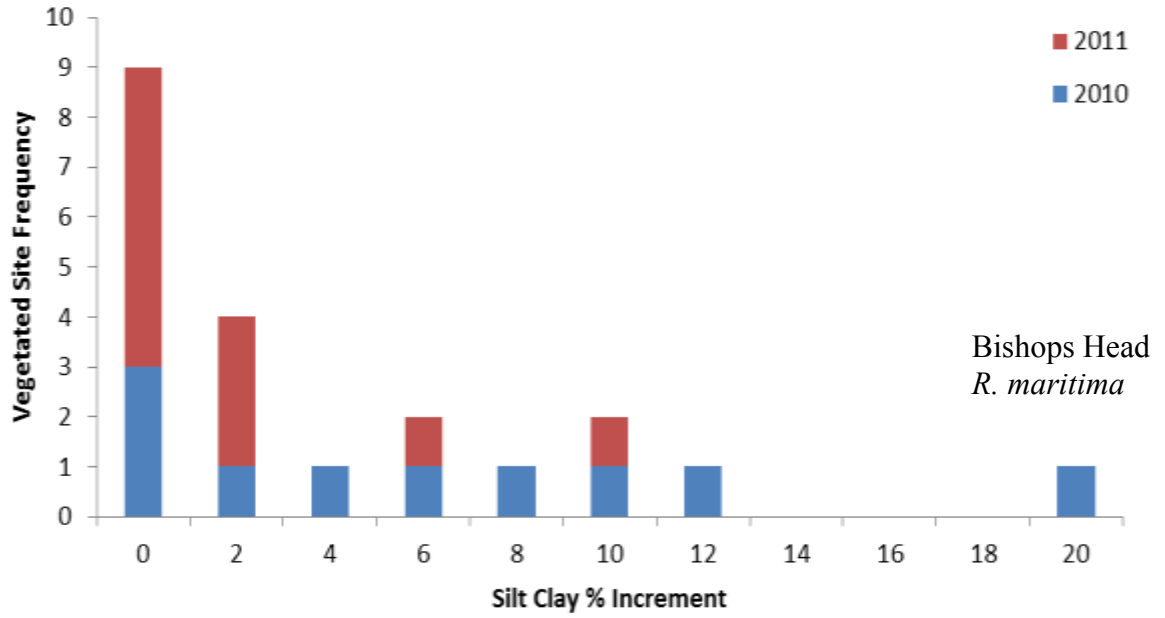


Figure 3.12 The frequency of vegetated sites growing in increments of sediment silt clay %.

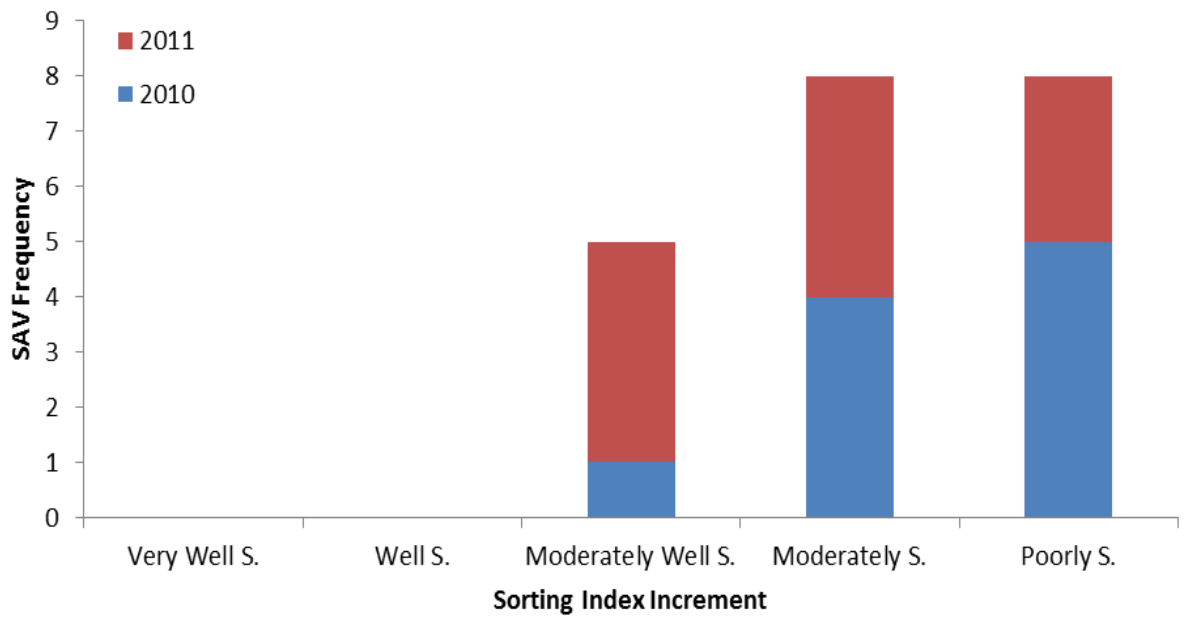


Figure 3.13 The frequency of vegetated sites growing in increments of sediment sorting index.

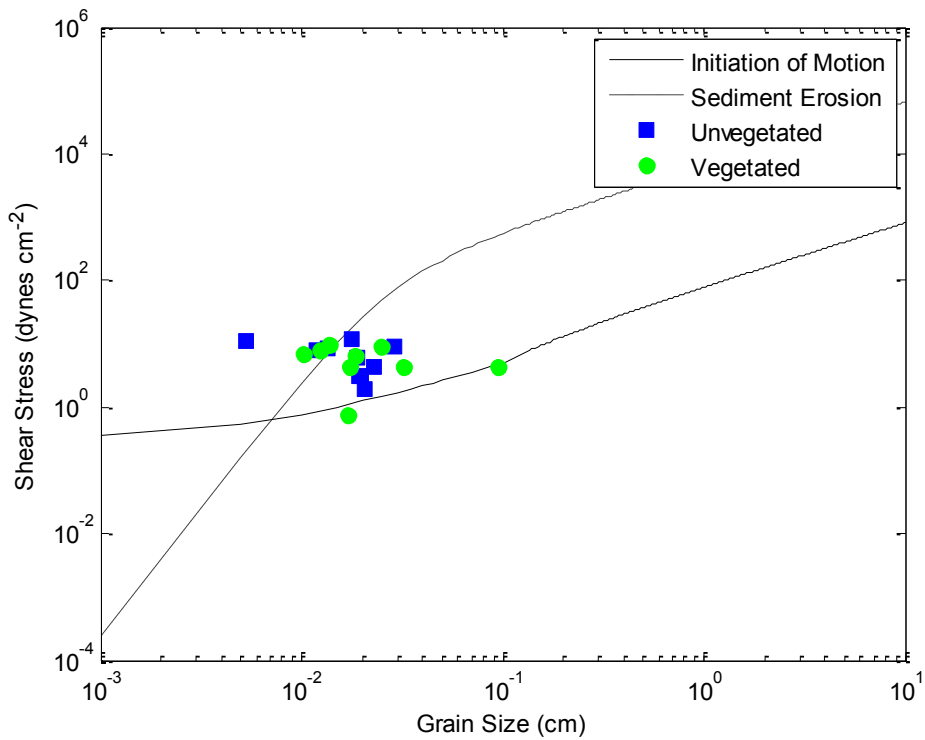


Figure 3.14 Modified Shields diagram relating the mean D50 grain size (cm) at each vegetated and unvegetated site to the calculated shear stress in comparison the empirically derived Shields critical threshold of sediment motion.

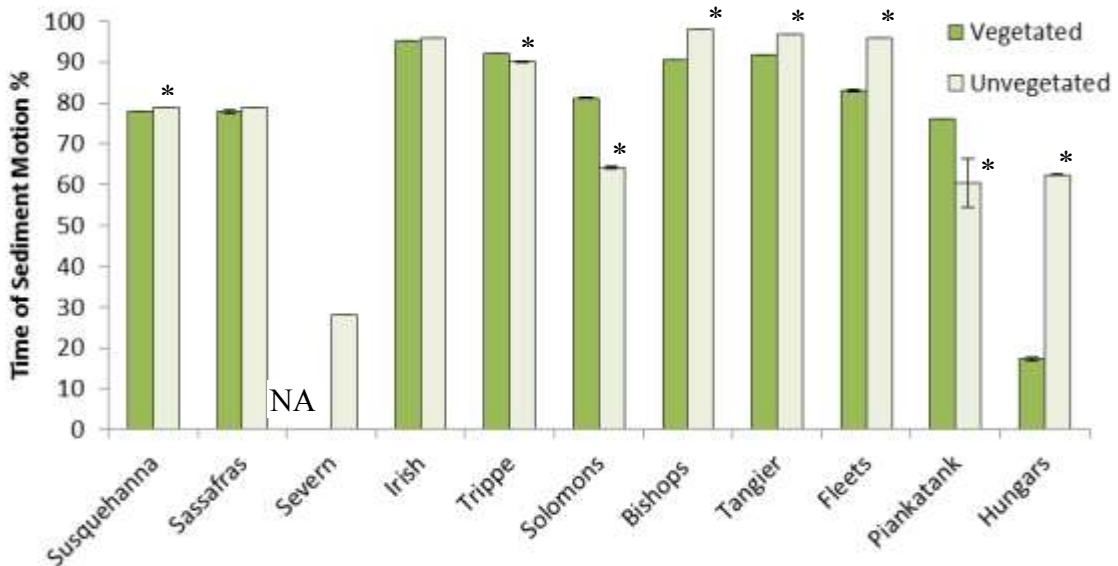


Figure 3.15 The percentage of shear stress events meeting or exceeding the Shields derived critical shear stress for the mean D50 at each vegetated and unvegetated site.

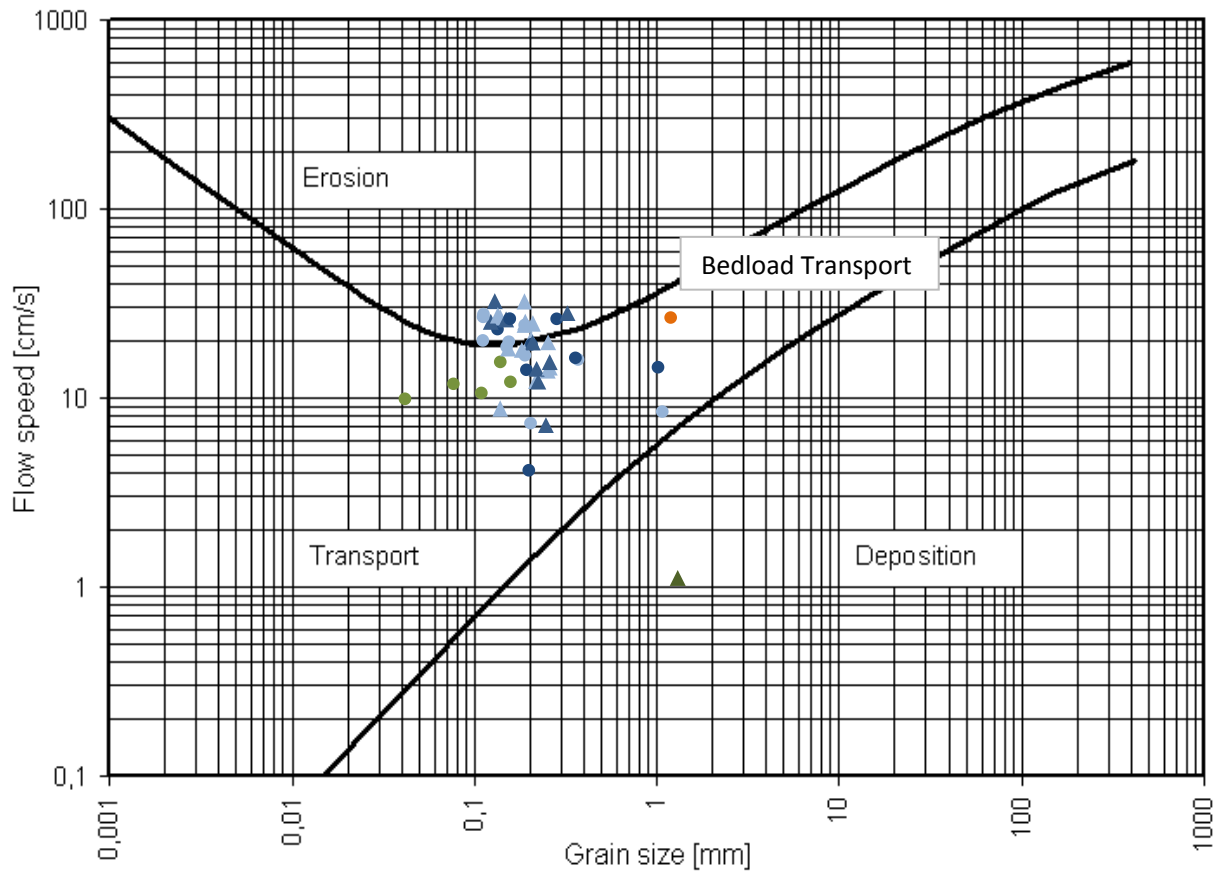


Figure 3.16 The Hjulstrom diagram represents different types of sediment motion by relating water flow speed and grain size. Circles represent vegetated sites while triangles represent unvegetated regions. Dark blue points represent the eleven sites sampled during this study. Light blue points represent wave data collected at the same site locations during different time periods. Green points represent data gather from other sources within the Chesapeake Bay. Orange points represent data from other ecosystems. D50 grain size was used on the x axis and maximum orbital velocity on the y axis.

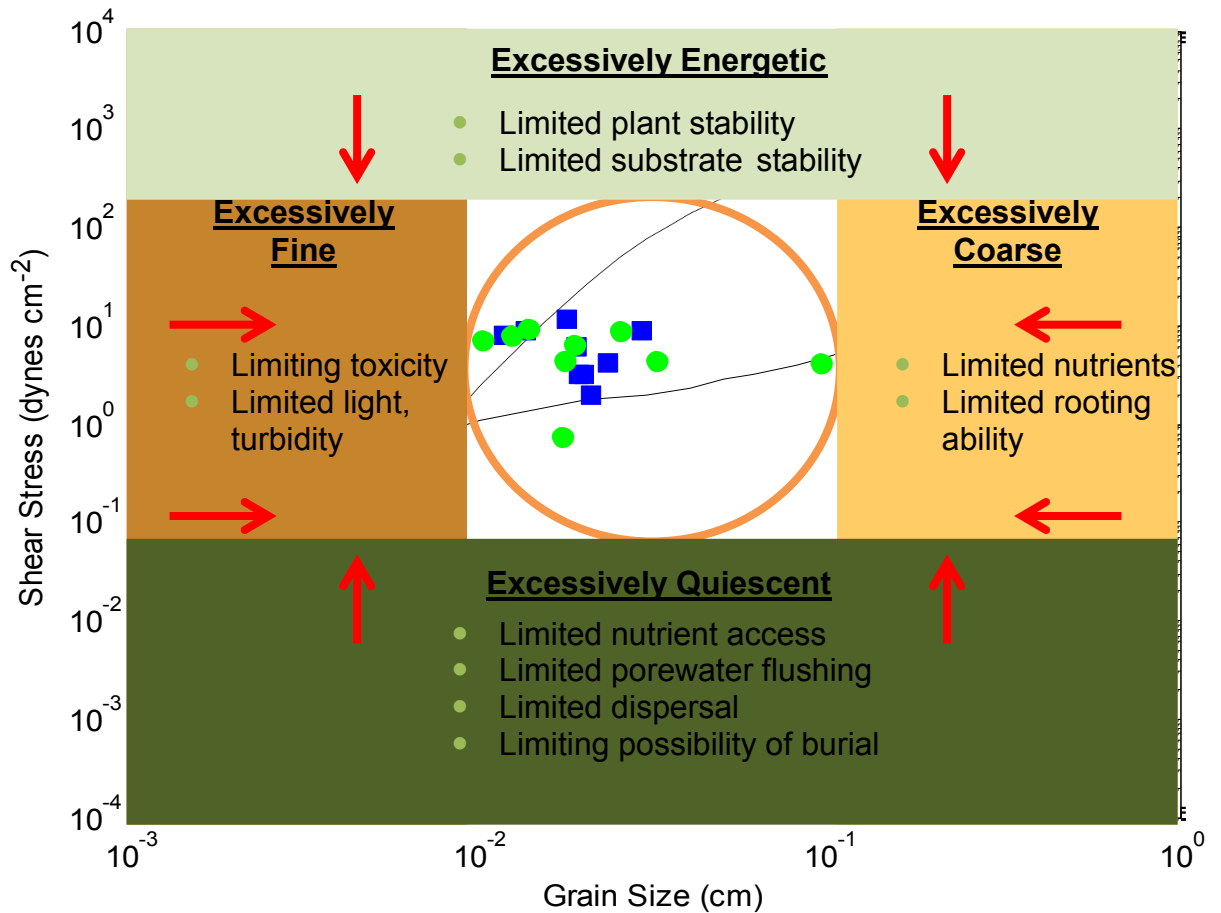


Figure 3.17 Modified Shields diagram representing limitations to SAV success.

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Chapter 4: Water Flow and Sediment Grain Size: Summary and Recommendations for Submersed Aquatic Vegetation Restoration

Summary

Loss of valuable SAV ecosystems in the Chesapeake Bay has contributed to the worsening of the environmental health of the Bay and has spurred an increased interest in restoration efforts (Heck and Orth 1980; Thom et al. 2005; Orth et al. 2006). Current SAV restoration methods have rarely (~10%) resulted in healthy self-sustaining SAV beds, potentially due to limited restoration site selection criteria (Fonseca et al. 1998; Orth et al. 2002; Fonseca 2011). This study assessed the importance of water flow and sediment texture as co-varying SAV habitat requirements to be considered in addition to the commonly considered light availability criteria when selecting restoration sites. An outdoor, circulating mesocosm experiment was conducted in order to assess biomass, density and morphological responses to combinations of two sediment types and three water flows for two common species of SAV in the Chesapeake Bay: *Zostera marina* and *Ruppia maritima* (Chapter 2). These conditions led to depositional conditions, bedload transport and erosion. In the field, wave-generated water flow and surface sediment grain size were quantified, SAV species assemblage was identified, shoot and root length were measured, and total, above- and below-ground biomass were

determined at 11 vegetated and nearby unvegetated sites located along the salinity gradient of the shallow, near-shore Chesapeake Bay (Chapter 3).

The results of this study were used to assess the importance of water flow and sediment texture, in relation to one another, as SAV restoration site selection criteria and to assess the relevance of sediment motion as a representation of this relationship and its importance to SAV restoration. Revised SAV habitat requirement criteria and restoration management recommendations were also suggested based on these results. The initial hypothesis of this study was based on the existing literature and stated that SAV will grow better in habitats characterized by water flow and sediment texture that promote sediment deposition. This hypothesis was rejected based on the inferior biomass, density and morphology developed by SAV grown under depositional conditions compared to those developed under conditions with some form of sediment motion (bedload transport or erosion).

The alternate hypothesis, that SAV is found, and biomass production is highest, in habitats characterized by moderate sediment transport, was supported by field observations as nearly all study sites were characterized by sediment bedload transport according to a modified Shields diagram (Figure 4.1). Both vegetated and unvegetated areas were characterized by bedload sediment transport while, individually, wave-generated water flow and sediment grain size were significantly different between vegetated and unvegetated areas at many study sites. This indicates that threshold levels of wave-generated water flow and sediment grain size that limit SAV colonization can be site specific. It also appears that SAV presence is limited by

not only sediment motion, representing the relationship between water flow and sediment grain size, but also by an additional, undetermined, habitat parameter.

The primary conclusions of both the outdoor mesocosm experiment and the field observations are: SAV is found, and biomass production is highest, in habitats characterized by moderate bedload sediment transport. However, the impact of water flow and sediment grain size on specific SAV responses often differed between the laboratory and the field. In the outdoor mesocosm experiment, *Z. marina* biomass, shoot density, root density and shoot length and *R. maritima* biomass were positively related to wave generated water flow while no significant relationships between a SAV response and water flow was observed *in situ*. Similarly, most SAV responses quantified for each species were lesser in coarser sediment in comparison to those in finer sediment in the outdoor mesocosm experiment, while no relationships were observed between SAV and sediment characteristics in the field. The variance in levels of habitat complexity between the controlled experimental conditions and the very heterogeneous natural environment may explain the differences in relationship between SAV responses and the habitat parameters. Nonetheless, it can be concluded that potential SAV restoration sites are not characterized by sediment deposition as previously thought, but by moderate bedload sediment transport based on this study.

Management Recommendations

General physiological requirements for SAV growth have been well studied. SAV requires sufficient light levels to reach leaf surfaces to allow for photosynthesis to saturate (Carter et al. 2000). Appropriate water flow and sediment characteristics are also necessary for SAV colonization and survival (Fonseca et al. 1983; Barko and

Smart 1986; Koch 2001). Despite this knowledge, most restoration projects consider only the light requirements of SAV when selecting sites to distribute seeds or transplanting shoots (Short et al. 2002; Orth et al. 2007; Fonseca 2011). The majority of SAV restoration efforts, in the Chesapeake Bay as well as ecosystems world-wide, do not result in the establishment of self-sustaining SAV colonies, which is most often explained by a limiting habitat parameter or poor site selection (Golden et al. 2010; Shafer and Bergstrom 2010; Fonseca 2011; Bologna and Sinnema 2012; Cunha et al. 2012). Despite some re-growth of SAV in the Chesapeake Bay since the last large scale decline in the 1970's, current SAV coverage remains less than half of the Chesapeake Bay Program bay-wide abundance goal of 185,000 acres (Chesapeake Bay Program 2013). A greater success rate for SAV restoration will be necessary to reach that goal. Here, the results of this study are used to suggest SAV habitat requirement criteria for co-varying water flow and sediment grain size to be considered in addition to light availability for the improvement of SAV restoration site selection methods.

In the Chesapeake Bay, potential SAV restoration sites should be selected based on: light availability, water flow and sediment grain size criteria. The light criteria has already been implemented ($K_d < 1.5 \text{ m}^{-1}$; Dennison 1987). Water flow and sediment grain size should be such that the combination of these parameters promotes moderate bedload transport according to the Shields diagram. This can be assessed visually by the presence of sand ripples (Miller et al. 1977) or more quantitative methods. In the Bay, SAV sites are characterized by sediment grain sizes between 75 and 300 μm (very fine and fine sand). SAV can also colonize areas with coarser

particles if it consists of fine sand armored by large cobbles. Some species are able to grow around and between the large cobbles rooting into the finer component of the sediment. According to the Shields diagram, the orbital velocities observed in natural SAV beds, between 0.1 and 0.26 m s⁻¹, generate bedload transport of very fine and fine sand. Due to the variety of different and unique SAV species occurring in different salinity zones, further adjustments may be necessary. In the oligohaline regions of the Bay, the upper limit of orbital velocities tolerated by SAV species such as *Vallisneria americana* and *Myriophyllum spicatum* is lower (0.15 m s⁻¹). Further research is necessary to determine wave tolerance during fall and winter months when winds are strongest.

SAV presence was not observed outside of the habitat parameter criteria stated above. The apparent hydrodynamic and geological limitations to SAV survival can be explained ecologically. Water flow lower than the suggested criteria may limit nutrient and oxygen exchange between above-ground plant material and the water column as well as limit reproduction and dispersal (Ackerman 1986; Fonseca and Kenworthy 1987; Koch 2001; de Boer 2007; Weitzman et al. 2013). SAV grown under stagnant water flow conditions produced significantly less biomass and fewer reproductive shoot than those grow under water flow levels within the suggested criteria. Excessively high water flow can limit plant stability through sediment erosion or drag exerted on plant material, particularly when below-ground biomass is low and above-ground biomass is high (Madeson et al. 2001; Wicks et al. 2009; Infantes et al. 2011). Excessively fine sediment has been found to limit SAV survival through the accumulation of toxic compounds in sediment porewater and can bury

seeds and shoots to the point of mortality (Barko and Smart 1983; Pezeshki 2001; Cabaco et al. 2008). Hydrodynamic disturbances can also cause very fine sediment to be suspended, limiting light availability to SAV (Kaldy et al. 2004). Coarser sediment than the suggested criteria may limit SAV survival due to inadequate porewater nutrient content (*sensu* Ye et al. 2009). Sediment transport as bedload, promoted by the habitat requirement criteria recommended in this study, may benefit SAV through porewater fluxes, seed burial dynamics and several more ecological processes which merit further investigation.

Conclusions

The need to improve SAV restoration methods and SAV habitat requirement criteria for parameters in addition to light availability have been increasingly recognized in the Chesapeake Bay and beyond (Koch 2001; Orth et al. 2010; McGraw et al. 2011; Fonseca 2011; Bologna and Sinnema 2012). The results of this study highlight the importance of not only considering water flow and sediment grain size habitat parameters to improve SAV restoration success, but the importance of considering synergism between related parameters. This study has further shown that established SAV beds are present in areas that are not quiescent and depositional as previously thought (Gacia and Duarte 2001; Koch 2001; Widdows et al. 2008), but are characterized by moderate bedload transport. Sediment motion processes appear to be closely related to key aspects of the SAV life cycle and should be further explored and applied to the improvement of SAV restoration management. By considering complex habitat requirements in addition to light availability such as the

co-varying water flow and sediment grain size, the probability SAV restoration success will increase and historic SAV population levels may one day be achieved.

Figures

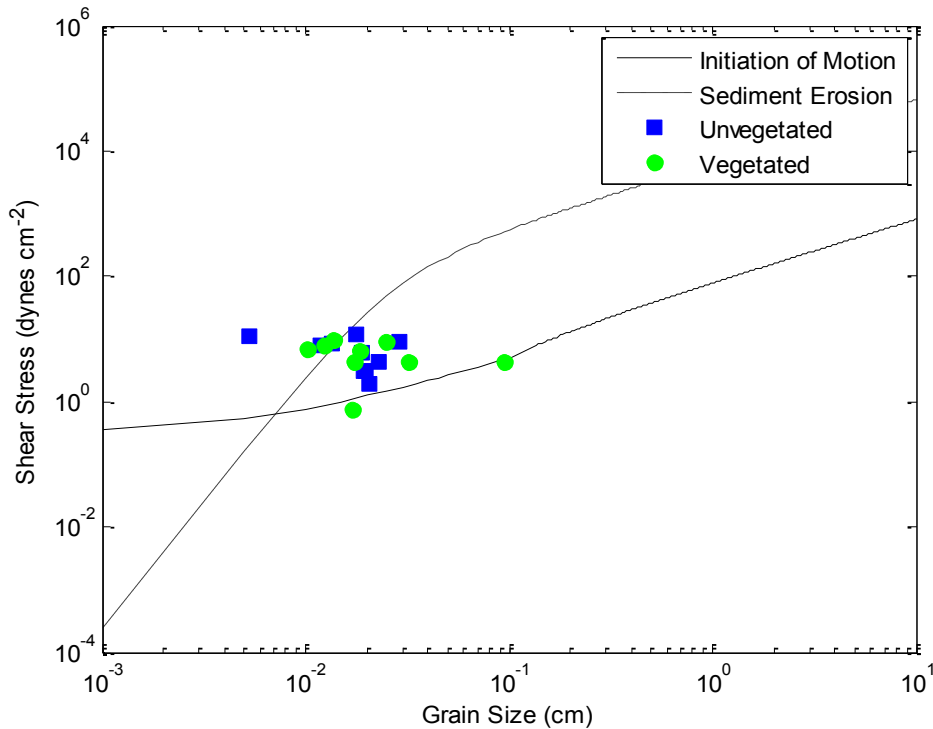


Figure 4.1 Modified Shields diagram relating the mean D50 grain size (cm) at each vegetated and unvegetated field study site and the calculated shear stress in comparison the empirically derived Shields critical threshold of sediment motion.

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Appendix

SAV Biomass

The distribution of SAV biomass was spatially and temporally variable (Figure 1A). The greatest biomass in the upper Bay grew at Susquehanna Flats in 2010 and consisted primarily of *Myriophyllum spicatum* (AG=16.2, BG=22.3 g m⁻²). The mid Bay region was dominated by the fast growing, tolerant and opportunistic *R. maritima*, which extended into the lower-Bay growing together with the dominant *Z. marina*. The most significant difference in biomass between sampling seasons occurred at Tangier Island and Hungars Creek where populations of *Z. marina* more than tripled and represented the highest overall biomass. Several sites, including Irish Creek, Fleets Bay and Piankatank River appeared to have been sampled after above ground SAV material had already senesced in 2010. No SAV was found at Trippe Bay and only small juvenile plants were collected at Solomons Island in 2011.

The ratio of above- to below-ground biomass was less than or equal to 3 for most sites, indicating that more above- than below-ground biomass was often produced (Fi). The presence of *M. spicatum* and reproductive shoots of *R. maritima* decreased this ratio at Susquehanna Flats and Hungars Creek respectively. *Z. marina* was the only species to develop greater below ground biomass than above at several sites.

SAV Shoot and Root Density

Unlike below ground biomass, root density far exceeded shoot density for most species at most sites sampled. Roots are often much smaller than shoots and some species naturally develop a cluster of roots for every shoot, although the fairly ubiquitous *R. maritima* usually grows only one root per shoot. Both shoot and root densities varied significantly (p-value=0.039 and 0.042) between sites and sampling seasons. In the lower bay, Tangier Island and Hungars Creek both developed extremely high shoot densities and particularly high root density in 2011, similar the trend in biomass.

SAV Morphology

Shoot and root length of strap bladed species exhibited little variations within species between sampling seasons or sites. Only *R. maritima* and *Z. marina* occurred at multiple study sites allowing statistical assessment of morphological measurements.

SAV distribution was very variable in 2010 and 2011. The biomass, density and often the species assemblage varied significantly between salinity regions in the Bay and between the two sampling years. In particular, *Z. marina* populations showed a large amount of variability. SAV distributions have often been observed to be very fluid. A large scale survey between 1985 and 1993 found significant differences in SAV biomass and coverage in year to year comparisons, *Z. marina* populations accounting for 85% of the changes (Moore et al. 2000). SAV populations also fluctuate throughout the growing season, biomass peaking in July and reaching a minimum in December. The SAV observations collected during this study capture

seasonal differences, 2010 data representing later summer to fall and 2011 data representing late spring to early summer. Surveys have found that higher salinity communities, such as *Z. marina* beds, dominate in winter, spring and summer while lower salinity communities, such as *R. maritima* and fresh water species, have the greatest biomass in the fall, a trend reflected in this study (Moore et al. 2000).

Orbital Velocity and SAV Biomass, Density and Morphology

Within SAV beds, wave activity appeared to impact the growth and morphology all species present and specifically *Z. marina* and *R. maritima*. Biomass, shoot and root density, shoot length and the ratio of above- to below-ground biomass all tended to decrease with increasing orbital velocity. Less SAV was able to grow under higher orbital velocities, and that which did grow in more hydrodynamically active areas adapted morphologically in ways that have been found to significantly reduce the effect of drag forces (Biehle et al. 1981; Puijalon et al. 2008; Puijalon et al. 2005). *Zostera noltii*, *Potamogeton pectinatus* and several species of macroalgae have been observed to reduce in above ground biomass, leaf length and density with increasing water flow (Chambers et al. 1991; Schaz and Asmus 2003; Steward 2006). Although root density also decreased, root length tended to increase with orbital velocity in *Z. marina* and *R. maritima*, likely anchoring the plants in response to increasing drag forces. The same behavior has been observed in *P. oceanica* and *C. nodosa* as well as kelp, in the former case through developing larger holdfasts (Roberson and Coyer 2004; Infantes et al. 2011). *R. maritima* was less impacted by orbital velocity than *Z. marina*, just as in earlier mesocosm experiments conducted with these species (Chapter 2).

Sediment Characteristics and SAV Biomass, Density and Morphology

Within the range of sediments found in vegetated areas, grain size, percentage of silt and clay, and sediment sorting appeared to impact SAV growth and morphology. Coarse sediments negatively impacted SAV growth, associated with lower biomass, shoot and root density and shoot length. Root length tended to increase with increasing sediment grain size, most likely as a response to lower availability of porewater nutrients. *Z. marina* grew longer roots in sandy sediment than in muddy sediment in controlled experiments (Jordan 2008). A similar trend was demonstrated when both *Hydrilla verticillata* and *Vallisneria americana* exhibited poorer growth in terms of biomass and density in coarser sediment with low organic content and nutrient availability (Ye et al. 2009). *Z. marina* was also more negatively impacted by grain size than *R. maritima*, decreasing in biomass, density and shoot length. The biomass, density and shoot length of *R. maritima* appeared unrelated to grain size while root length did increase. A greater allocation of growth resources to below-ground biomass in coarse sediment has been observed in a variety of species, including *C. nodosa*, as a function of nutrient availability (Cunha and Duarte 2007).

Interestingly, as *R. maritima* was less affected by grain size than *Z. marina*, *Z. marina* was less affected by the percentage of silt and clay than *R. maritima*. The density, biomass and ratio of above- to below-ground biomass of *R. maritima* tended to increase with the percentage of silt and clay while root length decreased. A study of the relationship of seedling success to sediments also found *R. maritima* positively related to silt clay percentage (Ailstock et al. 2010). The different sediment

characteristics that *Z. marina* and *R. maritima* tend to respond to can most likely be explained through nutrient acquisition methods.

SAV, especially *Z. marina*, tended to decrease in biomass and density while increasing in root length with increasing orbital velocity, limiting to SAV above 26 cm s⁻¹. Increasing sediment grain size was also associated with decreasing SAV biomass and density but increasing root length, especially in *Z. marina*. These qualitative trends support the hypothesis that SAV grown in fine sediment is morphologically suited to withstand low water flow and SAV grown in coarse sand is morphologically suited to withstand higher water flow. Unexpectedly, *R. maritima* appeared to respond more markedly to the percentage of silt and clay in sediments while *Z. marina* appeared to respond more directly to sediment grain size.

WEMo

A publicly available Wave Exposure Model (WEMo) was used to calculate long term predictions of wave climate statistics. The model was run using an ArcGIS Chesapeake Bay shoreline shapefile from NOAA, a 30-m by 30-m grid bathymetry file from the Chesapeake Bay Modeling Community (Lin et al. 1997), and wind data from the National Data Buoy Center at the Thomas Point, MD (Station TPLM2), Solomons Island, MD (Station SLIM2) and Norfolk, VA (Station 44059) buoy stations. Field validation of the model output was attempted as in Malhotra and Fonseca (2007). Model results were generated for each vegetated and unvegetated site based on three years of wind data at 5% wind exceedance, as recommended, and based on wind data from the specific dates of field deployment at 100% wind exceedance. For a more direct data comparison, time series of wave height was

generated for select representative sites located in open, bathymetrically simple areas. The model was run based on a 6 hour moving average of wind data at 5 and 100% wind exceedance for the specific period of field instrument deployment. For northern bay sites, wind data from Thomas Point was used, for mid bay sites Solomons Island wind data and for southern bay sites Norfolk Air Base wind data was used. The modeled and observed field results were graphically and statistically compared and found to be significantly different.

Validation of WEMo generated wave predictions to field collected wave data was not successful in this study. No relationship was found between field data and model output whether long term wind data or wind data limited to the time of deployment was input (Figure). Model-generated time series of wave height at simple, regionally representative sites were significantly different from field observed time series (Table A.1). See Appendix for detailed validation process, results, and possible explanation.

Tables

Table A.1 WEMo validation non parametric paired Wilcoxon test results.

Site	Type	Exceedance	P-value	Paired P-value
Sassafras	Veg	10%	$2.88e^{-7*}$	$8.99e^{-15*}$
Sassafras	Veg	100%	0.278	$1.37e^{-3*}$
Susquehanna	Veg	10%	$1.71e^{-4*}$	0.775
Susquehanna	Veg	100%	$1.95e^{-14*}$	$2.27e^{-8*}$
Sass, Sus	Unveg	10%	$5.46e^{-9*}$	0.116
Sass, Sus	Unveg	100%	$2.20e^{-16*}$	$2.66e^{-9*}$
Irish Creek	Veg	5%	$1.58e^{-7*}$	$1.66e^{-6*}$
Irish Creek	Veg	100%	$2.20e^{-16*}$	$2.20e^{-16*}$
Irish Creek	Unveg	5%	$9.66e^{-6*}$	0.344
Irish Creek	Unveg	100%	$2.20e^{-16*}$	$2.20e^{-16*}$
Piankatank	Veg	10%	$2.20e^{-16*}$	$2.20e^{-16*}$

Piankatank	Veg	100%	$2.20e^{-16*}$	$2.20e^{-16*}$
Piankatank	Unveg	10%	$2.20e^{-16*}$	$2.20e^{-16*}$
Piankatank	Unveg	100%	$2.20e^{-16*}$	$2.20e^{-16*}$

Figures

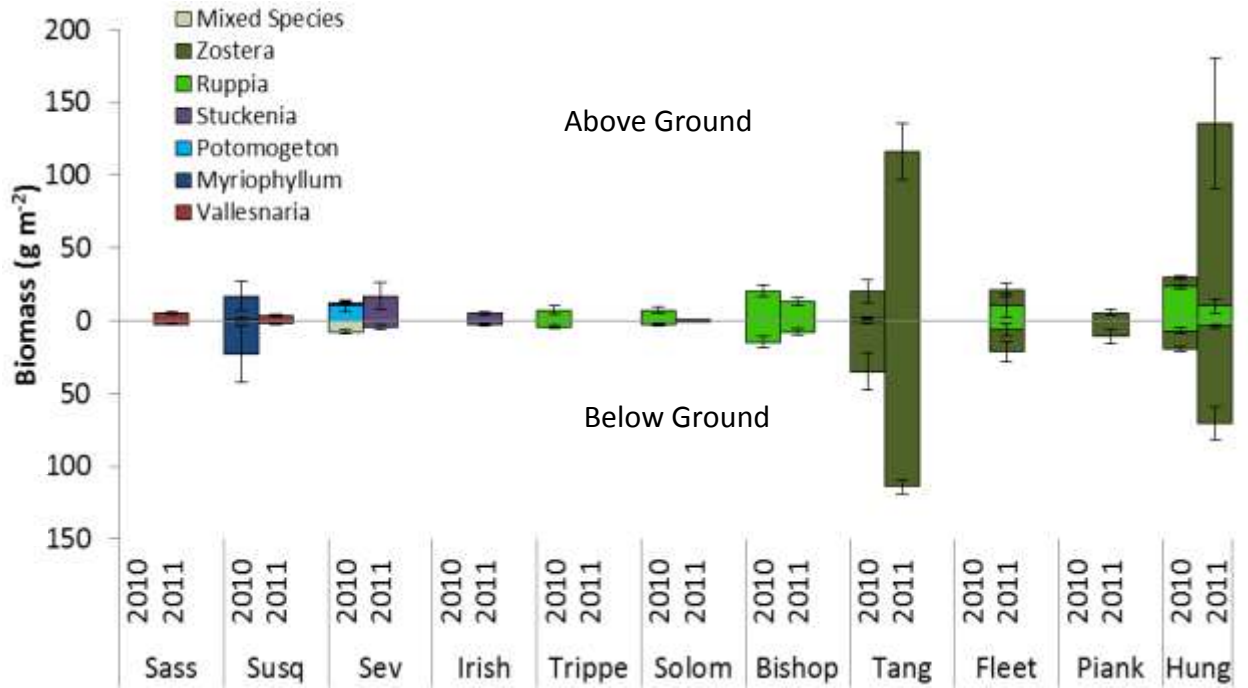


Figure A.1 Inter-annual variability (2010-2011) in mean above and below ground biomass ($\text{g m}^{-2} \pm \text{SD}$) of SAV.

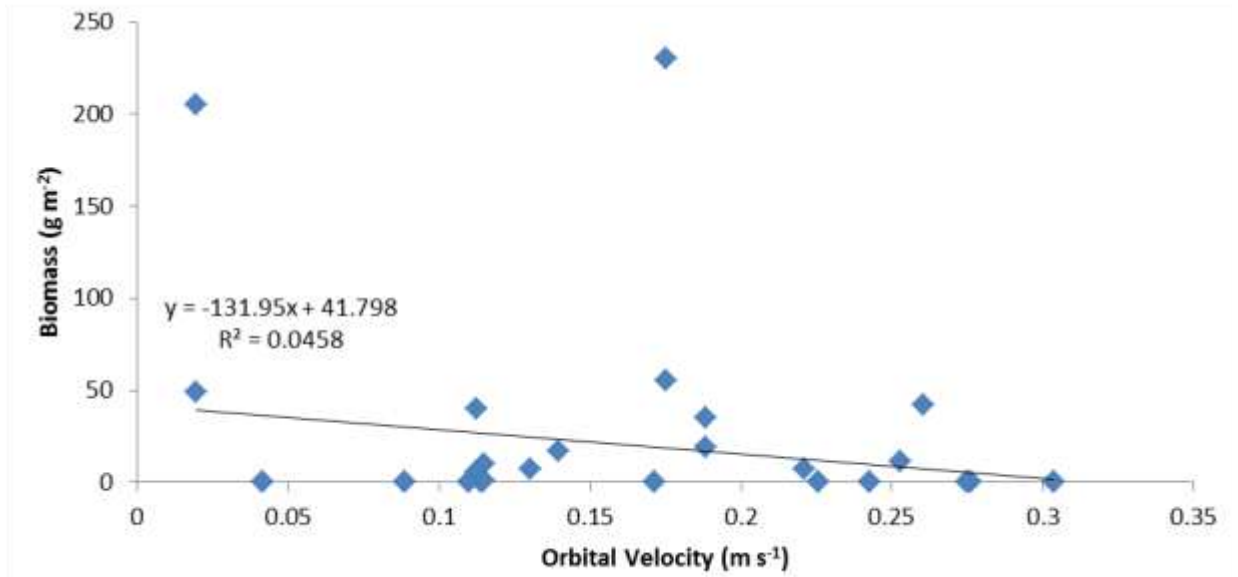


Figure A.2 The maximum near bottom orbital velocity (m s⁻¹) and total SAV biomass at study sites.

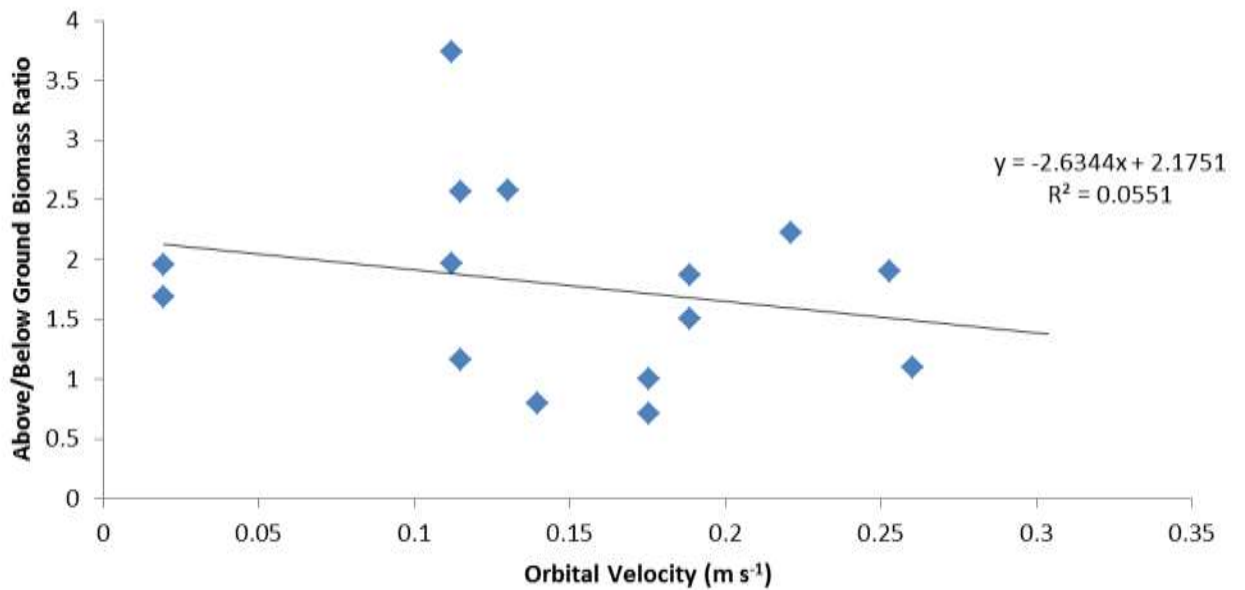


Figure A.3 The maximum near bottom orbital velocity (m s⁻¹) correlated to the ratio of total SAV above to below ground biomass sampled in 2010 and 2011.

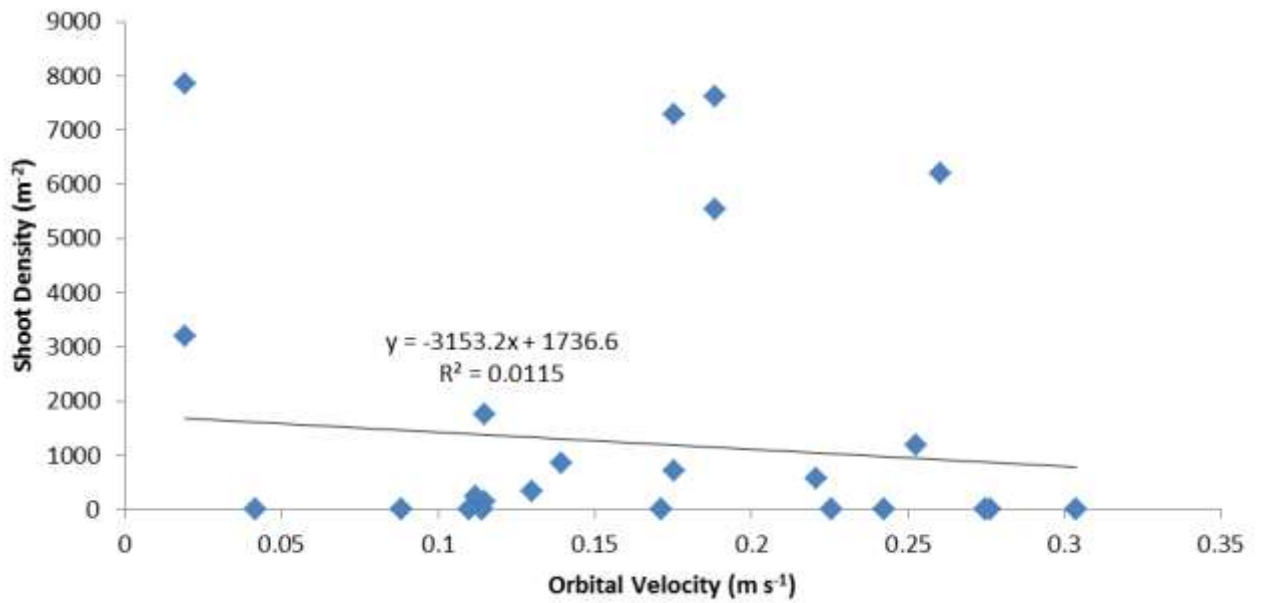


Figure A. 4 Maximum near bottom orbital velocity (m s⁻¹) correlated to strap bladed SAV shoot density (m⁻²) sampled in 2010 and 2011.

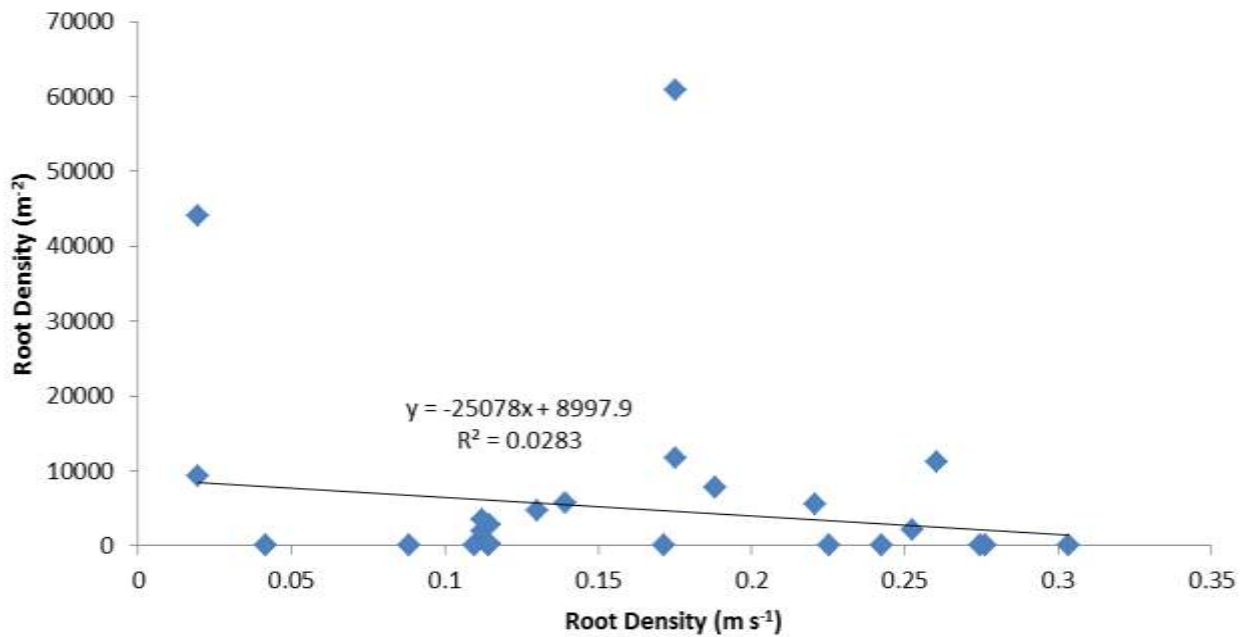


Figure A.5 Maximum near bottom orbital velocity (m s^{-1}) correlated to SAV root density (m^{-2}) sampled in 2010 and 2011.

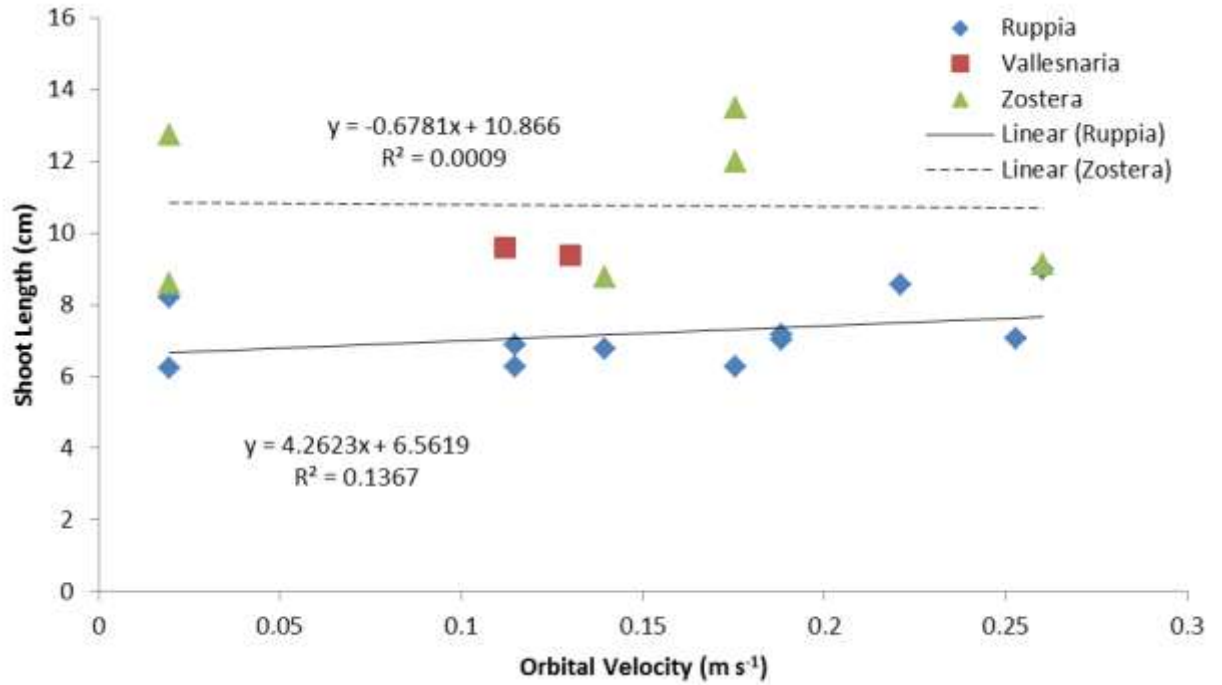


Figure A.6 The maximum near bottom orbital velocity (m s^{-1}) correlated to the shoot length (cm) of strap bladed species of SAV sampled in 2010 and 2011.

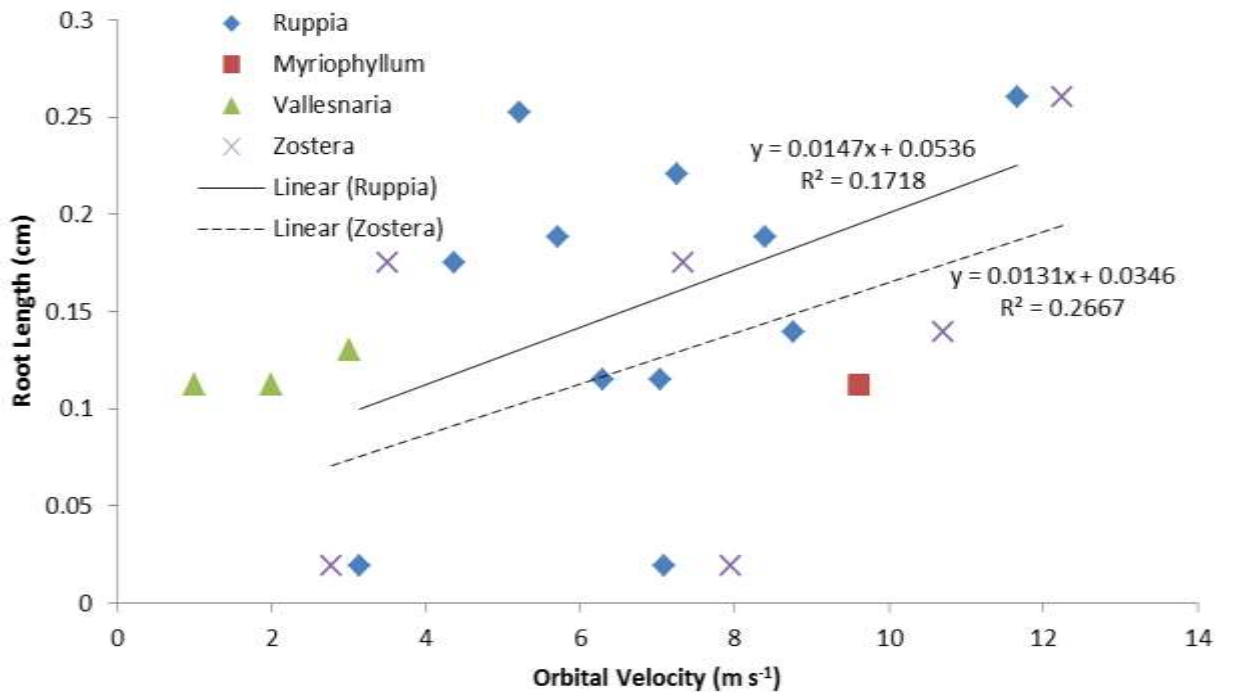


Figure A.7 The maximum near bottom orbital velocity (m s^{-1}) correlated to the root length (cm) of strap bladed species of SAV sampled in 2010 and 2011.

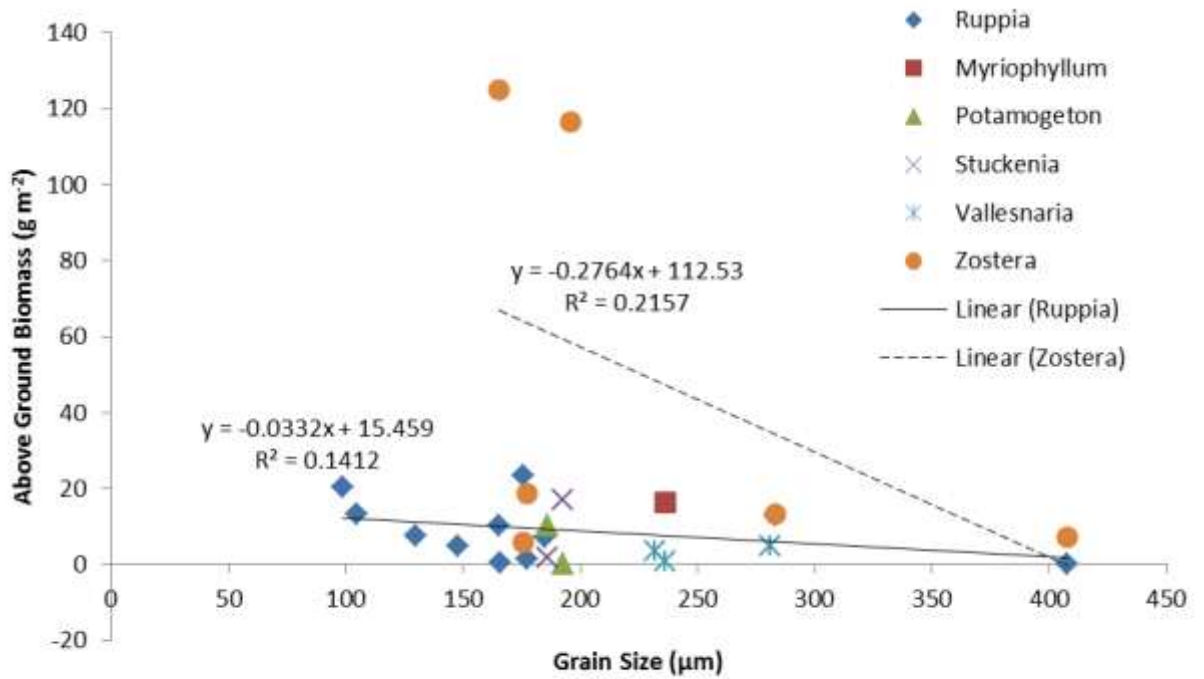


Figure A. 9 The D50 sediment grain size (μm) related to the above ground biomass (g m^{-2}) of individual species sampled in 2010 and 2011.

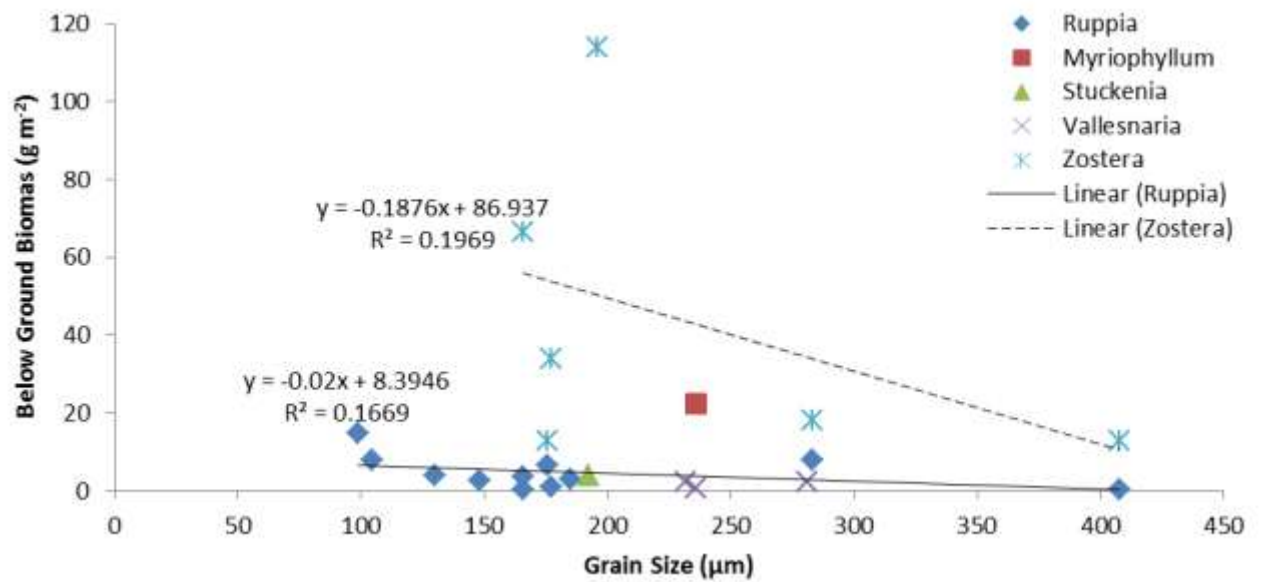


Figure A.10 The D50 sediment grain size (μm) related to the below ground biomass (g m^{-2}) of individual species sampled in 2010 and 2011.

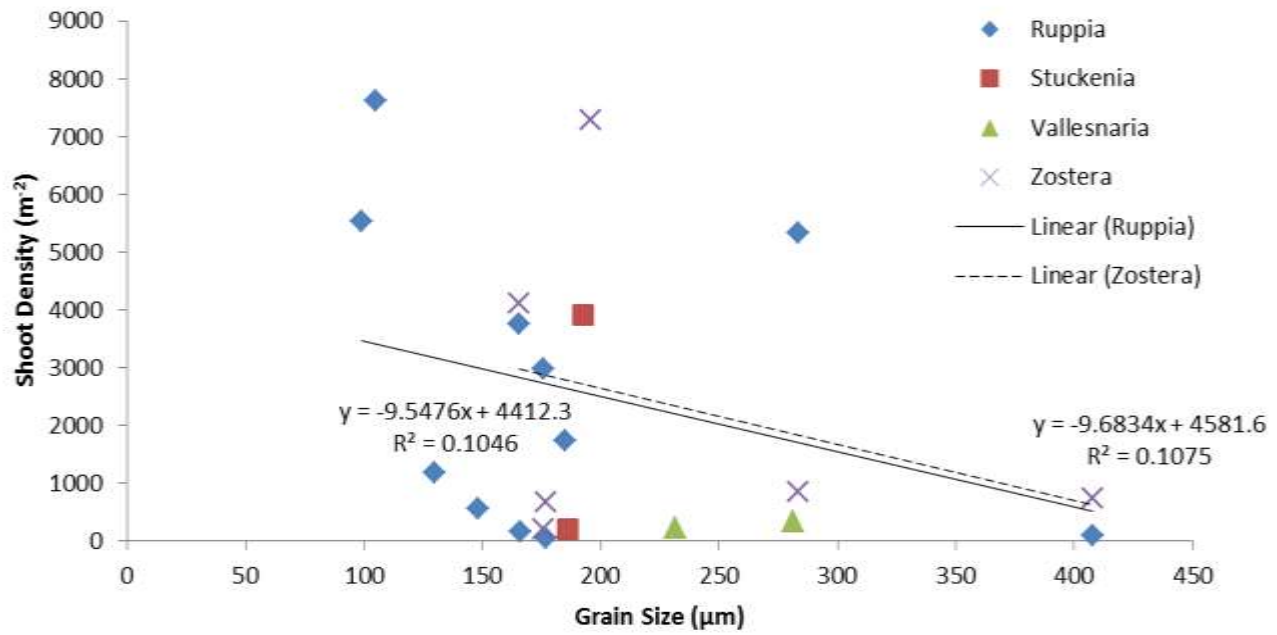


Figure A.11 The D50 sediment grain size (μm) related to the shoot density (m^{-2}) of strap bladed species sampled in 2010 and 2011.

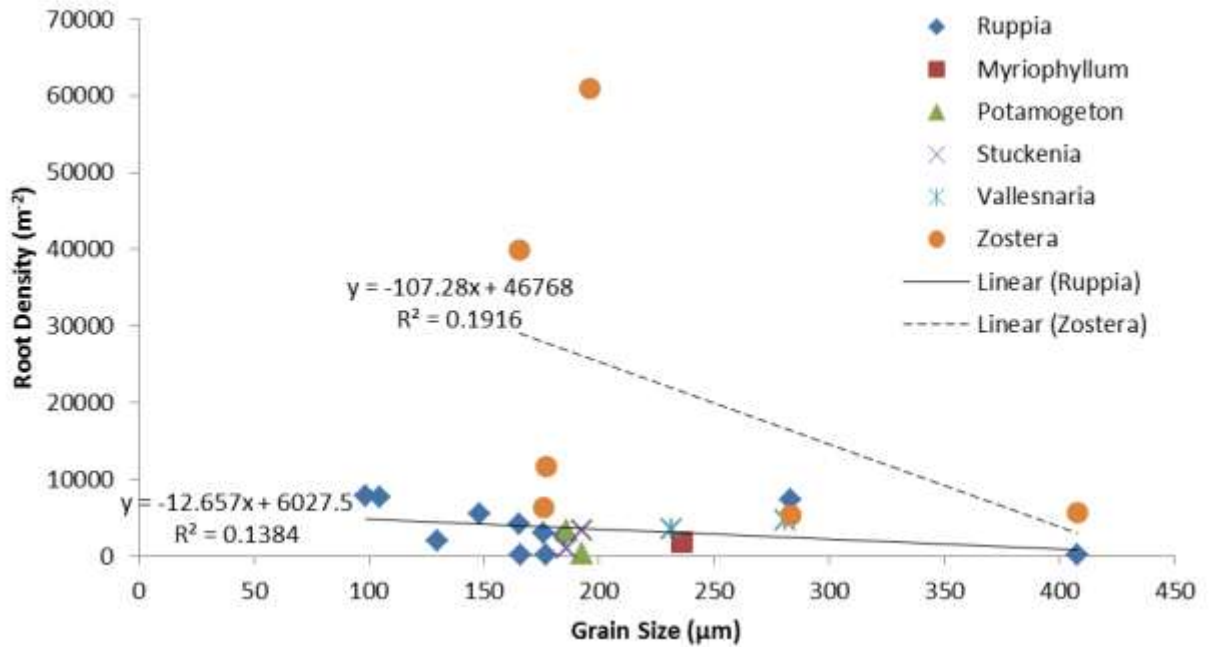


Figure A.12 The D50 sediment grain size (μm) related to the root density (m^{-2}) of individual species sampled in 2010 and 2011.

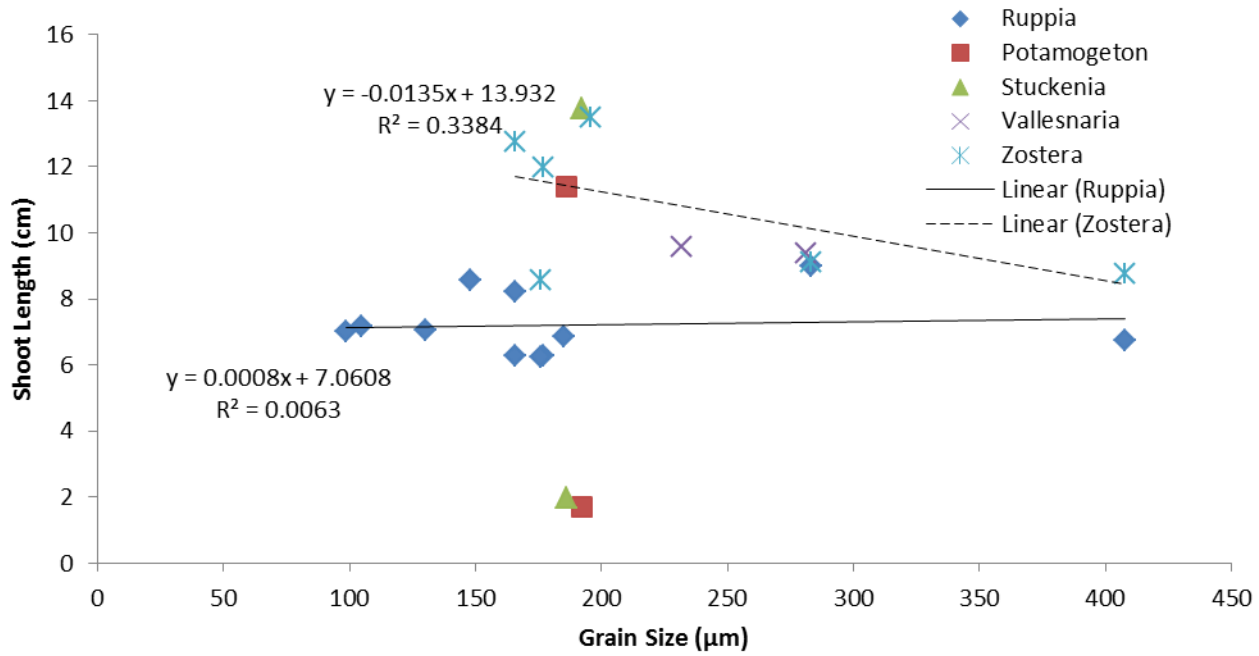


Figure A.13 The D50 sediment grain size (μm) related to the shoot length (cm) of strap bladed species sampled in 2010 and 2011.

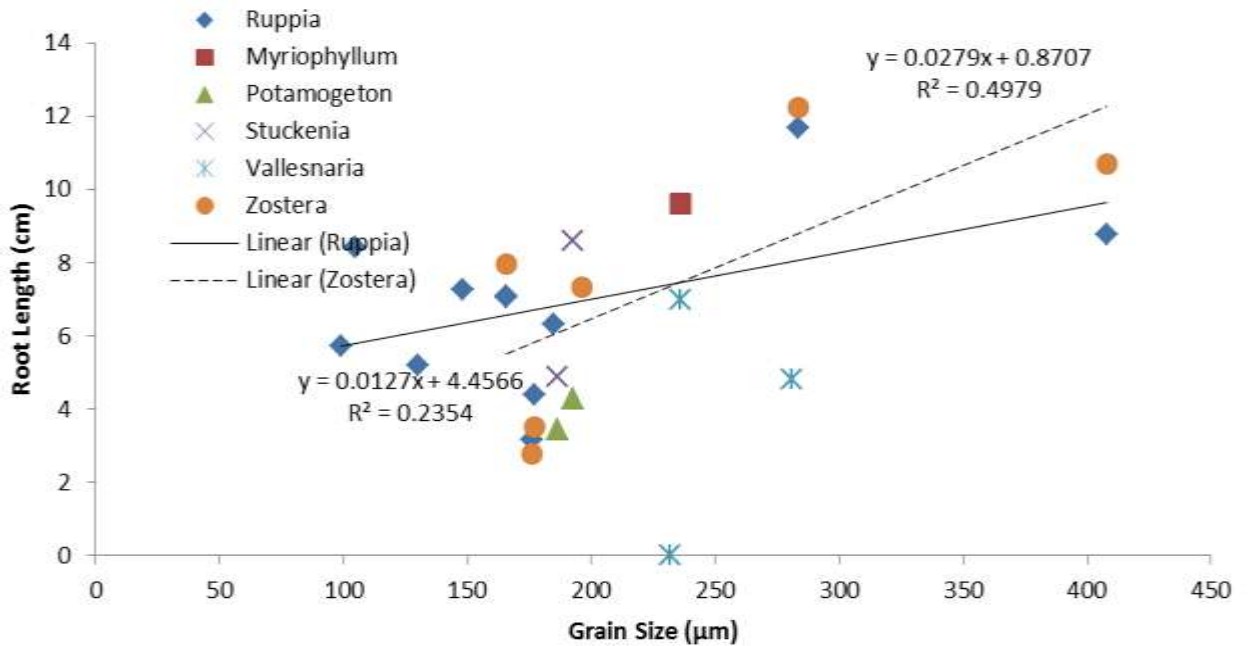


Figure A.14 The D50 sediment grain size (μm) related to the shoot length (cm) of strap bladed species sampled in 2010 and 2011.

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