Stability and bistability of seagrass ecosystems in shallow coastal lagoons: Role of feedbacks with sediment resuspension and light attenuation

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[¹] Shallow coastal lagoons are environments where a dynamic equilibrium exists between water quality and seagrass cover. Dense seagrass canopies limit the resuspension of bed sediments thereby creating a clearer water column and a positive feedback for seagrass growth. Positive feedbacks are often associated with the existence of bistable dynamics in ecosystems. For example, a bare and a seagrass-covered sediment bed could both be stable states of the system. This study describes a one-dimensional hydrodynamic model of vegetation-sediment-water flow interactions and uses it to investigate the strengths of positive feedbacks between seagrass cover, stabilization of bed sediments, turbidity of the water column, and the existence of a favorable light environment for seagrasses. The model is applied to Hog Island Bay, a shallow coastal lagoon on the eastern shore of Virginia. The effects of temperature, eutrophication, and bed grain size on bistability of seagrass ecosystems in the lagoon are explored. The results indicate that under typical conditions, seagrass is stable in water depths < 2.2 m (51% of the bay bottom deep enough for seagrass growth) and bistable conditions exist for depths of 2.2–3.6 m (23% of bay) where the preferred state depends on initial seagrass cover. The remaining 26% of the bay is too deep to sustain seagrass. Decreases in sediment size and increases in water temperature and degree of eutrophication shift the bistable range to shallower depths, with more of the bay bottom unable to sustain seagrass.


1. Introduction

[2] Shallow coastal lagoons, which represent an important transition between terrestrial and aquatic ecosystems, are particularly vulnerable to the rapid changes in population and land use occurring in coastal areas [Havens et al., 2001; Nixon et al., 2001; Valiela et al., 1997]. The subtidal seagrass meadows and estuarine salt marshes that dominate land-margin systems are among the most productive ecosystems known, and provide critical ecosystem services that include providing of habitat to a diverse and economically important faunal community, sequestering carbon and nutrients, and stabilizing shorelines. Eutrophication caused by the rapid changes in population and land use occurring in coastal areas [Havens et al., 2001; McGlathery et al., 2007; Nixon et al., 2001; Valiela et al., 1997], increases in water temperature [Keller, 2009; Najjar et al., 2000], water depth [Cazenave et al., 2008; Najjar et al., 2000] and storminess due to climate change [Hayden, 1999] can detrimentally impact subtidal seagrass meadows [Moore and Jarvis, 2008].

[3] Primary production in coastal lagoons is typically dominated by benthic plants (seagrasses and algae), except where external nutrient loading and phytoplankton populations can be high [McGlathery et al., 2007; Sandjensen and Borum, 1991]. The shallow depths of coastal lagoons make the lagoon-bottom sediment susceptible to current and wave suspension. The resulting high light attenuation in the water column can limit benthic primary productivity, particularly for species with high light requirements, such as seagrasses, which typically require about 20% of incident light at the sediment surface [Dennison et al., 1993; Duarte, 1991; Zimmerman et al., 1995].

[4] In general, turbidity in coastal lagoons is controlled by internal sediment resuspension [Lawson et al., 2007] because many coastal lagoons lack riverine discharge, a major control on turbidity in deeper estuaries. The magnitude and importance of resuspension may increase when rooted vegetation is absent because of the lack of the sediment stabilizing effects of the plants [Gacia and Duarte, 2001; Gacia et al., 2003; Heiss et al., 2000]. As such the dynamics of seagrass ecosystems may exhibit important positive feedbacks between vegetation and sediment suspension/deposition, and between nutrient loading and seagrass growth.

[5] Seagrass slows flow and shelters underlying sediment, consequently reducing its susceptibility to resuspension, and...
enhancing deposition of fine sediment, which are both factors that increase the transparency of the water column [Folkard, 2005]. Additionally, seagrass immobilizes nutrients produced in the sediment through remineralization, thereby reducing availability of nutrients in the water column that could promote algal growth and reduce light penetration to the seafloor [McGlathery et al., 2007]. Thus, seagrass positively influences light penetration, which, in turn, supports further seagrass growth. An increase in water column turbidity reduces light levels at the lagoon bottom with potentially detrimental effects on seagrass populations and consequent enhancement of sediment resuspension. It has been argued [van der Heide et al., 2007] that these positive feedbacks can rapidly shift a system from a state with clear water and a seagrass-covered bottom to an alternate state with turbid water and no seagrass cover. This state change can also be triggered by a loss in seagrass resilience associated with the reduction of light penetration resulting from increases in nutrient loads, with consequent algal growth and decreases in dissolved oxygen [McGlathery et al., 2007].

[6] Positive feedbacks between the state of the system (e.g., seagrass cover) and limiting resources (e.g., light) can induce the emergence of alternate stable states in ecosystem dynamics [Wilson and Agnew, 1992]. In the case of sea grass ecosystems the alternate states would exhibit either bare sediment beds with high suspended loads and poor light environments for seagrass growth, or a seagrass meadow with relatively clear water and enough light penetration through the water column to sustain seagrass growth.

[7] The emergence of bistability in ecosystems has important ecological implications. Bistable systems exhibit strong nonlinearities in their response to changes in environmental drivers and may undergo abrupt shifts from one state to the other as a result of only small environmental changes. Moreover, bistable ecosystems have only a limited resilience [Gunderson, 2000] in that they are able to recover from disturbances and return back to their pre-disturbance state only when the disturbance intensity (e.g., fraction of seagrass bed disturbed) is smaller than a critical value, while more severe disturbances would take the system into the attraction domain of the alternate stable state. Past the critical point, once the disturbances would take the system into the attraction domain of the alternate stable state. Past the critical point, once the external forcing causing the disturbance is eliminated the system will not be able to recover its pre-disturbance configuration [Scheffer et al., 2001; Scheffer and van Nes, 2004].

[8] In the case of shallow coastal lagoons, non-linear behavior could emerge from positive feedbacks between vegetation, sedimentation and environmental drivers [van der Heide et al., 2007]. However, feedbacks between water quality and seagrass ecosystems are understudied and the impact of these feedbacks on the stability and resilience of estuarine environments has seldom been assessed [van der Heide et al., 2007]. As a result, we currently do not have a comprehensive understanding of the susceptibility of these systems to changes in climate drivers and disturbances, including sea level rise, temperature increase, nutrient inputs, and seabed disturbance from storms and human activities. This limits the development and implementation of successful management and restoration strategies because the sensitivity of these systems to natural and anthropogenic drivers cannot be adequately predicted.

[9] This study investigates the strengths of positive feedbacks among seagrass cover, stabilization of bed sediments, turbidity of the water column, and the existence of a favorable light environment for continued growth of seagrasses. By assessing the strength of positive and negative feedbacks, we investigate whether shallow estuarine ecosystems are prone to catastrophic shifts to alternate “stable” states in response to gradual changes in environmental conditions and disturbance regime.

2. Hydrodynamic Model

[10] We develop a hydrodynamic model of vegetation-sediment-water flow interactions, and use this model to investigate the impact of changes in seagrass density on sediment resuspension, water column turbidity, and light environment under different conditions of sea level, bed sediment characteristics and eutrophication. The hydrodynamic model simulates the one-dimensional dynamics (in the vertical direction) of sediment entrainment/settling within the water column. It accounts for the effect of seagrass vegetation on these dynamics, including its effect on the velocity profile, eddy diffusivity, shear flow dispersion, and wave and current shear stress. At the same time it accounts for the effect of flow on the height of the deflected seagrass canopy. Values of suspended sediment concentrations calculated by the model (sections 2.1–2.4) are used to determine the degree of light attenuation within the water column (i.e., from the water surface to the top of the canopy, see section 2.5) and to calculate light availability and the suitability of environmental conditions to maintain seagrass meadows (see section 2.6). In the following subsections we describe the main components of the hydrodynamical model and its use in the calculation of light attenuation.

2.1. Suspended Sediment

[11] We use a one dimensional representation of the conservation of mass for suspended sediments in the form of the advection-diffusion equation where individual grain settling velocities, \(w_{s,j}\), and concentrations, \(C_{s,j}\), are calculated for each size class \(j\) [Dietrich, 1982]

\[
\frac{\partial C_{s,j}}{\partial t} = w_{s,j} \frac{\partial C_{s,j}}{\partial z} + \frac{\partial}{\partial z} \left( K_v \frac{\partial C_{s,j}}{\partial z} \right)
\]

(1)

where \(K_v\) is an average vertical diffusivity (see sections 2.3 and 2.4) and \(z\) is the height above the bed surface. The coupling of the suspended sediment concentrations to the bed sediment concentrations is expressed as a continuity of sediment flux boundary condition, where the entrainment flux, \(E_j\) (kg m\(^{-2}\) s\(^{-1}\)) is

\[
E_j = \rho_{s,j} c_{b,j} \beta (\tau_b - \tau_{cr})
\]

(2)

where \(\rho_{s,j}\) is the density and \(c_{b,j}\) is the bed fraction of sediment size class, \(j\), while \(\beta\) is a resuspension constant (m\(^2\) s\(^{-1}\) Pa\(^{-1}\)) [Sanford and Maa, 2001]. \(\tau_b\) (Pa m\(^{-2}\)) is the shear stress applied to the bed, and \(\tau_{cr}\) (Pa m\(^{-2}\)) is the critical shear stress for sediment detachment. The total amount of sediment in suspension may not exceed the total amount of sediment in an active layer at the bed surface [Harris and Wiberg, 1997].
in which case the available bed concentration for size class \( j \) is limited to
\[
C_{\text{bedavailable}, j} = \left( C_{b,j}d_{\text{active}} - \int_{a_j}^{Z} C_{b,j}d_z \right)
\]
where \( Z \) is water depth and \( z_a \) is bed roughness height.

2.2. Shear Stress Exerted on Bed Sediment

[12] The bed shear stress, \( \tau_b \), used in equation (2) is determined as the vectorial sum of the shear stresses exerted by currents (\( \tau_{\text{current}} \)) and waves (\( \tau_{\text{wave}} \)). The former is calculated as a function of the average current velocity, \( U_{av} \),
\[
\tau_{\text{current}} = \rho C_d U_{av}^2
\]
where \( \rho \) is the fluid density; the drag coefficient \( C_d \) is calculated following Lawson et al. [2007].

[13] Wave shear stress is determined from significant wave height, \( H_{\text{sig}} \), wavelength, \( L \), and period, \( T \), generated from the fetch–limited shallow water wave model of Young and Verhagen [1996] as
\[
\tau_{\text{wave}} = \rho \left( \frac{g}{2} \right) U_b^2
\]
where the wave orbital velocity, \( U_b \), at the bed is given by
\[
U_b = \frac{\pi H_{\text{sig}}}{4 \sinh(2\pi Z/L)}
\]
while the friction factor, \( f \), is calculated following Lawson et al. [2007]. Wave attenuation due to a seagrass canopy is incorporated by reducing the wave orbital velocity as a function of the number of shoots, \( N \), using a Monad equation with a half saturation constant \( N_{hs} \) of 1500 shoots m\(^{-2} \) [van der Heide et al., 2007].

[14] To combine the effect of waves and currents on total bed shear stress, the total shear stress applied to the bed by waves and currents is calculated as
\[
\tau_b = \sqrt{\tau_{\text{wave}}^2 + \tau_{\text{current}}^2}
\]
Values of \( \tau_b \) calculated with equation (7) are used in equation (2) to calculate the entrainment rate.

2.3. Current Flow and Deflection of the Seagrass Canopy

[15] To account for flow–induced deflection of the seagrass canopy, the deflected canopy height, sheer velocity and stress acting on a seagrass blade are calculated as in the work by Abdelrahman [2007], i.e., by balancing the forces of drag, lift, skin friction and buoyancy along a segmented blade of seagrass protruding from an immobile sheath (see Appendix A).

[16] The velocity profile is assumed to be logarithmic above the seagrass canopy, while within the canopy the velocity decreases non-logarithmically with decreasing height. Starting from the edges of a vegetated patch and moving a distance of one meter into the vegetation (in the direction of the flow), the velocity profile is calculated using an iterative procedure, that modifies the velocity profile for bare sediments to account for the effect of drag exerted by the seagrass blades upstream from the point in question (i.e., within one meter from the edges). Thus, although the model does not resolve the horizontal dimensions, it accounts for modification of flow by upstream vegetation.

[17] Conserving fluid momentum between the logarithmic velocity profile when seagrass is absent, \( U_{\text{bare}} \) and the flow modified by the drag imparted by the collection of seagrass blades allows for the velocity profile within the canopy and sheath layers, \( U_{\text{veg}} \), to be calculated as
\[
\rho l \cos \theta U_{\text{bare}} = \rho l \cos \theta U_{\text{veg}}^2 + F_{\text{N}} N_m
\]
where \( N_m \) is a modified one-dimensional shoot density function (number of shoots and blades per unit length) defined in the following section, and \( F_{\text{N}} \) is the horizontal component of the drag exerted by a single blade of seagrass (see equation (A2)). The velocity profile developed in the presence of seagrass, is then calculated solving equation (8) for \( U_{\text{veg}} \).

[18] The momentum lost within the canopy is added to the flow above the canopy and the velocity profile above the canopy is modified accordingly. The velocity, \( U_{\text{transfer}} \), required by the flow above the canopy to conserve the fluid momentum is calculated from the momentum balance equation
\[
\int_0^Z \rho U_{\text{bare}}^2 dz = \int_0^Z \rho U_{\text{veg}}^2 dz + \int_0^Z \rho \left( U_{\text{bare}}^2 + U_{\text{transfer}}^2 \right) dz
\]
where \( k_c \) is the height of the bent canopy (see Appendix A).

[19] Using a displacement height of 70% of the deflected canopy height [e.g., Campbell and Norman, 1998], the momentum lost in the canopy is distributed to the velocity field above the canopy assuming a logarithmic distribution of \( U_{\text{veg}} \) above the canopy, with \( U_{\text{veg}} = 0 \) at the displacement height. Linear regression of the logarithm of the height above the bed, \( z \), to the velocity above the canopy is used to determine the new shear velocity for the flow above the canopy. This approach takes an initial logarithmic velocity profile and runs it through a collection of blades to calculate the departing velocity profile. While this model is one-dimensional, the departing velocity depends on the distance into the seagrass meadow, allowing for calculation of velocities near both the middle and edge of a seagrass meadow.

2.4. Vertical Diffusivity With a Canopy

[20] When a dense canopy is present, vertical diffusivity within the canopy can be modeled as a function of shoot morphology and velocity [Lightbody and Nepf, 2006].
\[
K_{\text{canopy}} = \alpha U w \sqrt{C_d N_m w^2} \text{ for } (0 < z < k_c)
\]
with the coefficient \( \alpha \) ranging from 0.1 to 0.2, \( w \) being average blade width, and where \( N_m \) is a modified shoot density function
\[
N_m = 3.9N \int_{\alpha z}^{\beta z} \frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{(z-z_0)^2}{2\sigma^2}} dz
\]
which accounts for the existence of an average of 3.9 blades/shoot above the sheath [Abdelrhman, 2007]. In equation (11), \( l_{av} \) is the average total blade length set to 80% of the total canopy height and \( \sigma \) is the standard deviation of blade length set to 10% of the canopy height based on measured values from Abdelrhman [2007]. The density in the sheath layer \( z < z_{\text{sheath}} \) is set to the shoot density \( N \).

The vertical diffusivity above the canopy is calculated as \( K_z = \frac{K_{z_{\text{canopy}}}}{C_{13}} + \frac{D_{tz}}{C_{0}/C_{1}} + \frac{1}{C_{0}/C_{13}} (K_z) \) (for \( 0 < z < k_c \)).

In equation (13) the weighing coefficient, \( \gamma \), is calculated as

\[
\gamma = \int_0^N n \left( 1 - \frac{n}{N_{\text{req}}} \right) dn \tag{14}
\]

where \( n \) is shoot density and \( N_{\text{req}} \) is the required shoot density, i.e., the shoot density necessary for a given canopy to behave with diffusivities corresponding to equations (10) and (12).

Dense aquatic canopies have a non-dimensional cross-sectional area of 0.016 \( = ad \) [Ghisalberti and Nepf, 2006]. Using the minimal value of 0.016 and given the calculated deflected canopy height, \( k_c \), and plant morphology, \( N_{\text{req}} \) is determined as

\[
N_{\text{req}} = \frac{0.016}{w^2 k_c} \tag{15}
\]

\( N_{\text{req}} \) is time dependent since the deflected canopy height is time dependent. Under typical blade widths of 0.007 m and a deflected canopy height ranging from 0.15 m to 0.30 m, the modified shoot density required for the canopy to be considered dense varies from 280 shoots m\(^{-2}\) to 580 shoots m\(^{-2}\).

[22] Calculations of \( D_{tz} \) and, \( K_{z_{\text{canopy}}} \) apply only to the case of dense canopies. To model the transitional diffusivity within the canopy between the bare sediment scenario and the dense canopy scenario a weighted average is used.

\[
K_z = \gamma(K_{z_{\text{canopy}}} + D_{tz}) + (1 - \gamma)K_z \text{ for } (0 < z < k_c) \tag{13}
\]
2.5. Light Attenuation

[24] Light attenuation for photosynthetically active radiation (PAR), wavelengths (400–700 nm), in the water column is modeled using the Lambert-Beer law, where the light attenuation coefficient, \( K_d \) (m\(^{-1}\)), is a function of solar zenith, \( \mu \), total suspended solids, phytoplankton (chl \( a \)) and colored dissolved organic matter (CDOM). For this study we determine \( K_d \) based on the empirical relationship used by Lawson et al. [2007]

\[
K_d(\mu) = 0.052TSS + \text{chl} \times 0.0154 + \text{CDOM} \times 0.28 + 0.0384
\]

The case study presented in this paper refers to Hog Island Bay, a shallow coastal lagoon within the Virginia Coast Reserve (VCR), 37°25’N, 75°46’W. This reserve is a Long Term Ecological Research (VCR/LTER) site located on the Atlantic side of the Delmarva Peninsula and includes a number of lagoons bordered by *Spartina alterniflora* marshes both on the mainland and on the barrier islands. About 50% of the lagoons are less than 1 meter deep at mean low water [Oertel et al., 2000] and the tidal range is about 1.2 meters. Since the 1930’s, the southern lagoons of the VCR have been dominated by benthic algae due to a seagrass die off that occurred when the seagrasses of the VCR, already under stress from disease, were severely impacted by a hurricane and became locally extinct [Orth et al., 2006]. In the 1990’s small natural patches of seagrass were discovered, prompting both large-scale restoration efforts and attempts to understand the slow recovery of the seagrass populations in these lagoons. Currently meadows exhibits shoot densities from 412–529 shoots m\(^{-2}\) at depths up to 2 m (Tables 2a and 2b). This change in the trophic base from benthic algae to seagrass is expected to affect the entire system due to changes in production, nutrient cycling, water quality, sediment stability [Sfriso and Marcomini, 1997; Viaroli et al., 1996] and higher trophic levels [Lepoint et al., 2000; Norkko et al., 2000; Sfriso et al., 2001]. We are interested in both the potential for initial seagrass recovery in the VCR coastal lagoons and the resilience of restored seagrass meadows to stress associated with climate change (temperature, storminess) and eutrophication.

### Table 1. Variables

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>( h_{canopy} )</td>
<td>Canopy height (m)</td>
</tr>
<tr>
<td>( k_c )</td>
<td>Deflected canopy height (m)</td>
</tr>
<tr>
<td>( \tau_b )</td>
<td>Shear stress applied to the bed (Pa m(^{-2}))</td>
</tr>
<tr>
<td>( U )</td>
<td>Velocity (m/s)</td>
</tr>
<tr>
<td>( u^* )</td>
<td>Shear velocity (m/s)</td>
</tr>
<tr>
<td>( T )</td>
<td>Temperature (°C)</td>
</tr>
<tr>
<td>( K_d )</td>
<td>Light attenuation coefficient (m(^{-1}))</td>
</tr>
<tr>
<td>( I )</td>
<td>Irradiance in PAR (mol m(^{-2}) hr(^{-1}))</td>
</tr>
<tr>
<td>( Z )</td>
<td>Water depth (m)</td>
</tr>
<tr>
<td>( U_{av} )</td>
<td>Average tidal current velocity (m/s)</td>
</tr>
<tr>
<td>( K_v )</td>
<td>Vertical diffusivity (m(^{2}) s(^{-1}))</td>
</tr>
<tr>
<td>( K_{canopy} )</td>
<td>Vertical emergent canopy diffusivity (m(^{2}) s(^{-1}))</td>
</tr>
<tr>
<td>( D_v )</td>
<td>Vertical diffusivity due to vegetation induced shear layer and coherent vortices (m(^{2}) s(^{-1}))</td>
</tr>
<tr>
<td>( \bar{K_v} )</td>
<td>Weighted average vertical diffusivity for sparse canopies (m(^{2}) s(^{-1}))</td>
</tr>
<tr>
<td>( N )</td>
<td>Shoot density (shoots m(^{-2}))</td>
</tr>
<tr>
<td>( N_m )</td>
<td>Modified shoot density incorporating blade density (shoots m(^{-2}))</td>
</tr>
<tr>
<td>( N_{req} )</td>
<td>The shoot density required to assume a dense flow (shoots m(^{-2}))</td>
</tr>
</tbody>
</table>

the temperature, \( T \), is expressed in °C. These values are then compared to incident radiation, \( I \), at the canopy surface calculated as

\[
I = I_{\text{surface}} e^{-K_hd}
\]

with \( h_d = Z - k_c \) (Table 1).

\[\text{[27]}\] To obtain a first order estimate of growth of plant biomass, \( G_p \), we use the maximum specific growth rate \( G_{pmax} \) scaled as a function of the incident radiation and temperature

\[
G_p = G_{pmax}F_t(I)F_{\text{phot}}(T)
\]

where the scaling functions, \( F_t(I) \) and \( F_{\text{phot}}(T) \) are calculated as in the work by Bocci et al. [1997], Pastres et al. [2004], and Zharova et al. [2001]. We compare \( G_p \) to a respiratory loss term, \( L_{pp} \), which is expressed as a function of the maximum respiration term \( L_{resp} \) and temperature, to account for temperature effects on respiration reduction.

\[
L_p = L_{resp} \theta_{20}^{28-20}
\]

The daily maximum specific growth rate is assumed to correspond to a 10 hour day at optimum light and temperature conditions and is scaled to an hourly rate, whereas the respiratory loss is spread over the entire 24 hour day to acquire an hourly rate. Hourly net loss or growth is summed for the entire year to determine if a given set of conditions favors growth (\( G_p - L_p > 0 \)), or loss of biomass (\( G_p - L_p < 0 \)), for the year.

2.7. Numerical Solution and Model Application

2.7.1. Study Site

[29] The model was used to investigate seagrass dynamics in Hog Island Bay, a shallow coastal lagoon within the Virginia Coast Reserve (VCR, 37°25’N, 75°46’W). This reserve is a Long Term Ecological Research (VCR/LTER) site located on the Atlantic side of the Delmarva Peninsula and includes a number of lagoons bordered by *Spartina alterniflora* marshes both on the mainland and on the barrier islands. About 50% of the lagoons are less than 1 meter deep at mean low water [Oertel et al., 2000] and the tidal range is about 1.2 meters. Since the 1930’s, the southern lagoons of the VCR have been dominated by benthic algae due to a seagrass die off that occurred when the seagrasses of the VCR, already under stress from disease, were severely impacted by a hurricane and became locally extinct [Orth et al., 2006]. In the 1990’s small natural patches of seagrass were discovered, prompting both large-scale restoration efforts and attempts to understand the slow recovery of the seagrass populations in these lagoons. Currently meadows exhibits shoot densities from 412–529 shoots m\(^{-2}\) at depths up to 2 m (Tables 2a and 2b). This change in the trophic base from benthic algae to seagrass is expected to affect the entire system due to changes in production, nutrient cycling, water quality, sediment stability [Sfriso and Marcomini, 1997; Viaroli et al., 1996] and higher trophic levels [Lepoint et al., 2000; Norkko et al., 2000; Sfriso et al., 2001]. We are interested in both the potential for initial seagrass recovery in the VCR coastal lagoons and the resilience of restored seagrass meadows to stress associated with climate change (temperature, storminess) and eutrophication.
2.7.2. Model Simulations

[30] The model was run with an hourly time step (Figure 2) using hourly wind measurements from Hog Island Bay (37°27′N, 75°40′W) and hourly tides from Red Bank (37°26′N, 75°50′W). We used hourly water temperature and salinity measurements (37°23′N, 75°43′W 23) made by the Virginia Institute of Marine Science (VIMS), and PAR from the VCR-LTER flux tower at Fowling Point (37°24′N, 75°50′W). For each one-hour time step, sediment settling velocities were calculated based on water temperature, salinity and density. Velocity and diffusivity profiles were calculated with an iterative procedure to account for canopy deflection. The resultant diffusivity profile and excess shear were used in the implicit solution of the suspended sediment equation for all grain sizes on an hourly time step. The sediment concentrations were then integrated to determine the total suspended sediment. Light attenuation was calculated based on PAR at the water surface and the hourly-calculated light attenuation coefficient. Net growth or loss for that hour was then calculated. These hourly values were used to calculate total net yearly seagrass biomass growth/loss for a constant yearly shoot density. Parameters values were assigned using data available from literature as indicated in Table 3.

[31] The model is limited to water depths where the assumption that a logarithmic velocity profile above the seagrass is appropriate. Thus, the model can be applied only in conditions of seagrass submergence. To maintain validity, the depth limit is set to twice the normal canopy height. Considering a canopy height of 30 cm and a lowest minimum tidal elevation of approximately −1 m below mean sea level model application is limited to mean water depths = 1.6 m.

Due to deflection of the canopy, flow over the meadow occurs for roughly 70% of the water depth. Z. marina can withstand short durations of emergence [Duarte, 1991] and as such the actual range of suitable depths is dependent on canopy height, tidal range and light and nutrient availability. In most systems the typical depth range is 1–10 m with most meadows found from 2–3 m [Duarte, 1991]. Half of Hog Island Bay is deeper than 1.6 m, and depths shallower than 1.15 m account for 36% of the bay (Figure 3). The bare sediment model can be run for mean water depths ≥1.15 m. To fill the gap in depths between the applicability of the bare sediment model and the canopy model, an emergent vegetation hydrodynamic model would be needed that incorporates the transition from an above canopy logarithmic flow to a thin above canopy shear flow. The development of such a model is beyond the scope of this study.

3. Results

[32] Modeled suspended sediment concentrations decreased significantly with increasing seagrass shoot densities with very little suspension occurring at high shoot densities due to the decrease in bed shear and vertical mixing. Even low shoot densities had a strong effect, with 100 shoots m⁻² reducing total suspended sediments by 14% (with respect to the bare sediment case) for a 2 m mean water depth, and by up to 40% at 10 m mean water depth. Total suspended sediment is reduced by 98% at 1000 shoots m⁻². In addition the reduction in the vertical diffusivity due to the presence of a seagrass canopy decreased the time that sediment remained in suspension after large entrainment events. This allowed for faster clearing of the water column and a corresponding increase in the number of hours when light conditions were favorable for seagrass growth each year.

[33] Hours of light saturation, compensation and partial saturation were totaled for the year (Figure 4). When a canopy is present there is a 50% reduction in compensation hours across all water depths with an average increase of 720 hours with partial saturation conditions, i.e., about 90 additional days of adequate growth conditions. At shallow water depths (i.e., Z < 2 m) the number of hours with saturation conditions doubled when a seagrass canopy was present. At 3 m water depths there are no saturation hours under bare sediment or canopy conditions indicating that even under clear water conditions, light attenuation does not allow for saturation at depths > 3 m. However, there are enough partially saturated light hours (i.e., hours with L \textsubscript{c} < L \textsubscript{con} < L \textsubscript{k}) under typical conditions (i.e. typical winds, tides, water temperature, sediment, chl a, CDOM and light) in Hog Island Bay to allow for seagrass growth in water depths up to 3.6 m.

3.1. Alternate Stable States and Their Water Depth Dependence

[34] Under typical conditions for Hog Island Bay, the system favors the presence of a stable seagrass bed ("vegetated state") at locations with water depths, Z < 2.2 m. In this stable vegetated state, shoot density is not determined by light but by other limiting factors (e.g., nutrients). For Z > 3.6 m the light availability is not sufficient for the growth and survival of seagrasses because partial light saturation would occur

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Table 2a. Site Specific Values and Modeled Results for Bed Grain Size Distributions

<table>
<thead>
<tr>
<th>Observed</th>
<th>Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Φ Percent</td>
<td>Same as VCR Percent</td>
</tr>
<tr>
<td>2.5</td>
<td>4</td>
</tr>
<tr>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>3.5</td>
<td>18</td>
</tr>
<tr>
<td>4</td>
<td>32</td>
</tr>
<tr>
<td>4.5</td>
<td>17</td>
</tr>
<tr>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>5.5</td>
<td>5</td>
</tr>
<tr>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>6.5</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 2b. Site Specific Values and Modeled Results

<table>
<thead>
<tr>
<th>Observed</th>
<th>Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shoot densities</td>
<td>412–529 shoots m⁻²</td>
</tr>
<tr>
<td>Depth of meadows</td>
<td>Up to 2 m water depth relative to MSL</td>
</tr>
<tr>
<td>Average annual chl a</td>
<td>1.5–4.1 mg m⁻³</td>
</tr>
<tr>
<td>Light attenuation coefficient</td>
<td>0.47–2.9 m⁻¹</td>
</tr>
</tbody>
</table>
less than 50% of the time. In this case, bare sediment conditions are stable (Figure 5). For depths of 2.2 m < Z < 3.6 m the system exhibits bistable behavior. Depending on the initial seagrass cover conditions, the system converges to a state with either bare sediment or vegetated conditions. Overall, the light environment depends on seagrass stem density, $N$. However, when $N$ exceeds the limiting value, $N_{req}$ (equation (15)), an increase in stem density has only a minimal impact on suspended sediment concentrations and associated light attenuation.

Figure 2. Subset of hourly measurements used in the model, including (a) wind speed (m/s) and direction at 5 m height. (b) Tidal water level variation (m) around MSL from Red Bank. (c) Water temperature (°C). (d) Model simulations of total suspended sediment (mg/l). (e) Comparison between PAR (mol m$^{-2}$ hr$^{-1}$) measurements from the VCR-LTER flux tower at Fowling Point and modeled PAR (mol m$^{-2}$ hr$^{-1}$) reaching the top of the canopy due to light attenuation.

3.2. Effect of Sediment Grain Size

Bed sediment in Hog Island Bay is fine sand to fine silt with a D50 = 74 μm [Lawson et al., 2007]. Lagoons with finer bottom sediment exhibit higher suspended sediment concentrations at low water depths with no significant change in suspended sediment concentrations at water depths > 4 m due to the reduction of wave shear stress as water depth increases. This implies that sediment grain size is important at low water depths where wave action dominates bed shear stress. With a significantly finer bed, e.g. medium silt, D50 = 15 μm, the system is bistable from the shallowest water depth of 1.15 m that can be investigated by this model (due to the submer-

Table 3. Parameter Values and Sources

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value and Description</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$t_{cr}$</td>
<td>0.04 (Pa m$^{-2}$) is the critical shear stress to erode sediment.</td>
<td>Lawson et al. [2007]</td>
</tr>
<tr>
<td>$T_{opt}$</td>
<td>21°C Optimum Photosynthetic Temperature</td>
<td>Bach [1993], Bocci et al. [1997], Pastres et al. [2004], Verhagen and Nienhuis [1983], Zharova et al. [2001]</td>
</tr>
<tr>
<td>$T_{max}$</td>
<td>34°C Maximum Photosynthetic Temperature</td>
<td>Bach [1993], Bocci et al. [1997], Pastres et al. [2004], Verhagen and Nienhuis [1983], Zharova et al. [2001]</td>
</tr>
<tr>
<td>$I_{K20}$</td>
<td>2.8 mol m$^{-2}$ hr$^{-1}$ Saturation irradiance at 20°C in PAR</td>
<td>Bach [1993], Bocci et al. [1997], Pastres et al. [2004], Verhagen and Nienhuis [1983], Zharova et al. [2001]</td>
</tr>
<tr>
<td>$I_{C20}$</td>
<td>0.3 mol m$^{-2}$ hr$^{-1}$ Compensation irradiance at 20°C in PAR</td>
<td>Bach [1993], Bocci et al. [1997], Pastres et al. [2004], Verhagen and Nienhuis [1983], Zharova et al. [2001]</td>
</tr>
<tr>
<td>$\theta_{loss}$</td>
<td>effect of temperature on loss rate, set to 1.05</td>
<td>Bach [1993], Bocci et al. [1997], Pastres et al. [2004], Verhagen and Nienhuis [1983], Zharova et al. [2001]</td>
</tr>
<tr>
<td>$L_{res}$</td>
<td>Respiratory loss rate 0.000375 per hour</td>
<td>Zharova et al. [2001]</td>
</tr>
<tr>
<td>$G_{max}$</td>
<td>Maximum specific growth rate 0.0095 per hour</td>
<td>Bach [1993]</td>
</tr>
</tbody>
</table>
Figure 3. The distribution of depths in Hog Island Bay and the depths where the bare sediment model and the full model are applicable; the partially submerged area is at depths shallower than the tidal range such that full emergence of the seagrass would be expected at low tide.

Figure 4. Total hours of (a) saturation, (b) partial saturation, and (c) compensation as a function of water depth and the presence or absence of seagrass.
gence requirements discussed in section 2; Figure 3), to 3.6 m (Figure 6). In the case of coarser bed sediments, suspended sediment concentrations are smaller and the transition from stable seagrass beds to bistable seagrass cover–bare sediment conditions occurs in deeper waters.

3.3. Effect of Eutrophication

[37] Increasing the levels of chl $a$ to reflect eutrophication due to increased nutrient loading causes a decrease in the depths at which the bistable transition occurs due to an increase in background water column turbidity (Figure 7). Values of chl $a$ in Hog Island Bay typically range from 0 to 9 mg m$^{-3}$ [Lawson et al., 2007]. A set of simulations using different constant values of chl $a$ within this range (Figure 8) shows that the bistable transition zone changes from the water depth range of 2.3–3.6 m to 1.2–1.6 m. The bistable transition zone reaches the minimum model-resolved water depth limit of 1.6 m at chl $a$ concentrations of 5 mg m$^{-3}$. When chl $a$ exceeds 12 mg m$^{-3}$, the maximum measured value of chl $a$ in Hog Island Bay, the bistability range disappears and the system exhibits only a single stable state that supports no seagrass.

3.4. Effect of Water Temperature

[38] Water temperature has an important influence on photosynthesis and respiration rates, thereby potentially exerting a control on the stability and bistability of the system. The conditions that determine light stress for seagrass depend on temperature (section 2.6). When chl $a$ is set to 0 mg m$^{-3}$ bistable dynamics are observed for water depths in the range 2.2–3.6 m under current temperature conditions (i.e., using water temperature records from Hog Island Bay) (Figure 8). With a 3°C increase in water temperature, this bistable range shifts to 1.4–2.7 m. A 5°C increase makes the system bistable for water depths below 2.1 m. In this case, the stable vegetated state may exist only in conjunction with the alternate stable state of bare bed sediment. In contrast, decreasing the temperature favors growth and shifts the bistable transition zone to deeper water.

3.5. Edge Effects

[39] While this model does not resolve the horizontal dimension, the approach allows calculation of vertical profiles of diffusivity, sediment concentrations and light attenuation at varying distances from the edges of a seagrass meadow. Suspended sediment concentrations decrease as a function of distance from the edges of the meadow, with shoot density affecting the amount and rate of attenuation with depth into the meadow (Figure 9). Shoot densities of 100 shoots m$^{-2}$ with a 30 cm canopy height reduce suspended concentrations by 17% at 1 m distance from the edge of the meadow while 500 shoots m$^{-2}$ reduce suspended sediment concentrations by 96%. For the case of 1000 shoots m$^{-2}$, the canopy at 1 m distance from the edge has reduced suspended sediment concentrations by 99% when compared to the bare sediment. Closer to the edge of the meadow, however, the reduction is not as significant, with 1000 shoots m$^{-2}$ reducing suspended sediment concentrations by 70%.

4. Discussion

[40] The results of this study shed light on the stability and bistability of seagrass meadows in shallow coastal lagoon ecosystems and their sensitivity to changing environmental conditions. Hog Island Bay, the focus site for this study, currently exhibits conditions favorable for the growth and
Figure 6. Yearly specific growth rate as a function of depth for varying shoot densities with (a) medium silt sediment bed (mean $\varphi = 5.5$; Tables 2a and 2b). (b) Very fine grain sand sediment bed (mean $\varphi = 3.5$; Table 3).

Figure 7. Changes in the region of bistable behavior due to eutrophication with chl $a$ equal to (a) 0 mg m$^{-3}$, (b) 2 mg m$^{-3}$, (c) 5 mg m$^{-3}$, and (d) 9 mg m$^{-3}$.
maintenance of seagrass over most of the Bay. However, a change in light and temperature conditions that could be expected from climate change or eutrophication can induce bistability in much of the system. In the bistable regime, both vegetated and bare sediment conditions are possible stable states and the dynamics tend toward either one of these states depending on the initial seagrass cover. This shift from stable to bistable dynamics has profound implications for coastal

**Figure 8.** Changes in the region of bistable behavior with chl $a = 0$ and water temperature changes of (a) $-3^\circ$C, (b) $0^\circ$C, (c) $3^\circ$C, and (d) $5^\circ$C.

**Figure 9.** The existing fraction of suspended sediment as a function of distance into the meadow for 100 and 500 shoots m$^{-2}$ at 2.5 m water depth.
ecosystems as a reduction in seagrass cover has a negative impact on water quality and the provision of habitat for fauna [van der Heide et al., 2007].

[41] Our model shows that the stability and bistability of seagrass meadows in coastal lagoons such as Hog Island Bay depend on the environmental controls of water depth, temperature and light attenuation as it is influenced by phytoplankton concentrations and suspended sediments. Future sea level rise in the region of the VCR lagoons is estimated at 3.6 to 10 mm yr⁻¹ [Najjar et al., 2000]. Even small depth changes in this shallow system (0.1 m) predicted over 30 years can have profound effects on light availability and seagrass survival, in large part because of the importance of sediment suspension on light attenuation and much of the bay will fall into a bistable regime. The negative impact of sea level rise and increased water depth is partially mitigated by a secondary effect that benefits seagrass growth through a decrease in wave generated shear stress and hence turbidity. Eutrophication scenarios are expected to increase light attenuation by enhancing algal growth in the water column and on seagrass blades [McGlathery et al., 2007]. Our model gives a conservative estimate of eutrophication effects on seagrass cover and the change in stability of the system, as it only incorporates a modest increase in water column chlorophyll. Light attenuation by epiphytes on seagrass blades and benthic macroalgae can be equally important in shallow coastal systems [Hauxwell et al., 2001]. Regional climate change scenarios predict a 1.3°C change in sea-surface temperatures over the next 30 years [Najjar et al., 2000]. Due to the larger effect of temperature on respiration than on photosynthesis in Z. marina, this increase in sea surface temperature will shift the bistable range to shallower depths with more of the bay unable to sustain seagrass.

[42] Although suspended sediment concentration is currently the primary factor controlling light attenuation in Hog Island Bay in its current low-nutrient state [Lawson et al., 2007], this control would be diminished if seagrass restoration was successful throughout the bay and a dense seagrass canopy covers the sediment surface. In this case, eutrophication induced increases in phytoplankton chl a in the water column becomes the primary factor controlling light attenuation. Even a relatively moderate chl a concentration of 12 mg m⁻³, as long as it is sustained throughout the year, does not allow for conditions favoring seagrass growth in Hog Island Bay; a smaller constant value of 2 mg m⁻³ induced bistability for 20% of the bay. Boynton et al. [1996] report water column chl a concentrations for the more eutrophic Maryland lagoons ranging from 20–70 mg m⁻³, with summertime averages of 10–30 mg m⁻³.

[43] Our model indicates that, like warming trends, eutrophication would shift the bistable range of seagrasses toward shallower water depths. This is consistent with previous large-scale surveys linking the depth distribution of Z. marina to eutrophication (measured as water column total nitrogen or chlorophyll concentrations [Nielsen et al., 2002]). Because chl a and CDOM have important effects on the bistable range, temporal changes in the concentration of chl a and CDOM should be incorporated in future models.

[44] The disappearance of the stable vegetated state in deeper water in scenarios that reflect changes related to both climate and eutrophication effects indicates that bare sediment conditions are the only stable state in the deeper parts of the bay. The emergence of bistable dynamics in shallow waters limits the resilience of seagrass beds in areas with low water depths. In fact, in these conditions the system could abruptly and irreversibly lose its seagrass beds. In this case, the bed would be susceptible to other physical processes not accounted for by this model, including bed scouring and associated changes in water depth, which would, in turn, modify currents and waves [e.g., Fagherazzi et al., 2006; Fagherazzi and Wiberg, 2009].

[45] Some limitations of the methods used in this study need to be acknowledged. First, the model presented here provides a one-dimensional representation of sediment transport and deposition in the vertical direction within a seagrass meadow of varying shoot densities. Thus, important processes such as lateral transport of sediment are neglected. Advection and dispersion of sediment from barren sediment areas within the bay is a more likely source of suspended sediment above and within the canopy than is the bed below the canopy at shoot densities >250 shoots m⁻². This implies that the suspended sediment dynamics at the edge of seagrass meadows are important to the growth and maintenance of the meadow. These three dimensional dynamics of suspended sediment cannot be investigated with the modeling framework developed in this study.

[46] Second, a parameterization of flow in extremely sparse vegetation remains an important issue in environmental fluid dynamics [Luhar et al., 2008]. The approach utilized in this model treats the transition as a weighted average of two extremes with an increase in shoot density affecting turbulent diffusivity and the shape of the velocity profile. While this is a good first approximation, some measurements have shown an increase in resuspension at low shoot densities [Lawson et al., 2007] implying a more complicated transition than the one used in this study.

[47] Third, several aspects of seagrass growth and architecture were simplified in the model and could be further developed in future modeling efforts. The use of a yearly specific growth rate allows for a general understanding of vegetation growth and of the existence of alternate stable states in seagrass ecosystems. To simplify and explore feedbacks, the canopy height and shoot density were considered constant throughout the year, without accounting for important seasonal variations. Such variability implies greater susceptibility to light deficit during low density and low foliage time periods. Running the model with lower canopy heights would further limit the existence of stable vegetated conditions in deep water (i.e., the bistability range would be shifted toward shallower water) due to the decreased influence of the canopy on sediment resuspension. There was no inclusion of a rhizome biomass store which would allow for resilience of the seagrass under adverse conditions. Similarly, there was no incorporation of storm removal of biomass or other temporal variability in the plant morphology. Adding a time-dependent model for seagrass growth and loss involving both aboveground and below-ground biomass is needed to fully investigate the stability of the system. However, including a temporal growth model of seagrass would add additional parameters [Bocci et al., 1997; Zharov et al., 2001], not all of which are well constrained.

[48] Direct grazing on seagrasses is not significant in temperate seagrass ecosystems as it is in tropical ecosystems, and so this is not an important factor in the accuracy of the
model for these temperate lagoons. Previous work [McGlathery et al., 2007] has shown that the water column is typically net heterotrophic, except for short periods in mid-summer. Grazing on phytoplankton populations would increase the accuracy of the model in some more nutrient-enriched systems, however, the coastal bays of Virginia are nutrient-poor and phytoplankton populations are extremely low, so that including grazing or nutrient competition in the model for the Virginia coastal bays would not significantly increase its accuracy.

[40] Lasty, improvements in characterizing the light environment could be made, particularly with regards to incorporating grain size effects of light absorption, as both chl $a$ and CDOM are low in this system. A more sophisticated light attenuation model [Biber et al., 2008] that accounts for the nonlinearity of the attenuation process would improve the characterization of the light environment.

[50] The model presented here allows for a physically-based resolution of canopy bending and the feedback of canopy structure on the fluid dynamics. This approach is well suited to investigate sediment dynamics and the corresponding impact on the light environment. This modeling of the light environment along with the temperature conditions allows for sensible estimation of the specific net growth/loss rates of seagrass and for investigation of the conditions controlling stability and bistability of seagrass ecosystems in shallow bays.

5. Conclusion

[51] In general, the results of this modeling effort point toward the conditions that control the stability and bistability of seagrass meadows in shallow bays. The results show how the presence or absence of seagrass depends on water depth, sediment size, water temperature and degree of eutrophication. We found that (i) the response of the system to sea level rise is highly non-linear and seagrass meadows located in relatively deep waters are likely to undergo abrupt shifts to a bare sediment state; (ii) regions of shallow coastal lagoons with finer sediment are more likely bistable than regions with coarser sediment; (iii) increases in both temperature and eutrophication lead to increases in the proportion of shallow bays that exhibit bistable behavior, with a consequent decrease in resilience. Moreover, both eutrophication and warming would cause the migration of seagrass toward shallower parts of the bay, leaving the deeper sediment bed without seagrass cover.

Appendix A: Method Used for the Iterative Calculation of Canopy Bending

[52] The bending angle, $\theta$ (with respect to the vertical direction), of the uppermost stem segment was calculated from the force moment balance equation

$$\frac{1}{2} C_d \rho w U^2 \frac{F^2}{2} \cos^2 \theta + \frac{1}{2} C_l \rho U^2 \frac{F^2}{2} \sin^2 \theta - \frac{1}{2} (\rho - \rho_p) gw \frac{E^2}{2} \sin \theta = 0$$

(A1)

where $C_d$, $C_l$, $C_f$ are the coefficients for drag, lift and skin friction; $w$, $d$, $l$ are the width, thickness and length of the segment and $U$ is the velocity acting on the midpoint of the segment. $\rho_p$ is the density of the plant and set to 700 kg m$^{-3}$.

[53] The drag coefficient of the blade segment to the flow was modeled to vary linearly from 1.2 to 0 for $0^\circ \leq \theta \leq 90^\circ$. Treating the blade segment as an airfoil, the lift coefficient was varied linearly from 0.8 to −0.8 for $15^\circ \leq \theta \leq 105^\circ$. For blade segments with angles outside this range the lift coefficient was assumed to be zero. The skin friction coefficient was calculated based on the blade segment Reynolds number, $Re = \frac{ul}{\nu}$, as $C_f = 0.074$ [Abdelrhman, 2007].

[54] Effects of the ensemble of blades on the lift drag and skin friction coefficients were incorporated assuming a linear density-dependent sheltering effect with the above coefficients being reduced by a factor of 3 at shoot densities of 200. Abdelrhman [2007] used a reduction factor of 2 and reduction in terrestrial canopies due to sheltering have been found in the range of 3 to 4 [Abdelrhman, 2007].

[55] Once the bending angle was determined the forces acting on the uppermost segment were calculated as

$$F_x = -\frac{1}{2} C_d \rho w l U^2 \cos \theta - \frac{1}{2} C_f \rho w l U^2 \sin^2 \theta$$

$$F_z = \frac{1}{2} C_l \rho w l U^2 \sin \theta - (\rho - \rho_p) gw bl - \frac{1}{2} C_f \rho w l U^2 \sin^2 \theta \cos \theta$$

(A2)

and the deflection angle of the subsequent segment, $i$, was calculated accounting for force moments as in equation (A1) and of the effect of the reaction force of the segment, $i-1$, above exerted through the upper node of the segment, $i$. Thus, for the $i$-th segment the equilibrium equation becomes

$$\frac{1}{2} C_d \rho w l U^2 \frac{F^2}{2} \cos^2 \theta + \frac{1}{2} C_l \rho U^2 \frac{F^2}{2} \sin^2 \theta - (\rho - \rho_p) gw \frac{E^2}{2} \sin \theta$$

$$+ F_{x,i-1} \cos \theta - F_{z,i-1} \sin \theta = 0$$

$$F_x = \frac{1}{2} C_d \rho w l U^2 \cos \theta - \frac{1}{2} C_f \rho w l U^2 \sin^2 \theta - F_{x,i-1}$$

$$F_z = \frac{1}{2} C_l \rho w l U^2 \sin \theta - (\rho - \rho_p) gw bl$$

$$- \frac{1}{2} C_f \rho w l U^2 \sin^2 \theta \cos \theta - F_{z,i-1}.$$  

(A3)

[56] The segment corresponding to the seagrass sheath was considered immobile in all flow conditions and maintained zero deflection in any flow. Numerical solution of the coupled deflected canopy and flow equations requires iteration because, as it gets deflected, each segment experiences a different flow velocity, which, in turn, changes the forces acting on the segment.

[57] Acknowledgments. Partial support of this study was provided by the Virginia Coast Reserve LTTER project, which was supported by National Science Foundation grants BSR-8702333–06, DEB-9211772, DEB-9411974, DEB-0080381 and DEB-0621014.

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