

Modeling Seagrass Density and Distribution in Response to Changes in Turbidity Stemming from Bivalve Filtration and Seagrass Sediment Stabilization

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ABSTRACT: In many areas of the North American mid-Atlantic coast, seagrass beds are either in decline or have disappeared due, in part, to high turbidity that reduces the light reaching the plant surface. Because of this reduction in the areal extent of seagrass beds there has been a concomitant diminishment in dampening of water movement (waves and currents) and sediment stabilization. Due to ongoing declines in stocks of suspension-feeding eastern oysters (*Crassostrea virginica*) in the same region, their feeding activity, which normally serves to improve water clarity, has been sharply reduced. We developed and parameterized a simple model to calculate how changes in the balance between sediment sources (wave-induced resuspension) and sinks (bivalve filtration, sedimentation within seagrass beds) regulate turbidity. Changes in turbidity were used to predict the light available for seagrass photosynthesis and the amount of carbon available for shoot growth. We parameterized this model using published observations and data collected specifically for this purpose. The model predicted that when sediments were resuspended, the presence of even quite modest levels of eastern oysters (25 g dry tissue weight m^{-2}) distributed uniformly throughout the modeled domain, reduced suspended sediment concentrations by nearly an order of magnitude. This increased water clarity, the depth to which seagrasses were predicted to grow. Because hard clams (*Mercenaria mercenaria*) had a much lower weight-specific filtration rate than eastern oysters; their influence on reducing turbidity was much less than oysters. Seagrasses, once established with sufficiently high densities ($>1,000$ shoots m^{-2}), damped waves, thereby reducing sediment resuspension and improving light conditions. This stabilizing effect was minor compared to the influence of uniformly distributed eastern oysters on water clarity. Our model predicted that restoration of eastern oysters has the potential to reduce turbidity in shallow estuaries, such as Chesapeake Bay, and facilitate ongoing efforts to restore seagrasses. This model included several simplifying assumptions, including that oysters were uniformly distributed rather than aggregated into offshore reefs and that oyster feces were not resuspended.

Introduction

Seagrass beds have declined dramatically over the last three decades in many locations along the North American mid-Atlantic coast (Orth and Moore 1984), as well as worldwide (Short and Wylie-Echeverria 1996; Green and Short 2003). A major factor responsible for this decline is the eutrophication-induced lower light level reaching seagrasses as a consequence of the growth of epiphytes on the plant leaves and phytoplankton in the water column (Twilley et al. 1985), both of which contribute to light attenuation (Dennison et al. 1993). Another factor that has the potential to decrease water clarity is sediment resuspension. Seagrass meadows efficiently attenuate waves (Fonseca and Cahalan 1992; Koch 1996) and reduce current velocity (Fonseca et al. 1982; Gambi et al. 1990; Koch 1996; Koch and Gust 1999; van Keulen and Borowitzka 2002). This leads to the deposition

of particles within seagrass meadows (Grady 1981; Kemp et al. 1984; Newell et al. 1986; Posey et al. 1993), a reduction in the concentration of particles in suspension in the areas colonized by seagrass (Ward et al. 1984), and therefore allows more light to become available for seagrass photosynthesis (Kemp et al. 1984; Dennison et al. 1993; Moore et al. 1994). If seagrasses start to decline due to adverse environmental conditions, more sediment may be resuspended and water clarity will decline even further. Once seagrasses become established, these positive feedbacks help the beds become self-stabilizing, i.e., seagrasses promote their own growth because their presence improves water clarity.

Although an increase in suspended particles (via resuspension) in seagrass habitats has the potential to reduce plant growth, studies on the sediment dynamics in seagrass beds have focused mainly on depositional processes (reviewed by Fonseca 1996). Data on sediment resuspension leading to reduced light availability are mostly

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limited to extreme events, such as hurricanes and cyclones (Tilman et al. 1994; Dawes et al. 1995; Preen et al. 1995). Seagrass beds may tolerate sporadic high turbidity and resulting low light availability (Moore et al. 1997) in the summer and when colonizing clear waters (more hours exposed to saturating light levels). Under conditions where seagrasses are exposed to extremely low light conditions (late in the season when days become shorter, in deep waters, or high turbidity environments such as Chesapeake Bay, U.S.), even a short-term turbidity event can result in the loss of seagrasses (Williams 1988). In addition to the stochastic extreme sediment resuspension events associated with storms, resuspension of sediments in seagrass beds is an integral component of daily sedimentary processes (Koch 1999).

Bivalves, such as oysters and clams, as a direct result of their suspension-feeding activity, serve to reduce concentrations of phytoplankton and suspended inorganic particles, thereby increasing light penetration through the water column (for reviews see Dame 1996; Newell 2004). Preceding the major losses of seagrass beds that have taken place along the mid-Atlantic coast there was a century-long decline in the abundance of suspension-feeding eastern oysters, *Crassostrea virginica*, in the same region (MacKenzie 1996). Newell (1988) estimated that pre-1900 eastern oyster populations filtered approximately 80% of Chesapeake Bay shallows per day during summertime but, because of the precipitous decline in oysters throughout the last century, the rate has been reduced to less than 1%. The loss of this ecosystem service may be a crucial contributing factor to the reduction in water clarity that has led to the severe decline in areal extent of seagrass beds in Chesapeake Bay. A dramatic example of the possible synergism between suspension-feeding bivalves and submerged aquatic macrophytes occurred in the tidal freshwater reaches of the Potomac River, Maryland, U.S.). There, non-native asiatic clams, *Corbicula fluminea*, attained such high abundances during the early 1980s that they removed sufficient phytoplankton (Cohen et al. 1984) to reduce turbidities and increase light penetration to the sediment surface. It has been suggested that this was a contributing factor in allowing submerged aquatic macrophytes that were previously light-limited, to become reestablished in the Potomac River (Phelps 1994).

There is considerable interest in the possible ecological benefits associated with bivalve populations reducing estuarine turbidities but this is a complex non-linear process in which the interactions between animals and plants control the light availability to benthic plants. It is difficult to apply

this idea to environmental management without some type of predictive model that can incorporate the complex interactions involved. Our first objective was to develop a simple mathematical model that predicted possible changes in seagrass shoot density with increased light availability stemming from an enhancement of the biomass of bivalve suspension feeders. Our second objective was to predict changes in light extinction associated with changes in turbidity and sediment resuspension associated with the seagrass beds themselves (i.e., resulting from effects of seagrass shoot density on wave action). Although some of the functional relationships needed to parameterize the model were available from literature sources, some specific relationships were not available. To obtain these necessary data, we undertook a series of field measurements in a seagrass bed (*Ruppia maritima*) in Chesapeake Bay and laboratory feeding studies on eastern oysters and hard clams (*Mercenaria mercenaria*).

Methods

SEAGRASS PROCESSES

We measured the influence of seagrasses on sediment resuspension in a *R. maritima* bed in Duck Point Cove (38°13.4'N, 76°03.1'W), near Bishop's Head Point, Maryland, in the mesohaline portion of Chesapeake Bay. We studied sediment resuspension processes during two separate 10-d deployments at a site vegetated by *R. maritima* and at an adjacent unvegetated reference site that was 100 m away and at the same water depth (1 m at low water). One deployment was in summer, when the vegetation was reproductive and occupied the entire water column, and the other in autumn, when the plants only occupied a small fraction of the water column. At the beginning and end of each study period, seagrass density (random 25 × 25 cm quadrat counts, n = 5) and canopy height (direct measurement using a ruler) were measured.

At the seagrass and reference site we installed platforms to support automated water samplers (ISCO) used to collect ~0.9 l of water every 2 h from 3 cm above the sediment surface. The automated water sampler collected ~0.3 l every 40 min and combined 3 samples in one bottle to represent a 2-h average. These samples were then retrieved every other day. Measured aliquots were filtered through ashed and dried pre-weighed GF/C filters, dried (60°C), and weighed again to determine total seston. The filters were heat treated (450°C for 24 h) and the resulting weight loss used to estimate the organic fraction of each sample.

Additional abiotic parameters were measured concurrently with water sampling, including light

TABLE 1. Change in light attenuation coefficient (K_d) associated with feeding by different biomass (aggregate dry tissue weight [g] of n animals) and numbers (n) of eastern oysters (3 separate experimental runs) and hard clams (2 separate runs) feeding at three acclimation temperatures. Particle Clearance Rates (PCR; 1 h^{-1}) were calculated using a Coulter Counter to measure rates of particle disappearance. Changes in K_d and PCR were converted into weight specific rates as described in the text. nd = no data.

Species Temperature	n	Tissue Dry Wt (g)	Change in K_d 24 h^{-1}	Change in K_d $24 \text{ h}^{-1} \text{ g}^{-1}$	PCR (1 h^{-1})	PCR ($1 \text{ h}^{-1} \text{ g}^{-1}$)
Oyster 15°C	14	37.5	0.384	0.016	18.54	0.76
	14	37.5	0.348	0.014	27.57	1.13
	14	37.5	0.415	0.017	26.88	1.11
Oyster 20°C	13	27.03	0.223	0.011	6.25	0.32
	13	27.03	0.646	0.033	65.48	3.34
	13	27.03	0.396	0.020	82.24	4.2
Oyster 25°C	6	10.68	0.593	0.072	79.35	9.58
	6	11.04	0.768	0.091	59.59	7.05
	6	9.3	0.638	0.086	58.83	7.97
Clam 15°C	20	35.4	0.072	0.003	3.12	0.13
	20	35.4	0.055	0.002	nd	nd
Clam 20°C	20	36	0.108	0.005	17.2	0.73
	20	36	0.139	0.006	19.68	0.83
Clam 25°C	20	19.89	0.109	0.005	5.29	0.27
	20	20.6	0.068	0.003	4.49	0.22

availability and wave characteristics. Spherical irradiance sensors (LiCor model 193SA), deployed near bottom (Z) and at 0.3 m above the bottom sensor (O) in the vegetated and unvegetated sites, recorded ambient light levels every 15 min from which we calculated the light attenuation coefficient (K_d) based on the Lambert-Beer equation: $K_d = -[\ln(\text{light Z}/\text{light O})]/0.3$.

Wave gauges (Macrowave, Coastal Leasing) were deployed on the sediment surface in the unvegetated and vegetated sites. These recorded the pressure exerted on the sensor (i.e., water height = waves) for 13 min every hour at a 5 Hz frequency. A Fast Fourier Analysis (PC Spec, Coastal Leasing) of these data allowed us to determine wave height and tidal level in the vegetated and unvegetated areas. The critical erosional threshold (critical friction velocity, τ_c) of the sediments within the seagrass bed was determined in the laboratory using a microcosm that generated homogeneous friction velocities, τ (Huettel and Gust 1992). Field-collected sediment was placed in the microcosm and covered with water. Then τ levels were gradually increased and water samples collected after 10 min of exposure to each τ level. Seston concentrations were determined in these water samples as described above and the inflection point, where seston concentrations increased exponentially with friction velocity, was defined as τ_c . Seston, light, seagrass, and wave data were used to explore the effects of seagrass shoot density and canopy height on sediment resuspension in the model.

LABORATORY STUDIES OF THE INFLUENCE OF BIVALVES ON TURBIDITY

Adult eastern oysters (8–10 cm shell height) were collected from the Choptank River, Mary-

land. Hard clams (5–6 cm shell height) were grown in Plantation Creek, Virginia. Both species of bivalve were collected in March and August 2000 and acclimatized to laboratory conditions for 14–20 d prior to use in the feeding studies. In March, one group of each species was held at the field ambient water temperature of 15°C and one group was acclimated to 20°C. In August, animals were maintained only at field ambient water temperature (25°C). Oysters were held in flowing ambient estuarine water (salinity 12–15) with a natural seston complement. Clams were held in non-flow-through aerated tanks with 20 salinity water made by mixing estuarine water with 32 salinity seawater, with 20% water exchanged every second day. Clams were fed *Isochrysis galbana* (T-Iso) at 2% of dry body weight per day as a maintenance ration. Clams were put into 12 cm deep plastic beakers containing coarse sand into which they deeply buried during the acclimatization period.

The influence of eastern oysters and hard clams on turbidity and light penetration was evaluated in 1 m deep 1,000 l tanks filled with estuarine water. These tanks had a mixing system consisting of rotating, reversing paddles, with speed, direction, and duration controlled by computer to simulate mixing in nature. This system ensured homogeneous mixing of the water column without resuspending sediment from the bottom as described by Sanford (1997). Light was provided by high output fluorescent lamps that produced irradiance of c. 200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ just beneath the water surface.

In separate experiments, groups of oysters and clams were placed on the bottom of tanks and allowed to feed undisturbed for 2 h. Table 1 lists the

number of bivalves, their aggregate dry tissue weight, and the number of experimental runs performed at each temperature (note: for some runs the same group of oysters and clams were measured on different days). Additional identical tanks were maintained without any bivalves to serve as controls to measure changes in turbidity due to gravitational settling of particles. Hard clams buried in the sand-filled plastic beakers were placed directly on the tank bottom and oysters were placed on the tank bottom without sediment. For between 10 and 24 h following acclimatization, photosynthetically available radiation (PAR) was periodically measured using a scalar irradiance sensor (LiCor) positioned just beneath the water surface (O) and at 0.5 m (Z) beneath the surface. The fluorescent lights were only switched on for the 10 min period required to take readings and were then turned off to reduce any phytoplankton growth during the experimental runs. We measured light levels ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) 4 times at each depth from which we calculated the mean extinction coefficient (K_d) in each tank, based on the Lambert-Beer equation (see above).

Regression equations of K_d against time for each data set were used to calculate the absolute change in K_d (increase in light penetration) for a 24 h period. The change in K_d for the control tank associated with particle settlement was then subtracted from the experimental values. There was diminution in light intensity associated with distance from the artificial light source. We estimated this diminution, together with the attenuation due to the water, in these same tanks by replacing the natural river water with tap water containing no suspended particles and, as before, measuring light just under the water surface and 0.5 m further into the tank. This K_d value was subtracted away from all of the experimental values. Note that this correction only altered the absolute magnitude of the K_d values and not the relative change in K_d between the experimental and control tanks.

Water was collected concurrently with the light measurements using a siphon hose positioned close to the middle of the tank. Abundance of particles $>2 \mu\text{m}$ (size above which clams and oysters can retain a large percentage of suspended particles) was counted on subsamples using a Coulter Multisizer II. At the end of each experiment, oyster and clam tissues were individually dissected from shells into preweighed aluminum pans and dried at 80°C for 2 d for determination of each animal's total dry tissue weight.

Particle concentrations measured using the Coulter Multisizer at intervals in each tank were transformed by logarithm and used to prepare a linear regression of particle disappearance over

time for each tank. These equations were used to predict the initial (time 0; C_i) and final (time 24 h; C_f) log transformed particle concentrations in each tank. Similar calculations were performed for the control tanks without bivalves (time 0; C_{ci} and time 24 h; C_{cf}) in order to correct for particle settlement during the feeding period. These values were then used to calculate aggregate Particle Clearance Rate (PCR; 1 h^{-1}) using the following equation (Coughlan 1969):

$$\text{PCR}(1 \text{ h}^{-1}) = \{(\log_e C_i - \log_e C_f) - (\log_e C_{ci} - \log_e C_{cf})\} \left(\frac{V}{t} \right)$$

where V = tank volume (1,000 l) and t = duration of feeding period. By fitting regression curves to the sequential measurements of light penetration we also estimated the change in K_d per 24 h, which is a measure of how rapidly bivalves increased light penetration.

Values for PCR and change in K_d were converted into rates for a standard size bivalve of 1 g dry weight using the standard allometric relationship (Bayne and Newell 1983; Bayne et al. 1985): $X = y/W^b$, where X = weight corrected rate for a 1 g dry tissue weight bivalve, y = measured rate, b = weight exponent, and W = average individual dry tissue weight of the bivalves in the tank. A weight exponent of 0.56 was used for eastern oyster data (Newell unpublished data) and 0.287 for hard clam (Grizzle et al. 2001; average of values in their Table 8.1 measured at 17°C , 20°C , and 25°C).

MODEL DEVELOPMENT

These field and laboratory data were used, together with literature information, to construct a numerical model that simulated seston concentration, water clarity, and seagrass shoot density as a function of bivalve biomass and filtration, sedimentation, and sediment resuspension. Values used for the various model parameters are listed in Table 2. The model consisted of two equations, one of which described the rate of change in seagrass shoot density (D_{sg}):

$$\frac{dD_{sg}}{dt} = u_m [1 - e^{(-I_{avg}/I_k)}] D_{sg} - r D_{sg} \quad (1)$$

where u_m is the maximum growth rate (s^{-1}) of the seagrass (see below for description of how we estimated this parameter for *R. maritima*), I_{avg} is the average irradiance over the length of the shoot, I_k is the light saturation parameter for seagrass photosynthesis, and r is a coefficient characterizing respiratory losses of the seagrass.

A second equation described the rate of change of seston concentration (S):

TABLE 2. Model parameters, units, and values.

Description	Abbreviation	Units	Value	Source
Maximum seagrass growth rate	μ_m	s^{-1}	1.44×10^{-5}	See text for derivation
Light saturation parameter for seagrass growth	I_k	$\mu\text{mol m}^{-2} s^{-1}$	200	Koch and Dawes 1991
Seagrass respiration coefficient	r	s^{-1}	1.53×10^{-6}	Koch and Dawes 1991
Incident PAR at the water surface	I_o	$\mu\text{mol m}^{-2} s^{-1}$	1,000	input parameter
Shoot-specific light attenuation	a_{sg}	$m \text{ shoot}^{-1}$	0.01465 0.000985	reproductive (long) shoots vegetative (short) shoots derived a posteriori
Distance from water surface to the bottom	z_{bot}	m	input	input parameter
Distance from water surface to the top of shoot canopy	Z_{top}	m	input	input parameter
Shoot height	$Z_{bot}-Z_{top}$	m	0.15 and 1.0	observed vegetative and reproductive shoot heights
Background light absorption coefficient	k_x	m^{-1}	0.607	unpublished data
Seston light absorption regression coefficient	m_1	$(g \text{ m}^{-3}) m^{-1}$	0.0259	unpublished data
Erosion rate constant	M	$g (\text{Pa m}^{-2} s^{-1})^{-1}$	0.00389	Sanford and Chang (1997) 50% of their value to produce realistic results measured in this study
Critical shear stress for resuspension	τ_c	Pa	0.196	
Critical seagrass density for damping	D_{crit}	shoots m^{-2}	1,000	Koch, unpublished data
Water density	ρ	$g \text{ m}^{-3}$	1,000	Constant
Kinematic viscosity	ν	$m^2 s^{-1}$	0.000001	Constant input
Wave height at deep boundary	H_{db}	m	input	
Wave period	T	s	2.1	measured this study
Sediment sinking rate	w_s	$m \text{ s}^{-1}$	1.3972×10^{-5}	Sanford and Chang 1997
Bivalve biomass	B_b	$g \text{ m}^{-2}$	input	input parameter
Bivalve clearance rate	c_b	$m^3 s^{-1} g^{-1}$	input	Average of rates at 20°C and 25°C (Table 1)

$$\frac{dS}{dt} = \frac{[M(\tau_b - \tau_c) - w_s S - C_b S B_b]}{Z_{bot}} \quad (2)$$

where M is the erosion rate (modified from Sanford and Chang 1997), τ_b and τ_c are the bottom shear stress and the critical shear stress for sediment resuspension, respectively, w_s is the sinking rate of seston (Sanford and Chang 1997), C_b the bivalve filtration rate, B_b the biomass of bivalves, and Z_{bot} the distance from the water surface to the bottom.

The model was cast in a vertically integrated form with spatial units of m^2 (i.e., depth was specified, not explicitly modeled). Seagrass growth or death, represented as a change in shoot density (D_{sg} ; shoots m^{-2}) and seston concentration (S ; $g \text{ m}^{-3}$) were dynamically modeled, with D_{sg} determined in Eq. 1 by the balance between light-controlled growth and respiration, and S determined in Eq. 2 by the balance between sediment resuspension, deposition, and bivalve filtration. Bivalve abundance (B_b) was not dynamically modeled; instead the mass of bivalves m^{-2} was an input parameter. For simplicity, the distribution of bivalves was

assumed to be homogeneous throughout the seagrass bed, which is true for hard clams but not for oysters that generally live offshore aggregated on reefs. Equation 2 had feedback to Eq. 1 through S , which partly determined I_{avg} in Eq. 1. Equation 1 had feedback to Eq. 2 through the wave attenuation of seagrasses (i.e., a reduction in τ_b and, consequently, S).

Calculations of I_{avg} included light attenuation due to seston (K_s), self-shading by the seagrasses (K_{sg}), and all other light absorbing substances associated with water, dissolved matter, and phytoplankton (K_x). We partitioned light attenuation vertically into two parts, attenuation above the seagrass canopy (K_1) with attenuation due only to K_x and K_s :

$$K_1 = K_x + K_s \quad (3)$$

and attenuation within the seagrass canopy (K_2) that also included K_{sg} :

$$K_2 = K_x + K_s + K_{sg} \quad (4)$$

For simplicity, we assumed that K_x was constant. We estimated $K_s = m_1 S$ from seston concentration with

m_1 derived from field and laboratory measurements. We estimated $K_{sg} = a_{sg}D_{sg}$ using a seagrass shoot density-specific light attenuation coefficient, a_{sg} . The incorporation of this self-shading effect allowed us to model maximum seagrass density as a function of depth and light attenuation in the overlying water column and within the vegetation. Although a_{sg} can vary with tidal level, which causes changes in canopy height, and water flow (e.g., bending of seagrass leaves by water currents; Fonseca et al. 1982), in our model a_{sg} only varied as a function of seagrass shoot density and shoot height, which are the main factors influencing a_{sg} .

The average light over the length of the seagrass shoots was determined by first calculating the irradiance at the top of the canopy, Z_{top} , where light was attenuated by K_x and K_s :

$$I_{top} = I_0 e^{-K_1 Z_{top}} \quad (5)$$

and then averaging the light from Z_{top} to the bottom, Z_{bot} according to:

$$I_{avg} = I_0 e^{-K_1 Z_{top}} \frac{(e^{-K_2 Z_{top}} - e^{-K_2 Z_{bot}})}{K_2 (Z_{bot} - Z_{top})} \quad (6)$$

where I_0 was the irradiance at the water surface.

We used the value we measured for field-collected sediments for the critical bottom shear stress for resuspension, τ_c (a constant). The bottom shear stress, τ_b , was determined primarily by waves:

$$\tau_b = \frac{f_w \rho u^2}{2} \quad (7)$$

Where τ_b is the maximum bottom shear stress due to waves, f_w is the wave friction factor, u is the maximum wave-induced bottom velocity, and ρ is the density of the water (Sanford 1994). Because we considered both shallow, transitional waves and deepwater waves we used Airy's linear wave theory to calculate u as a function of wave height, period, and wavelength. We then calculated f_w as a function of Reynold's number (Re) using Jonsson's diagram assuming a smooth bottom (Madsen 1976):

$$Re = \frac{u A_b}{\nu} \quad (8)$$

where A_b is the distance along the bottom over which motion was induced by each wave and ν was the kinematic viscosity. The wave friction factor was also used to calculate the rate at which waves were damped as they propagated over a shallow unvegetated bottom, where the rate of energy dissipation, d , in the bottom boundary layer was given by

$$d = \frac{f_w \rho u^3}{4} \quad (9)$$

(Sanford and Grant 1987). In practice, wave damping was calculated from the wave energy flux, E , starting at the deep boundary (i.e., the seaward end of the model domain):

$$E = \frac{\rho h^2 v_g}{8} \quad (10)$$

where h was the wave height and v_g the surface group wave velocity. As the waves propagated shoreward energy was removed in each successive grid cell, j , due to dissipation in the bottom boundary layer:

$$E_j = E_{j-1} - d_{j-1} \Delta x \quad (11)$$

where Δx was the width of each cell. As the wave propagated, the wave height was recalculated (dissipated) for each grid cell according to Eq. 10. In the model runs reported here, waves were propagated and attenuated manually, by running a linear series (from offshore to onshore) of models, and feeding the resulting wave height from each successive calculation into the next. A simple parameterization of wave breaking in shallow water was also incorporated by checking to see if $h/Z_{bot} > 0.8$ in each grid cell. If it was, then we set $h = 0.8 \times Z_{bot}$ and recalculated E according to Eq. 10.

The wave attenuation effects due to the presence of seagrasses were incorporated by increasing bottom roughness which increased f_w (Fonseca and Cahalan 1992). This was done by choosing different relative bottom roughness curves on Jonsson's diagram (Madsen 1976) that gave wave dissipation rates consistent with those observed in our field studies (see below). We set a seagrass shoot density threshold, D_{crit} , such that seagrasses had no influence upon waves when $D_{sg} < D_{crit}$ (Fig. 1).

MODEL PARAMETERIZATION

The seagrass model was parameterized using data derived primarily from *R. maritima*, though, in the few situations in which essential data for this species was not available, information from other seagrasses was used (Table 2). The geometry of the modeled domain was a bottom with a 1:120 slope, with the distance from the water surface to the bottom (Z_{bot}) varying from 3 m depth at 360 m offshore to 0 m depth at the shore. Seagrass canopy height was specified as either 0.15 m for vegetative shoots or 1.0 m for reproductive shoots based upon our measurements of *R. maritima* plants in Chesapeake Bay. The maximum growth rate (μ_m) for *R. maritima*, the light saturation parameter for growth (I_k), and the respiration coefficient (r) were derived from photosynthesis versus irradiance measurements (Koch and Dawes 1991). Specifically, μ_m was derived by taking the maximum oxygen

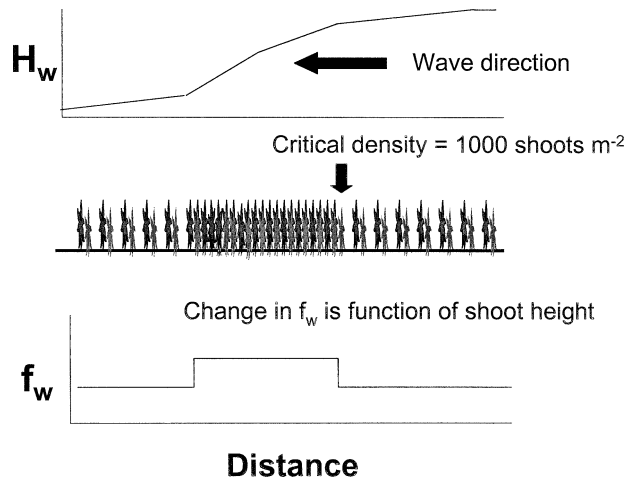


Fig. 1. Schematic diagram showing how waves are progressively attenuated as they propagate inshore, and how seagrass shoot density increases bottom friction when shoot densities exceed 1,000 shoots m^{-2} . H_w is wave height and f_w is bottom friction factor.

evolution rate and dividing by a photosynthetic quotient of 1.1 to derive carbon fixation, and then dividing again by the measured carbon biomass of the plants to derive growth rate. Similar conversions were applied to calculate the respiration rate from oxygen consumption in the absence of light.

Incident PAR at the water surface (I_o) was specified to represent a typical, summertime, daily-average value in the Chesapeake Bay region. The background light absorption coefficient (K_x), which was considered to include everything except seston and seagrass attenuation, was set to give a phytoplankton euphotic depth (1% I_o) of 7.58 m when $S = 0$. The seston light absorption regression coefficient (m_1) was set based upon field data collected in our vegetated field site during a deployment, where K_s was regressed against S to determine the slope, m_1 . The seagrass shoot attenuation coefficient, a_{sg} , was set a posteriori to give a maximum model output seagrass density of 3,000 vegetative shoots m^{-2} with $S = 0$ in 1 m of water with no waves present. This maximum shoot density was based upon our observations of *Ruppia* beds in the mesohaline Bay which sometimes achieve, but rarely exceed, 3,000 shoots m^{-2} . We derived an a_{sg} value of 0.000985 $m \text{ shoot}^{-1}$ for 0.15 m vegetative seagrasses and 0.01465 $m \text{ shoot}^{-1}$ for the 1 m tall reproductive plants. In order to validate these parameters, we calculated that a canopy of 3,000 shoots m^{-2} , has a_{sg} values of 3 and 44 m^{-1} for vegetative and reproductive shoots, respectively. This is broadly comparable to the a_{sg} value of 32.32 m^{-1} recorded by Enriquez et al. (2002) for a dense *Thalassia testudinum* bed.

The erosion rate constant, M , was originally tak-

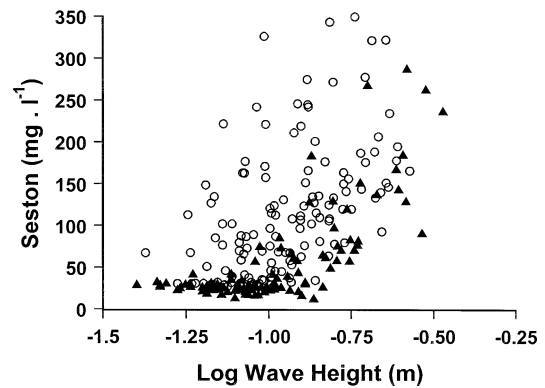


Fig. 2. Measured seston concentrations ($mg \text{ l}^{-1}$) in a *Ruppia maritima* bed at Duck Point Cove as a function of wave height (m) in June (\circ), when the plants were reproductive and the elongated shoots occupied the entire water column, and in October (\blacktriangle) when the plants were vegetative and shoots occupied only a small fraction of the water column.

en from Sanford and Chang (1997; their Table 1). Their coefficient produced seston concentrations in our model that were too high compared to field studies and it was reduced by half to give more reasonable concentrations in the model. An adjustment of this magnitude is not unreasonable given the large uncertainty in these coefficients (Sanford personal communication).

The critical seagrass shoot density required for wave damping to occur (D_{crit}) was set based upon our field observations (Koch unpublished data) that, when shoot densities were less than 1,000 shoots m^{-2} , *R. maritima* has little or no effect upon waves compared to unvegetated control areas regardless of water depth. Bivalve clearance rates, C_b , were set at two different levels representing particle clearance rate by hard clams (0.5 $l \text{ h}^{-1} \text{ g}^{-1}$) and by eastern oysters (6.0 $l \text{ h}^{-1} \text{ g}^{-1}$). These were an average of our measured values for each species at 20°C and 25°C (Table 1). We modeled a range of different bivalve biomasses (B_b) for both species in order to explore the effect of changing bivalve abundance, although bivalves were always assumed to be uniformly distributed throughout the modeled domain.

Results

SEAGRASS PROCESSES

Seston concentrations in the seagrass bed at Duck Point Cove were a function of wave height (Fig. 2), with waves as small as 10 cm capable of resuspending sediment. Plant characteristics also affected seston concentration (Figs. 2 and 3), with higher levels (ANOVA, $F = 38.1$, $p < 0.0001$) and more scatter in the seston concentrations in June when plants were in the tall reproductive form than in October when they were in the shorter veg-

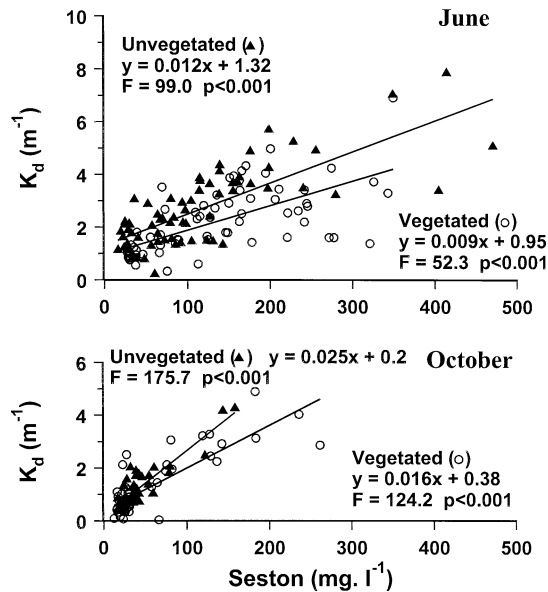


Fig. 3. Light attenuation coefficients (K_d) as a function of seston concentration (mg l^{-1}) at locations with (○) and without (▲) *Ruppia maritima* at Duck Point Cove. Upper panel is for June when the plants were reproductive and the elongated shoots occupied the entire water column. Lower panel is for October when the plants were vegetative and shoots occupied only a small fraction of the water column. The slope and F value for the best fit linear regression equations are annotated by each data set. Note: when the shoots were vegetative (October) no major resuspension events occurred; the maximum seston concentrations observed were lower than the time the shoots were reproductive (June).

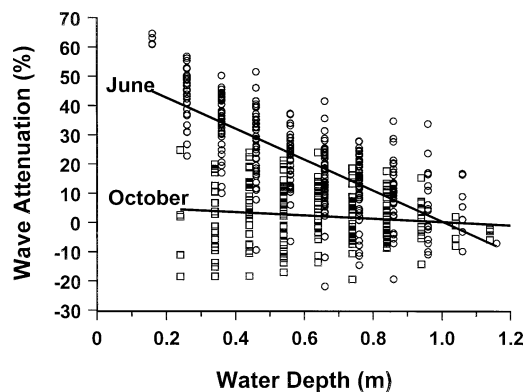


Fig. 4. Percent wave attenuation as a function of water depth (m) in a *Ruppia maritima* bed in June (○) when the plants were reproductive and the elongated shoots occupied the entire water column, and October (□) when the plants were vegetative and shoot height was short and occupied only a small fraction of the water column. The equations for the best fit linear regression line were $y = -53.14x + 55.61$ ($F = 384.3$, $p < 0.001$) and $y = -6.03x + 6.05$ ($F = 3.94$, $p < 0.05$) for June and October, respectively. Note: water depths for June were increased by 0.04 m and those for October were decreased by 0.04 m in order to allow both data sets to be clearly plotted on the same graph.

etative form. There was not a significant difference in seston concentration between vegetated and unvegetated areas (ANOVA, $F = 0.07$, $p > 0.05$ in June; $F = 1.43$, $p > 0.05$ in October).

The critical bottom shear stress ($\tau_c = 1.4 \text{ cm s}^{-1} = 0.196 \text{ Pa}$) did not differ for sediments collected in the vegetated and the unvegetated sites. Wave attenuation in the vegetated area was strongly dependent on water depth and the characteristics of the seagrass bed (Fig. 4). During high tide, wave attenuation (expressed as a percentage of the wave height in the unvegetated area) was low; at low tide, wave attenuation was high. In June when plants were reproductive and occupied the entire water column, wave attenuation was higher than in October when the vegetation was short and dense (Fig. 4). A maximum wave attenuation of 50% was observed when the plants were occupying the entire water column. Wave attenuation only started to be observed when the shoot density (short vegetative shoots) reached $1,000 \text{ shoots m}^{-2}$ (Koch unpublished data).

LABORATORY STUDIES OF THE INFLUENCE OF BIVALVES ON TURBIDITY

Feeding activity by eastern oysters and hard clams increased light penetration through the water column. On a weight-specific basis, oysters increased light penetration to a much greater extent than clams with larger values for change in K_d ($24 \text{ h}^{-1} \text{ g}^{-1}$), indicating a greater reduction in suspended particle load (Table 1). For oysters there was an extremely pronounced temperature effect, with lowest changes in K_d being recorded at 15°C and greatest change recorded at 25°C . In hard clams, temperature had a less pronounced influence, with feeding being similar at 20°C and 25°C . Particle clearance rates followed the same general pattern as the data for changes in K_d (Table 1). In order to parameterize the model we calculated an average clearance rate of $0.5 \text{ l h}^{-1} \text{ g}^{-1}$ for hard clams and $6.4 \text{ l h}^{-1} \text{ g}^{-1}$ for eastern oysters. These were an average of our measured values for each species at 20°C and 25°C (Table 1) and reflect average bivalve feeding activity over the seagrass growing season. Note that for eastern oysters the value of $0.32 \text{ l h}^{-1} \text{ g}^{-1}$ measured at 20°C was excluded from calculating this average because it was inexplicably ten fold lower than the two other values measured for oysters under the same conditions.

MODELING

We modeled the influence of different wave heights (i.e., sediment resuspension) on the depth to which seagrasses might grow under three scenarios: when there was no wave attenuation by sea-

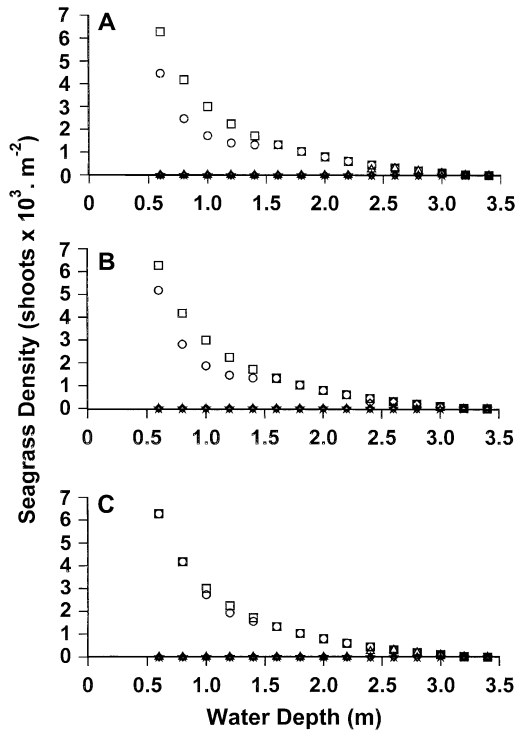


Fig. 5. Model predictions showing the self-stabilizing effect of *Ruppia maritima* when subject to different wave heights (0 m = \square , 0.1 m = \circ , 0.2 m = \triangle , 0.3 m = \star , and 0.4 m = \diamond). The x-axis represents water column depth (m) increasing with distance from shore, and the y-axis represents seagrass shoot density (shoots $\times 10^3 \text{ m}^{-2}$). Three scenarios are presented: A) no wave attenuation by seagrasses, B) reduced wave attenuation due to short vegetative shoots, and C) maximum wave attenuation due to long reproductive shoots.

grasses (i.e., when shoot density $< 1,000 \text{ shoots m}^{-2}$ or canopy height $\ll \ll$ water height); when wave attenuation was relatively low (i.e., vegetative shoots occupied only a small fraction of the water column); and when wave attenuation was at its maximum (i.e., long reproductive shoots occupied the entire water column). The model predicted that when waves were $\geq 0.2 \text{ m}$ (note that sediment resuspension started when waves $\geq 0.1 \text{ m}$) seagrass growth was completely precluded at all water depths due to sediment resuspension and light attenuation under all three scenarios (Fig. 5). When seagrasses exerted no self-stabilizing effects, and there was no wave action, seagrasses were predicted to start to grow in depths shallower than $\sim 2.5 \text{ m}$. Even with wave heights of 0.1 m, light levels in these shallow waters were still adequate for seagrasses to reach intermediate shoot densities. The short (15 cm) vegetative shoots had little influence on wave attenuation, resulting in only a minor increase in the depth to which seagrasses could grow compared to the scenario with no self-stabilization. When tall reproductive shoots were present and

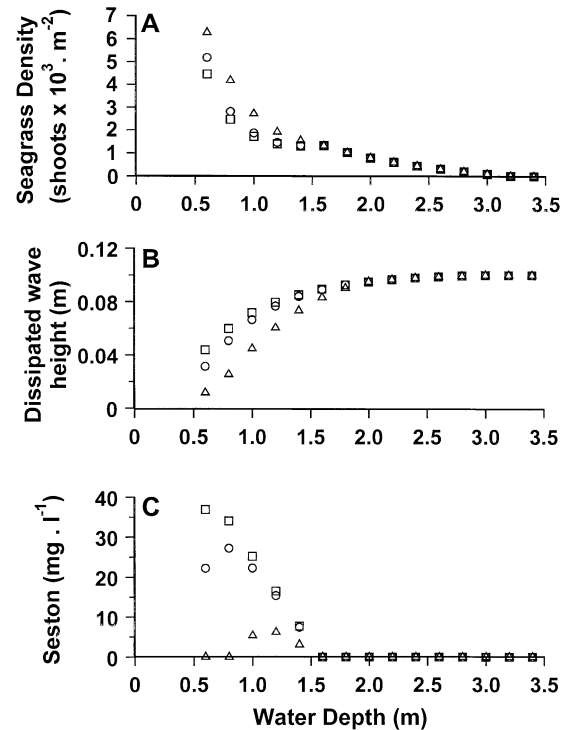


Fig. 6. Model predictions of the effects of wave damping associated with *Ruppia maritima* (no plants = \square , 15 cm high vegetative shoots = \circ , and reproductive shoots that reach the water surface = \triangle) exposed to 0.1 m waves on shoot density (A), wave height (B), and sediment resuspension (C) from nearshore to offshore (3.5 m water depth).

occupied the entire water column the wave attenuation effect was quite pronounced. For example, a comparison of the 0.0 and 0.1 m wave height scenarios (Fig. 5) indicated that the shoot density was reduced nearshore even by relatively small 0.1 m waves when the plants only occupied a small fraction of the water column. Waves of the same height had little influence when reproductive shoots were present with seagrasses predicted to attain the same shoot density as in the no-wave scenario.

In order to explore the underlying influences that seagrasses have on physical and geological processes we modeled the influence of shoot height and predicted shoot densities on wave attenuation and seston concentrations when exposed to 0.1 m waves (Fig. 6). As predicted the tall reproductive shoots attenuated waves more quickly and, consequently had a much more pronounced effect on seston concentrations nearshore than when the seagrass shoots were in the short vegetative phase.

Particle filtration by hard clams had very little influence on predicted seagrass distributions, even at simulated high abundances, whereas the effect

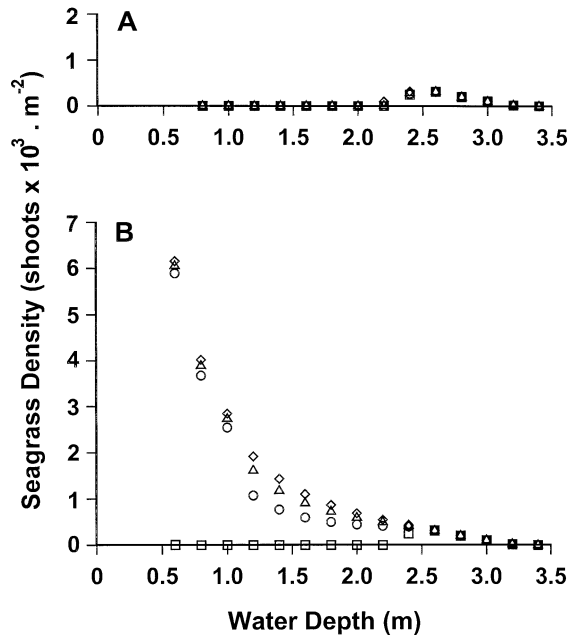


Fig. 7. Predicted effects of A) hard clams and B) eastern oysters at varying population biomasses ($0 = \square$, $25 = \circ$, $50 = \triangle$, and $100 = \diamond$ g dry tissue wt m^{-2}) on seagrass shoot density (shoots $\times 10^3 m^{-2}$) assuming a constant wave height of 0.1 m. Note that no wave-induced resuspension occurred in areas with depths >2 m, so seagrass shoot density was predicted to increase at these depths.

of eastern oysters was substantial over a range of abundances (Fig. 7). This result stems from the fact that oysters had an order of magnitude higher filtration rate than clams (6.4 versus $0.5 l h^{-1} g^{-1}$) causing seston concentrations to decline more substantially, and leading to greater water clarity. We used a constant wave height of 0.1 m in these simulations and assumed that no wave-induced sediment resuspension occurred in areas with water depths >2 m. Seagrass shoot density was predicted to increase slightly at these depths because of reduced turbidities, even in the simulations with no oyster biomass and in all simulations with hard clams. The effect of oyster filtration was so pronounced that oysters could substantially mitigate the effects of wave-induced sediment resuspension (Fig. 8). Even at modest abundances ($25 g m^{-2}$), eastern oysters facilitated the growth of seagrasses inshore, and at high oyster abundances ($75 g m^{-2}$) seagrasses reached high shoot densities nearshore, even when subjected to 0.4 m waves. In the absence of oysters, these high wave conditions had been classified as unsuitable for seagrass growth (Fig. 5).

Discussion

The reduction in turbidity that allows sufficient light to sustain seagrass growth can be obtained

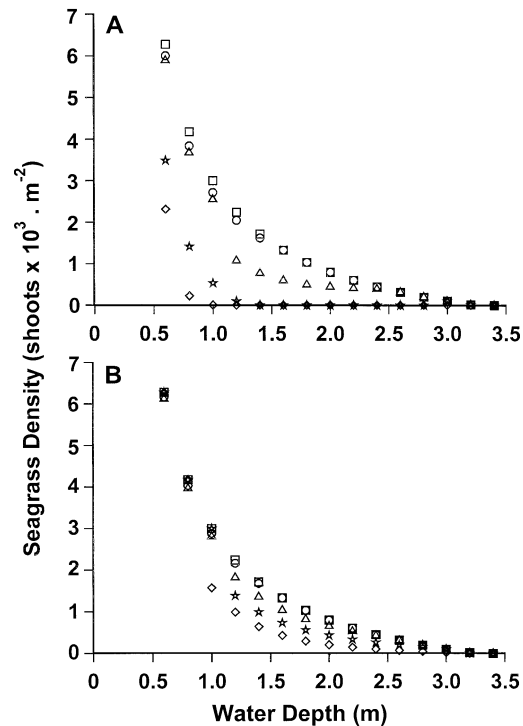


Fig. 8. Model predictions showing how filtration by eastern oysters associated with two different biomass levels A) 25 and B) $75 g$ dry tissue wt m^{-2} influences seagrass shoot density (shoots $\times 10^3 m^{-2}$) over a range of wave heights ($0 m = \square$, $0.1 m = \circ$, $0.2 m = \triangle$, $0.3 m = \star$, and $0.4 m = \diamond$).

either by an increase in the deposition of suspended particles (Moore et al. 1994) or a decrease in the resuspension of particles (Hemminga and Duarte 2000). Both processes are attained via a reduction in hydrodynamic forces in seagrass-colonized areas but a minimum seagrass shoot density seems to be necessary in order to attenuate waves to the point that there is an appreciable reduction in resuspension. At our study site (1 m deep), even waves as small as 10 cm caused sediment resuspension. No appreciable wave attenuation was observed until the density of *R. maritima* reached $1,000$ shoots m^{-2} (Koch unpublished data). At shoot densities less than this critical shoot density, sediment resuspension did not differ between the vegetated and unvegetated areas (i.e., there was no positive feedback between the plants and their environment). Once the seagrass bed reached densities above the critical shoot density, wave attenuation became evident, especially during storm events.

The fraction of the water column occupied by the seagrass canopy has a major impact on wave attenuation (Fonseca and Cahalan 1992). As some seagrasses, such as *Zostera marina* and *R. maritima*, tend to develop long reproductive shoots that oc-

copy the entire water column, we expected that wave attenuation and seston concentration would co-vary over the year. While we found that wave attenuation followed the expected pattern (Fig. 4; higher when plants were reproductive than when they were vegetative), seston concentrations did not conform to the predicted pattern. In October, when the seagrasses at our study site were in their vegetative state (short, occupying only a small fraction of the water column), seston concentrations were relatively low until the waves reached heights >10 cm (Fig. 2). Above that threshold, seston concentrations due to resuspension tended to increase with wave height. In June when the plants were reproductive and occupied the entire water column, seston concentrations were unexpectedly not a function of wave height and reached relatively high levels even when wave heights were below the critical resuspension level (Fig. 2). We anticipated that under these conditions, seston concentrations would be significantly reduced as observed by Ward et al. (1984) and Granata et al. (2001). We believe that our observation of high and variable seston concentrations when the plants were reproductive was a result of the dislodgement of particles that had settled on the plant surface during quiescent conditions followed by resuspension when exposed to even small waves or water currents. When waves propagate through a seagrass bed they cause sediment resuspension when the waves touch the bottom (Brown et al. 1989), but particles higher in the water column, such as those deposited on seagrass leaves, apparently responded to the wave effect much earlier than particles on the sediment surface. These results suggest that studies of sediment budgets in seagrass beds need to consider particles deposited on the leaves.

For all temperatures tested, changes in the light attenuation coefficient (K_d) and bivalve particle clearance rates (PCR), calculated from the number of particles filtered from suspension, were at least an order of magnitude greater for eastern oysters than for hard clams (Table 1). The eastern oyster is one of the most active and highly selective of all bivalve suspension feeders with feeding activity being minimal at temperatures <10°C, but this gradually increases rapidly to a maximum at temperatures >25°C (for review see Newell and Langdon 1996). Hard clams are less sensitive to environmental temperatures than oysters, with clearance rates showing little change between 10°C and 25°C (Grizzle et al. 2001). Eastern oysters maintain high feeding activity at even high particle loads of 25 mg l⁻¹, although at these loads most of the filtered material is not ingested but is rejected as pseudofeces (Newell and Langdon 1996). In response to increasing seston concentrations other suspension

feeding bivalves, such as hard clams, mainly regulate their ingestion rates by reducing clearance rates and not so much by rejecting excess particles as pseudofeces (Hawkins et al. 1998; Grizzle et al. 2001). When assessing the ecosystem effects of bivalve populations, it must be remembered that the species of bivalves that can exert the greatest influence on water clarity are those, such as eastern oysters, that maintain high clearance rates even under turbid conditions. The prevailing water temperature must also be considered as the low feeding rates of eastern oysters at temperatures <15°C mean that in winter and early spring they will not appreciably reduce turbidity.

The model we developed indicated that there was a positive feedback effect of seagrass wave attenuation, and hence reduced sediment resuspension, on seagrass shoot density. With the model parameterized to represent *R. maritima* this effect was significant only when long reproductive shoots were present, and even then only for relatively small, low energy waves (≤ 0.1 m). At higher wave heights, damping by the seagrasses had no effect on sediment resuspension. It appears that seagrasses can have a self-stabilizing effect, but this may be easily overridden by other factors that increase turbidity, such as nutrient enrichment enhancing phytoplankton biomass or periods of increased storminess. It is also possible that the dislodgement of particles deposited on the plant surface led to this result.

The effect of bivalve filtration on seagrass distributions can be quite profound, but the effect was pronounced only with eastern oysters because of their comparatively high clearance rates. Hard clams have relatively little impact on seagrass shoot densities because they do not filter sufficient water volume to increase water clarity appreciably. Our model results support the idea that loss of local eastern oyster filtration effects (i.e., decimation of oyster reefs in the vicinity of seagrass habitats) could, potentially, have a strong negative impact on seagrass populations. These results also suggest that coordinating oyster and seagrass restoration efforts could facilitate recovery of seagrasses in more energetic environments. We caution that the oyster distributions in the model were assumed to be uniform throughout the modeled spatial domain. This is not realistic because eastern oysters are usually aggregated into reefs often found in slightly deeper waters offshore from the shallow areas colonized by seagrass meadows and the filtration effect would usually be focused outside of the seagrass beds. These simulations are more realistic for *M. mercenaria*, which often grows within and around seagrass beds (Peterson 1986).

The oyster abundances of 25–75 g dry tissue m⁻²

used in our simulations are much greater than present day abundances in Chesapeake Bay but smaller than historical abundances. The total standing stock of oysters (>7.6 cm shell height and 1 g dry tissue weight) in Maryland's portion of Chesapeake Bay in 2002 was estimated to be 342.3×10^6 g dry tissue weight (Jordan personal communication). Assuming that these oysters are uniformly distributed over the 800 km² of oyster habitat in Maryland (Smith et al. 2001), oysters are currently at a population density of 0.43 oysters m⁻². Newell (1988) estimated 1988 oyster stocks to be 1% of historical densities present in Chesapeake Bay prior to commercial exploitation in the 19th century. This suggests that there were 43 oysters m⁻² on pre-exploitation oyster reefs, although even these abundances are well below those actually observed in unexploited oyster reefs. For example, Dame (1976) reported that intertidal reefs in North Inlet, South Carolina, had an oyster biomass of between 300 to 500 g dry tissue m⁻². Our modeled oyster abundances are also below abundances currently being attained by Maryland Oyster Recovery Partnership as part of ongoing intensive oyster restoration activities in many of the tributaries in the middle and upper Chesapeake Bay. Although such restoration activities are relatively small in areal extent (1,000–4,000 m²), oysters in areas of low disease prevalence have high survival and growth, allowing oyster densities in excess of 150 oysters > 7 cm shell height m⁻² (quantitative data on these eastern oyster restoration sites are available at www.life.umd.edu/biology/paynterlab).

One important caveat is that our model assumes that once seston particles are filtered by bivalves the particles are permanently removed from the water column. In situations where waves reach the sediment surface or there are strong bottom water currents that is not a valid assumption. Under such circumstances the friction velocity (u_*), which is a function of current velocity and bed roughness, can be above the critical velocity required to suspend particles of that particular mass. The feces of bivalves are tightly consolidated into mucus-bound pellets and their pseudofeces are more loosely bound by mucus (Newell and Langdon 1996). In locations with sufficient physical mixing these pellets can become disaggregated into smaller particles that will sink more slowly and be resuspended at lower friction velocities. Where bottom friction velocity is below the critical erosion velocity, fecal and pseudofecal material does undergo a consolidation process and become incorporated into the sediments (Widdows et al. 1998). Once consolidated, a much greater bottom shear stress is required to resuspend the cohesive material (Sanford and Chang 1997). Despite the clearly recognized im-

portance of bivalve biodeposition in benthic-pelagic coupling, exactly how much of the material is transferred to the sediment surface, how much is resuspended, and how much becomes incorporated in the surficial sediment remains poorly characterized. Research is required to quantify fecal and pseudofecal pellet sinking rates and physical conditions leading to their resuspension in order to more accurately model the role of bivalves in reducing turbidity in shallow water systems.

We developed our model in order to explore some of the simpler effects of different bivalve abundances and filtration rates on water clarity and seagrass density. The model can also be used to determine how different levels of wave height might alter the turbidity and light available for seagrass growth. In ongoing modeling studies we are specifying a more realistic distribution of eastern oyster biomass in reefs offshore from the seagrass meadows. These future studies will also include consideration of the potential wave damping effects of the oyster reef structure, in addition to the filtration capacity of the oysters themselves. Oyster reefs can act as natural breakwaters that substantially reduce wave energy, sediment resuspension, and shoreline erosion (McCormick-Ray 1998). Ultimately we intend to develop a spatially explicit version of this model with a sediment (erosion, transport, and deposition) term that can be used to help design oyster and seagrass restoration projects in a manner that provides synergistic benefits.

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SOURCES OF UNPUBLISHED MATERIALS

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