

Modeling the Effects of Oyster Reefs and Breakwaters on Seagrass Growth

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Abstract Seagrass beds have declined in Chesapeake Bay, USA as well as worldwide over the past century. Increased seston concentrations, which decrease light penetration, are likely one of the main causes of the decline in Chesapeake Bay. It has been hypothesized that dense populations of suspension-feeding bivalves, such as eastern oysters (*Crassostrea virginica*), may filter sufficient seston from the water to reduce light attenuation and enhance seagrass growth. Furthermore, eastern oyster populations can form large three-dimensional reef-like structures that may act like breakwaters by attenuating waves, thus decreasing sediment resuspension. We developed a quasi-three-dimensional Seagrass-Waves-Oysters-Light-Seston (SWOLS) model to investigate whether oyster reefs and breakwaters could improve seagrass growth by reducing seston concentrations. Seagrass growth potential (SGP), a parameter controlled by resuspension-induced turbidity, was calculated in simulations in which wave height, oyster abundance, and reef/breakwater configuration were varied. Wave height was the dominant factor influencing SGP, with higher waves increasing sediment resuspension and decreasing SGP. Submerged breakwaters parallel with the shoreline improved SGP in the presence of 0.2 and 0.4 m waves when sediment resuspension was dominated by wave action, while submerged groins perpendicular to the shoreline improved SGP under lower wave heights (0.05 and 0.1 m)

when resuspension was dominated by along-shore tidal currents. Oyster-feeding activity did not affect SGP, due to the oysters' distance from the seagrass bed and reduced oyster filtration rates under either low or high sediment concentrations. Although the current implementation of the SWOLS model has simplified geometry, the model does demonstrate that the interaction between oyster filtration and along-shore circulation, and between man-made structures and wave heights, should be considered when managing seagrass habitats, planning seagrass restoration projects, and choosing the most suitable methods to protect shorelines from erosion.

Keywords Seagrass · Oyster filtration · Suspended sediment · Waves · Nearshore processes · Modeling

Introduction

Seagrasses provide important ecosystem services to coastal marine systems. They influence their environments through wave attenuation, the stabilization of sediments, increased settling of seston (suspended particulate matter), and nutrient cycling (Ward et al. 1984; Rybicki et al. 1997). Seagrasses provide food for waterfowl (Lubbers et al. 1990) and nursery habitat for many organisms, including juvenile blue crabs (*Callinectes sapidus*; Orth and van Montfrans 1987). Seagrasses worldwide have declined over the past half-century (Short and Wyllie-Echeverria 1996; Green and Short 2003). Abundance of submersed aquatic vegetation from freshwater to marine areas of Chesapeake Bay, USA, believed to have once been over 200,000 ha, decreased catastrophically in the 1960s and 1970s (Orth and Moore 1983) to a low of 16,000 ha in 1984 (Gallegos 2001). There are many factors that limit seagrass distribution, including

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dislodgement by waves, desiccation above the low tide line, inability to grow in sediment with high organic content, and light blockage by epiphytes growing on the leaves (Barko and Smart 1983; Idestam-Almquist and Kautsky 1995; Jones et al. 2000; Koch 2001). Light attenuation from seston, however, is thought to be the most important factor limiting seagrass growth in Chesapeake Bay (Kemp et al. 1983; Dennison et al. 1993; Koch 2001), with impairment of survival at seston concentrations higher than $\sim 15 \text{ mg l}^{-1}$ (Batiuk et al. 1992).

Seston is composed of inorganic particles (e.g., clay particles) and organic material, such as phytoplankton. Phytoplankton biomass is a function of inorganic nutrient concentrations and seasonal factors such as light level and grazer activity (Lalli and Parsons 1997). Suspended sediments may come from land runoff or shore erosion, but in shallow waters much of the suspended sediment in the water column comes from the resuspension of bottom sediment (Langland and Cronin 2003).

Due to the need for adequate irradiance to support photosynthesis, seagrass beds are confined to shallow waters where their survival within the intertidal zone is limited by tolerance of desiccation (Koch 2001) and/or wave exposure (Koch et al. 2006). Wave motion tends to be highest in these shallow waters where, in combination with tidal currents, water movement imposes a shear stress on bottom sediments. If bottom shear stress exceeds a critical value (dependent on sediment grain size), sediment will be resuspended, increasing turbidity and light attenuation (Wright 1995). The water depth to which seagrasses can colonize is determined by the light intensity at the sediment surface (Duarte 1991) and the continuous shifting of sediment particles when waves reach the bottom (Koch et al. 2006).

Seagrass meadows can reduce suspended sediment concentrations; friction from seagrass leaves reduces current velocity and attenuates waves, thus reducing the stress on bottom sediments, decreasing resuspension, and promoting sediment settling within the seagrass bed (Fonseca and Fisher 1986; Fonseca and Cahalan 1992; Rybicki et al. 1997). Seagrass beds may also increase particle settling shoreward of the bed (Chen et al. 2007). This baffling of wave energy contributes to the seagrass' ecological importance by enhancing recruitment of marine organisms (Eckman 1983; Peterson 1986).

Eastern oyster (*Crassostrea virginica*) populations may be a possible aid to seagrass growth and survival because oysters can directly and indirectly reduce seston concentrations. Oysters are suspension feeders, actively filtering seston particles from the water column (reviewed by Newell and Langdon 1996) and rejecting the particles they cannot use as feces or pseudofeces. These mucus-bound aggregates settle around 40 times faster than non-aggregate

particles, which means that the bivalves can exert a direct effect on seston concentrations (Newell et al. 2002). The structure of the oyster reef can indirectly affect seston concentrations by attenuating wave energy (Dame et al. 1984), thus increasing particle settling and reducing resuspension. Man-made breakwaters similarly serve to attenuate wave energy and enhance particle settlement (Zyserman and Johnson 2002).

Our objectives were to explore how the interaction of waves, tides, breakwaters, oyster reefs, and oyster filtration could influence sediment resuspension and growth potential of the seagrass *Ruppia maritima*. We applied a numerical approach that built upon two previous modeling studies. In the first study, which used a one-dimensional model where oysters were assumed to be co-located with a *R. maritima* bed, oyster filtration caused significant reductions in wave-resuspended sediment (Newell and Koch 2004). In the second study, which used a quasi-three-dimensional model, a *R. maritima* bed influenced sediment resuspension and deposition within and behind the seagrass bed (Chen et al. 2007), indicating that spatial processes could influence the effect of wave attenuation on sediment resuspension. Based on these two studies, we hypothesized that the influence of oyster filtration on seagrass growth would be affected by the spatial separation of oysters and seagrass beds and that different reef or submerged breakwater configurations would have varying effects on sediment concentrations within seagrass beds, thereby influencing seagrass growth potential.

Methods

We developed the Seagrass-Waves-Oysters-Light-Seston (SWOLS) model and applied it in an idealized model domain. The SWOLS model is a coupled biological-physical model that integrates the nearshore hydrodynamic and sediment transport model package Nearshore Community Model (NearCoM) with biological components (Newell and Koch 2004). The NearCoM program runs the spectral wave model REFDIF-S (Kaihatu et al. 2002; Kirby et al. 2005), the nearshore circulation model SHORECIRC (Shi et al. 2003, 2007; Svendsen et al. 2004), and the sediment transport model SED (Chen et al. 2007). Waves and tidal currents (predicted in REFDIF-S and SHORECIRC) influence sediment settling rates and bottom shear stress, which affect suspended sediment concentrations, light attenuation, and growth potential of the seagrass *R. maritima* (predicted in SED). In turn, the seagrass bed slows near-bottom water currents and causes wave attenuation by increasing bottom friction. The program simulates an idealized mid-Chesapeake Bay, Maryland, USA near-shore region with a non-reproductive *R. maritima* bed,

waves, and along-shore tidal movement, and it allows inclusion of an oyster reef or submerged breakwater or groins. *R. maritima* was chosen because our SWOLS model builds on previous models (Newell and Koch 2004; Chen et al. 2007), which focused on *Ruppia* and also because an extensive data set for wave attenuation by this seagrass exists for Chesapeake Bay (Chen et al. 2007; Koch, unpublished data). Although the highest seagrass-induced wave attenuation was predicted in the summer (June/July) when this species has a greater canopy due to the presence of long reproductive shoots (Chen et al. 2007), we chose to simulate the shorter non-reproductive form as it represents the most common shoot form throughout the year.

The domain for the wave/circulation model was 720 m × 17,010 m, decreasing linearly in depth from 3.5 m near the channel boundary to 0.5 m at the shore (Fig. 1). The sediment model domain occupied a subset of this space (680 m × 11,010 m) to eliminate circulation boundary effects on the sediment transport model predictions. Suspended sediment concentrations were “looped” at the cross-shore boundaries; any suspended sediment that crossed one cross-shore boundary was brought back into the model domain at the other cross-shore boundary. Cross-

shore lengths of grids cells were 10 m; along-shore lengths were 30 m. Wave characteristics and tidal current velocities were parameterized to simulate conditions found in Chesapeake Bay (Lawrence P. Sanford, University of Maryland Center for Environmental Science, Horn Point Laboratory (UMCES HPL), pers. comm.). Wave frequency was fixed at 0.25 s^{-1} , and wave heights were set at 0.05, 0.1, 0.2, and 0.4 m. Wave angle was 5° from perpendicular to the shore. Tidal current boundary conditions that influence along-shore current velocities were adjusted to give maximum along-shore velocities between 35 and 40 cm s^{-1} . The optimum tidal current boundary conditions were determined by running a suite of model simulations and systematically changing boundary condition values until current speeds matched those reported for nearshore regions in Chesapeake Bay in unpublished data (Lawrence P. Sanford, UMCES HPL, pers. comm.).

The location and dimensions of the submerged breakwater and groins were selected to represent observed sizes of constructed breakwaters or restored oyster reefs, within the constraints of the model. This yielded an along-shore breakwater that was 780 m long and 40 m wide, with a height occupying 50% of the water column (1 m in height in a 2-m deep water column). The breakwater’s wave-facing slope was 20 m long in the cross-shore direction, and its shore-facing slope was 10 m. Cross-shore groins were placed to either side of the seagrass bed, starting at the shore edge of the model. The groins were 400 m long and 90 m wide and were spaced 1,620 m apart. The slope facing the seagrass bed was 30 m long in the along-shore direction, the tide-facing slope was 60 m, and the wave-facing end of the groin was 20 m. The groin height remained 50% of the height of the water column, increasing as depth increased (Fig. 1). Typical breakwaters in the Chesapeake region are 200–500 m long and 20–30 m wide, and typical groins are 50–100 m long and 10–20 m wide (Lawrence P. Sanford, UMCES HPL, pers. comm.). The breakwater and groins simulated in the SWOLS model were wider than these typical structures to avoid artifacts in the wave model which can be caused by steep changes in slope. The groin length was chosen to ensure that the structure was large enough to hold appropriate abundances of oysters at depths $>1.5 \text{ m}$ (where oysters are typically found in Maryland’s Chesapeake Bay). The breakwater length was set to be half that of the seagrass bed length to ensure that the influence of the breakwater would be detectable in model simulations.

Suspended sediment was modeled to identify how waves and circulation patterns influence sediment resuspension and deposition. The settling velocity of suspended sediment in the model was set to 0.3 mm s^{-1} , a value observed in Chesapeake Bay (Sanford et al. 2001). Suspended sediment was advected using the Lagrangian tracer routine with the QUICKEST numerical scheme (Ekebjaerg and Justesen 1991).

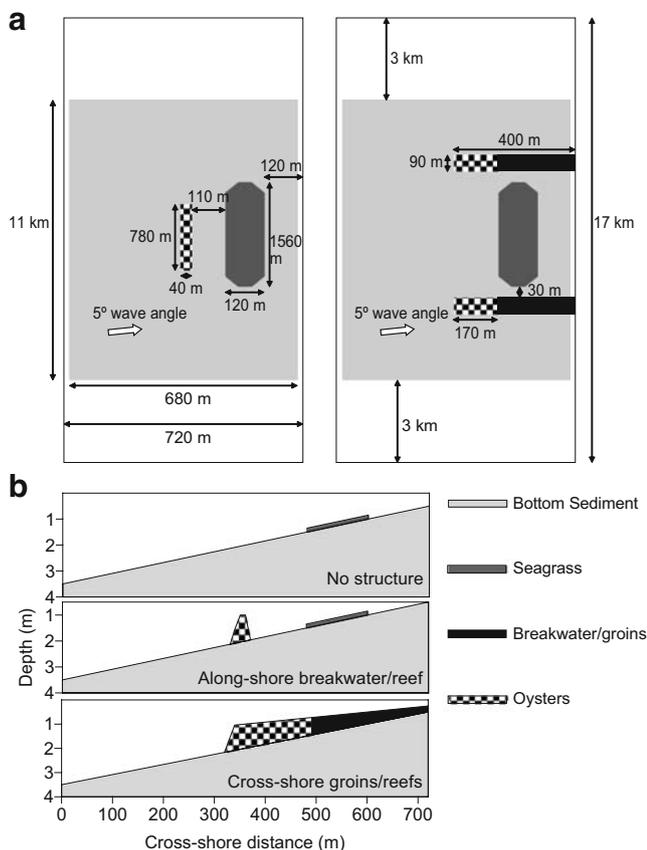


Fig. 1 Plan (a) and cross-sectional views (b) of the model domain with the location of the seagrass bed and along-shore (left, a) and cross-shore (right, a) reefs/breakwaters

The suspended sediment (S , kilograms) filtered by the oysters in each grid cell during each time step was calculated with the following equation:

$$S = p \times f \times B \times C \times dt$$

where p is the proportion of the maximum filtration rate depending on sediment concentration (Jordan 1987; Cerco and Noel 2005), f is the temperature-dependent oyster filtration rate (cubic meter kilogram oyster per second), B is the biomass of oysters (kilogram) in each grid cell, C is the suspended sediment concentration (before oyster filtration, in kilogram per cubic meter), and dt is the length of the sediment model time step (5 s). Oysters were assumed to have a 7.6-cm shell length. The model was run at a temperature of 28.5°C, so that $f=0.0028 \text{ m}^3 \text{ kg-oyster}^{-1} \text{ s}^{-1}$ and oysters were filtering at high summer-time rates (Newell and Koch 2004). The maximum filtration rate was chosen to allow the oysters to have the greatest possible effect on sediment concentrations in the model. Suspended sediment-dependent filtration rates were included using variable p . Oyster filtration was at its maximum rate ($p=1$) if sediment concentrations were between 5 and 35 mg l^{-1} . At concentrations under 5 mg l^{-1} , the filtration rate was 10% of maximum ($p=0.1$); between 35 and 100 mg l^{-1} , it was at 20% ($p=0.2$); and over 100 mg l^{-1} , it was assumed that oysters ceased filtering any sediment ($p=0$; Jordan 1987; Cerco and Noel 2005).

Oysters were arranged in either an along-shore or cross-shore configuration. In the along-shore configuration, the oysters covered the same area as the along-shore breakwater with an abundance of 100 oysters m^{-2} . In the cross-shore configuration, the oysters covered the same area as the deepest 170 m of the cross-shore groins, stretching from the deep end of the groins to a minimum depth of ~1.5 m (see Fig. 1). Oysters in the upper Chesapeake Bay would likely not survive in locations shallower than 1.5 m (which are depths at which seagrasses occur) due to exposure to freezing temperatures during aerial exposure in the winter (Shumway 1996). Oyster abundance in this case was 102 oysters m^{-2} so that the total number of oysters would be identical to the 3.12 million oysters in the along-shore configuration. This is equivalent to 10,400 bushels of whole live oysters; a bushel, the customary harvest unit (1 MD bushel $\equiv 0.046 \text{ m}^{-3}$), contains ~300 oysters of 7.6 cm shell length. Concentrations of erodible sediment were specified to be 3 kg m^{-2} throughout the sediment domain but were set to 0 on the oyster beds and breakwaters, since bottom sediment in nature is low on flourishing oyster reefs (Smith et al. 2005) and breakwaters. Oyster abundance and size were not changed in the model simulations that included oysters.

The modeled seagrass bed was 1,560 m long and octagonal in shape so that square corners would not create artifacts in current velocities and sediment transport

predictions. The seagrass bed was located between depths of 1.0 and 1.5 m (*R. maritima* is only found shallower than 1.5 m in Chesapeake Bay). The seagrass bed was placed toward the deep end of its range to avoid potential boundary effects closer to the shore. This resulted in the bed being 120 m in width, placed 120 m from the shore edge of the domain. The simulated seagrass represented the non-reproductive shoots of *R. maritima*, which were 0.15 m tall with densities of 1,270 shoots m^{-2} , reflecting densities observed in the field during the spring and shoot heights throughout most of the year (excluding summer flowering; Koch, unpublished data). Seagrass shoot height and density were not varied in the different model simulations. See Chen et al. (2007) for simulations with seasonal variation in *R. maritima* shoot height and density.

Seagrass growth potential was used to quantify seagrass habitat quality as affected by sediment resuspension. Seagrass growth potential (SGP, shoots per square meter per second) is a measure of the rate of change in shoot density (D , shoots per square meter), calculated as

$$\text{SGP} = u_m \left(1 - e^{-I_{\text{avg}}/I_k} \right) D - rD$$

where u_m (per second) is the maximum growth rate of the seagrass, I_{avg} is the average irradiance reaching the seagrass, I_k is the saturation irradiance for seagrass photosynthesis, and r (s^{-1}) represents losses due to respiration. The light availability term (I_{avg}) was determined by seston concentration, seagrass self-shading, and other light-absorbing substances assumed to be constant, as parameterized in Newell and Koch (2004).

A suite of simulations was conducted to investigate how wave height, reef configuration, and the presence/absence of oysters influenced seagrass habitat quality (Table 1). Base case simulations were run with only seagrass (“Seagrass” simulation) at the four wave heights (0.05, 0.1, 0.2, and 0.4 m). Simulations with the following configurations were also conducted at the four wave heights: “Along-shore breakwater”, “Cross-shore groins”, “Along-shore oyster bed” (with “bed” here implying no three-dimensional structure), “Cross-shore oyster beds”, “Along-shore oyster reef” (with “reef” here meaning that the simulation includes the breakwater structure), and “Cross-shore oyster reefs”. The only difference between the “Along-shore breakwater” and the “Along-shore oyster reef” setups, and between the “Cross-shore groins” and the “Cross-shore oyster reefs” setups, was the addition of oysters on the structure. This allowed direct assessment of the influence of oyster filtration on seagrass growth potential in the presence of breakwaters/groins. To determine the importance of the displacement of the oyster bed from the seagrass bed, two additional simulations were conducted using 0.1-m waves with an oyster bed of the

Table 1 Model simulations

Simulation	Breakwater/reef structure	Oyster configuration	Wave heights (m)
Seagrass	None	None	0.05, 0.1, 0.2, 0.4
Along-shore oyster bed	None	Along-shore	0.05, 0.1, 0.2, 0.4
Cross-shore oyster beds	None	Cross-shore	0.05, 0.1, 0.2, 0.4
Co-located oyster bed	None	Along-shore, in seagrass bed	0.1
Adjacent oyster bed	None	Along-shore, 10 m from seagrass	0.1
Along-shore breakwater	Along-shore	None	0.05, 0.1, 0.2, 0.4
Cross-shore groins	Cross-shore	None	0.05, 0.1, 0.2, 0.4
Along-shore oyster reef	Along-shore	Along-shore	0.05, 0.1, 0.2, 0.4
Cross-shore oyster reefs	Cross-shore	Cross-shore	0.05, 0.1, 0.2, 0.4

Model simulations were conducted with different breakwater/reef structures and oyster configurations, which consisted of either a single along-shore feature or two cross-shore features. For the breakwater/reef structure column, “None” indicates a smooth bottom except for seagrass. For the oyster configuration column, “None” indicates that no oysters were present. Each simulation was conducted with the wave heights indicated

same dimensions as the “Along-shore oyster bed”. In one, the oysters were placed in the center of the seagrass bed (“Co-located oyster bed”); in the other, the edge of the oyster bed was located 10 m from the edge of the seagrass bed (“Adjacent oyster bed”). All simulations had durations of 50 h, which included four tidal cycles and could represent a sustained wind-induced wave event. Model results were summarized as (1) seagrass growth potential averaged over the area of the seagrass bed and plotted against time, and (2) seagrass growth potential averaged over time and plotted at each grid point in the seagrass bed.

Statistical analyses were performed to determine if oyster beds, breakwaters, or oyster reefs resulted in a significant change in spatially averaged SGP (i.e., averaged over the whole seagrass bed for each time step) compared to the reference model configuration (“Seagrass”). Analysis of variance tests (ANOVAs) were conducted with SGP as the dependent variable. Spatially averaged SGP at 0.25-h intervals during the last two tidal cycles of each simulation were used to ensure initial conditions did not bias the analysis. In each ANOVA, the explanatory variable was classified as reference (“Seagrass”) or treatment (either “Along-shore oyster bed”, “Cross-shore oyster beds”, “Along-shore breakwater”, “Cross-shore groins”, “Along-shore oyster reef”, or “Cross-shore oyster reefs”). Non-parametric Kruskal–Wallis one-way ANOVAs were conducted (PROC NPAR1WAY, SAS v. 9.1) because several parametric repeated measures ANOVA models did not pass ANOVA model fit tests.

Results

Results of the numerical simulations indicated that wave height had the greatest effect, via sediment resuspension, on seagrass growth potential. Average SGP over the whole bed

was positive in all simulations with 0.05 m waves and negative in all simulations with 0.1, 0.2, and 0.4 m waves (see Fig. 2 for results from the “Seagrass” reference simulations). There was no large decrease in SGP when waves increased from 0.2 to 0.4 m, likely because high suspended sediment concentrations at 0.2 m had already reached the threshold at which seagrass growth was almost completely inhibited.

The along-shore breakwater had no significant effect on the spatially averaged SGP in conditions with 0.05 and 0.1 m waves when compared to the “Seagrass” base case simulation (Table 2, Figs. 3a, b). The time-averaged plots of the difference in SGP (i.e., SGP averaged over the entire simulation period for each individual grid point in the seagrass bed) show that in the lower wave simulations, the along-shore breakwaters resulted in increased SGP directly behind the breakwater but reduced SGP to either side of the breakwater (Fig. 4). In contrast, the along-shore breakwater had a significant, positive effect on SGP in simulations with

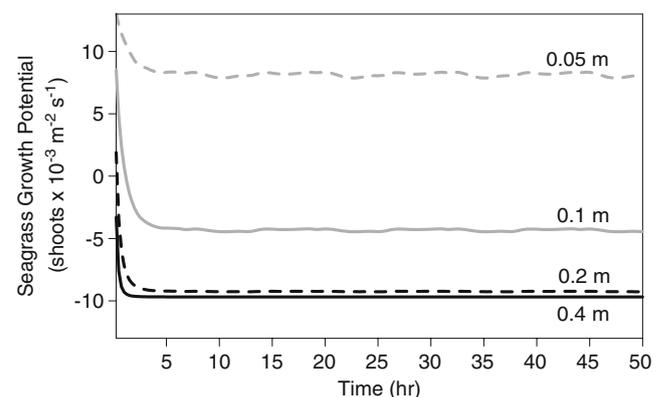


Fig. 2 Average seagrass growth potential for the entire bed over time at different wave heights (indicated near each line) for the “Seagrass” simulations (see Table 1) without oysters or breakwaters (i.e., only seagrass)

Table 2 Statistical analysis results

Wave height (m)	Oyster beds		Breakwaters		Oyster reefs	
	Along-shore	Cross-shore	Along-shore	Cross-shore	Along-shore	Cross-shore
0.05	0.00 (0.99)	0.01 (0.93)	2.49 (0.11)	15.61 (<0.0001)	2.49 (0.11)	15.63 (<0.0001)
0.1	0.00 (0.98)	0.02 (0.90)	3.51 (0.06)	23.10 (<0.0001)	3.51 (0.06)	23.58 (<0.0001)
0.2	0.00 (1.00)	0.01 (0.92)	22.49 (<0.0001)	1.13 (0.29)	22.49 (<0.0001)	0.88 (0.35)
0.4	0.00 (1.00)	0.00 (0.97)	149.25 (<0.0001)	108.57 (<0.0001)	149.25 (<0.0001)	109.49 (<0.0001)

Kruskal–Wallis one-way ANOVAs were conducted to determine if oyster beds, breakwaters, or oyster reefs resulted in a significant change in seagrass growth potential (SGP) when compared to the reference model configuration at different wave heights. The dependent variable was spatially averaged seagrass growth potential during the last two tidal cycles of each simulation. The explanatory variable was classified as reference (“Seagrass”) or treatment (either “Along-shore oyster bed”, “Cross-shore oyster beds”, “Along-shore breakwater”, “Cross-shore groins”, “Along-shore oyster reef”, or “Cross-shore oyster reefs”). Table entries include the χ^2 test statistic with the associated probability value in parentheses. Boldface indicates a significant difference in SGP between the reference and treatment simulations ($\alpha=0.05$)

0.2 and 0.4 m waves (Table 2, Figs. 3c, d and Fig. 4), with the effect most pronounced in the simulation with 0.4 m waves. In this simulation, the along-shore breakwater reduced wave heights by an average of 4% within the seagrass bed (in some regions of the bed reducing wave height by as much as 11%) compared to the simulation

without breakwaters. This resulted in a 0.3% increase in average SGP in this simulation compared to the reference case, which translates to an additional 2.5 shoots $m^{-2} day^{-1}$.

The “Cross-shore groins” significantly increased SGP relative to the “Seagrass” base case simulation under all wave conditions except 0.2 m waves (Table 2, Figs. 3 and 4). The greatest improvement in SGP occurred in the cross-shore groin simulation with 0.05 m waves, in which average SGP increased by 1.0% compared to the reference case (an additional 7.2 shoots $m^{-2} day^{-1}$). In the 0.05- and 0.1-m wave cases, the SGP difference between reference and cross-shore groin simulations (Fig. 3a, b) peaked just before maximum tidal current velocities, indicating that the cross-shore groins reduced sediment resuspension most when tidal current velocities were high. The effect of the tides on SGP fluctuations decreased as the wave height increased. This helps explain why the cross-shore groins, which shelter the seagrass from the along-shore tidal currents, were less effective in improving SGP in the higher wave cases (Fig. 4): waves dominated sediment resuspension in the higher wave cases, so the influence of the cross-shore groins on SGP was reduced.

The addition of oysters to the simulations had no significant effect on the seagrass growth potential (Table 2, Fig. 4); the effect of oyster reefs on SGP resulted from the physical structure of the reef, not the filtration by oysters. The largest difference caused by the addition of oysters was in the “Cross-shore oyster beds” simulation with 0.1 m waves, where SGP increased by a bed-wide average of 0.01%, the equivalent of 0.04 shoots $m^{-2} day^{-1}$ (Fig. 4). The lack of influence of the oysters in these simulations was caused by reductions in filtration rates associated with high sediment loads (Newell and Langdon 1996) and by tidal currents moving the filtered water away from the seagrass bed. In the 0.05-m wave height conditions, the concentration of suspended sediment was so low that the oysters were only filtering at 10% of their full capacity.

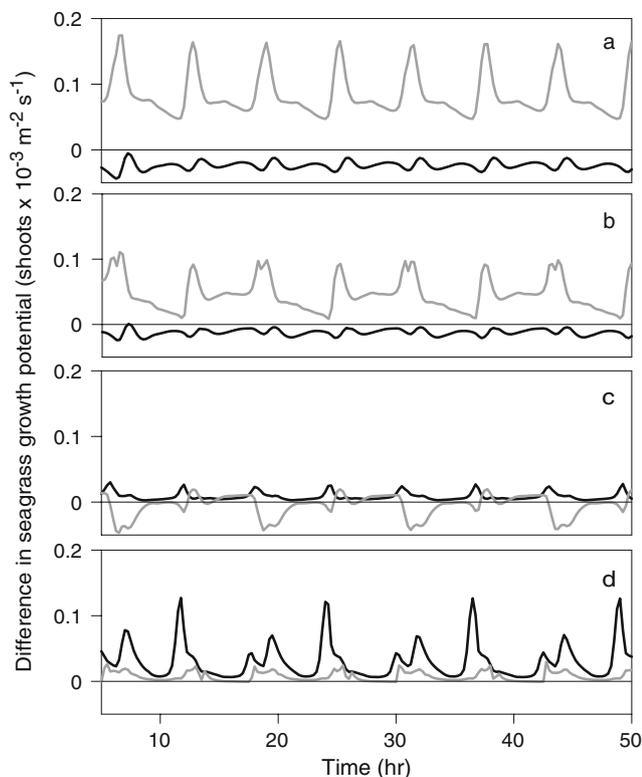
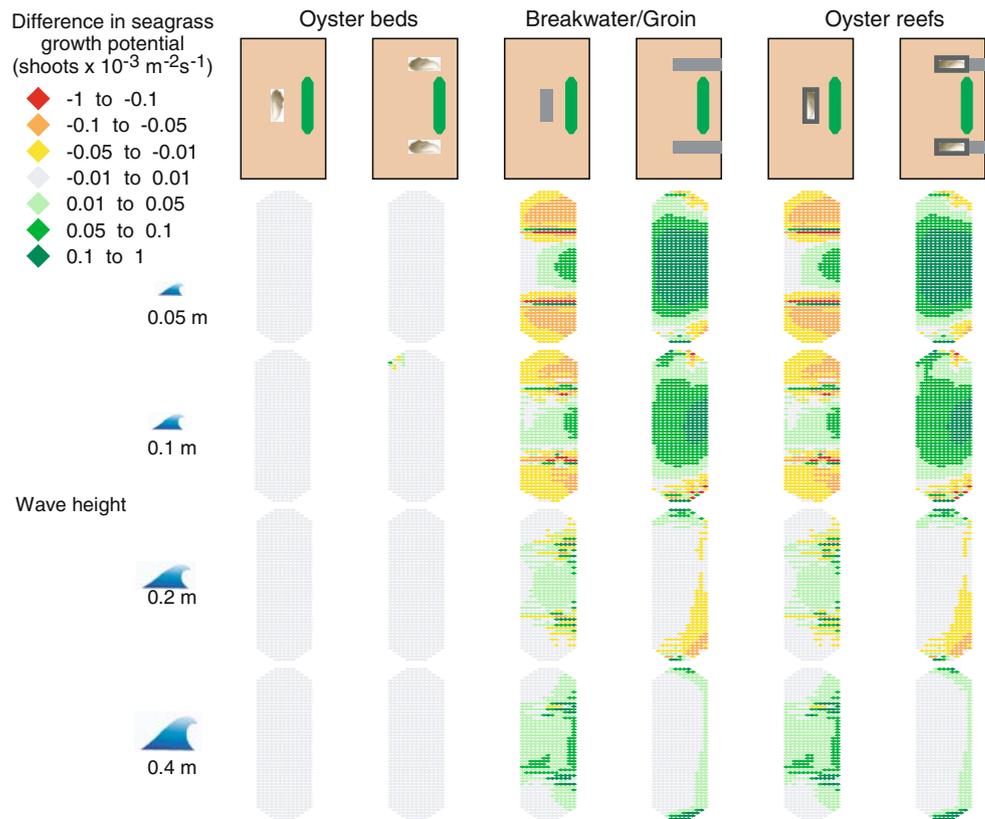


Fig. 3 Difference in seagrass growth potential between simulations with coastal structures and reference simulations with no structure. Seagrass growth potential was averaged over the entire seagrass bed for different wave heights: a 0.05 m, b 0.1 m, c 0.2 m, and d 0.4 m waves. Black lines indicate along-shore breakwater results minus reference (“Seagrass”) results. Gray lines indicate cross-shore groins results minus reference (“Seagrass”) results

Fig. 4 Difference in seagrass growth potential (SGP) for each simulation compared to the reference “Seagrass” simulation. The rows contain results of simulations with the same wave height. The *columns* contain results of simulations with the same model configuration. For each element in the matrix, SGP averaged over time at each grid point in the seagrass bed in the “Seagrass” reference simulation was subtracted from the equivalent averaged SGP value at each corresponding grid point in the specified simulation. Note that the color scale is not uniformly spaced



In the 0.2- and 0.4-m wave height cases, the suspended sediment concentrations were so high that the oysters were only filtering at 20% of their full capacity. The only simulations in which the oysters were filtering at full capacity were the 0.1-m wave height cases. In these simulations, we found that the oysters were reducing the suspended sediment concentrations over the oyster bed, but the plume of water with reduced sediment load was swept away by the tidal current in the along-shore direction, never passing over the seagrass bed (Fig. 5).

In an extreme scenario, when oysters were moved into the seagrass bed (“Co-located oyster bed” simulation), the average SGP increased by 24% (translating to an additional 89 shoots $\text{m}^{-2} \text{day}^{-1}$) compared to the “Seagrass” base case (Fig. 6). When oysters were 10 m from the seagrass bed (“Adjacent oyster bed” simulation), the average SGP was only 0.07% higher than the “Seagrass” base case (Fig. 6).

Discussion

Wave height was the dominant factor influencing SGP. Higher waves increased bottom sediment resuspension and thereby increased turbidity and, consequently, reduced light available to support seagrass growth. The model predicted that the cutoff between positive and negative seagrass growth occurred between 0.05 and 0.1 m wave heights in

conditions where maximum along-shore tidal currents were between 35 and 40 cm s^{-1} . The model may be overestimating the effect of waves on seagrasses, since based on the collected field data, the critical significant wave height threshold for seagrasses in the polyhaline region of the Bay has been estimated to be 0.3 m (Koch et al. 2008). The discrepancy is likely the result of the many complexities not included in the model, such as complicated shorelines and bathymetry, multiple sinking velocities of particles, and the organic content of the sediment. Although the model did not capture all of the complexities associated with the nearshore environment, it did allow assessment of the relative influence of oyster reefs and breakwater configurations on suspended sediment and SGP.

The influence of along-shore breakwaters and cross-shore groins on SGP differed and depended upon wave height. The cross-shore groins resulted in the greatest increase in SGP in the low (0.05 and 0.1 m) wave simulations, when along-shore tidal currents dominated sediment resuspension. Under higher wave conditions, waves (which were 5° from perpendicular to the shore) were the dominant factor in resuspending sediment. The along-shore breakwater provided better protection from waves under these conditions, reducing suspended sediment concentrations over the seagrass bed and increasing SGP. The ultimate effect of either structure at a specific site depends on the tidal and wave conditions over the course of

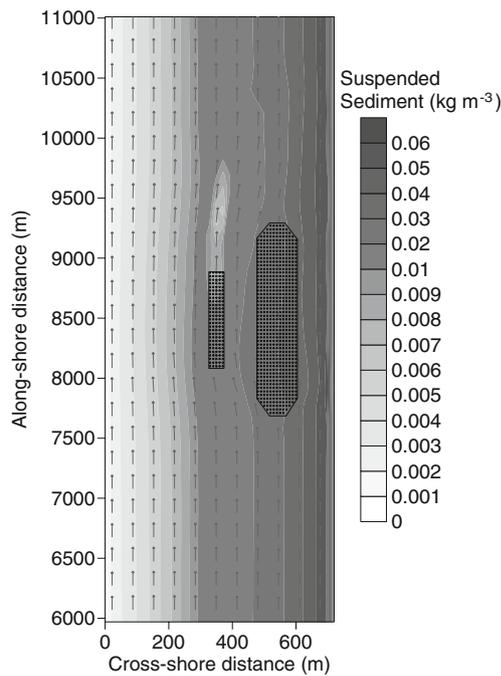


Fig. 5 Concentration of suspended sediment for the 0.1-m waves, along-shore oysters with no breakwater case (“Along-shore oyster bed”) at hour 21. The plume of water with reduced sediment caused by filtration in the oyster bed (rectangle) is swept in the along-shore direction by the tidal current, thus never passing over the seagrass bed (octagon)

the seagrass growing season. Therefore, model results suggest that it would be important to measure tidal current velocities and determine the wave climate in order to design an optimum breakwater configuration that would minimize sediment resuspension at a specific site. It should be noted that other detrimental effects of coastal structures need to be considered in the design of breakwaters. For example, the excessive accumulation of fine and organic particles shoreward of coastal structures (Martin et al. 2005) has the potential to be detrimental to benthic organisms, including seagrass, in some locations (Barko and Smart 1983, 1986; Koch 2001).

The lack of influence of oysters on SGP was largely due to the distance between the oysters and seagrasses and the advection of filtered water away from the seagrass bed. Only in the simulation in which the oysters and seagrass were co-located did the increase in water clarity associated with oyster filtration noticeably increase SGP. This is a situation that may be approximated in off-bottom aquaculture of oysters but, once again, other parameters need to be considered, such as the changes in sediment geochemistry associated with oyster aquaculture. Model results also suggest that because oyster filtration declines at high suspended sediment concentrations, their feeding activity may only influence nearshore water clarity in a narrow range of suspended sediment concentrations. Consequently,

oysters will have little effect in reducing turbidity during periods of high waves that cause sediment resuspension. It is important to note that we modeled oysters filtering suspended sediment and did not include organic particles such as phytoplankton. Phytoplankton can be an important component of the seston that does not settle as quickly as the suspended sediment modeled in these simulations (model settling velocity = 0.3 mm s^{-1}). In the SWOLS model, phytoplankton was included as a constant background concentration that affected light attenuation (Newell and Koch 2004), a reasonable assumption for simulations with a 50-h duration. It is possible that if phytoplankton were modeled as a dynamic variable that contributed to seston concentrations, the oysters would have had a more noticeable effect on seagrass growth, as they did in the Cerco and Noel (2007) model that included a dynamic phytoplankton component.

Spatial scale, resolution, and model parameterization were largely responsible for the discrepancy between our results and the results of previous model studies. Models developed by Newell and Koch (2004) and Cerco and Noel (2007) predicted that oysters would improve seagrass growth due to their ability to increase water clarity through filtration. In the Newell and Koch (2004) model, oysters were assumed to be co-located with seagrass and had a strong impact on seagrass growth. In comparison, in our study, when oysters or oyster reefs were displaced from the seagrass bed (as in nature), we found that they had almost no impact on SGP. Additionally, the oyster filtration rate in Newell and Koch (2004) did not vary in relation to the suspended sediment concentrations, whereas oyster filtration was reduced or eliminated at high or very low suspended sediment concentrations in our study. The Cerco and Noel (2007) model also grouped oysters and seagrasses

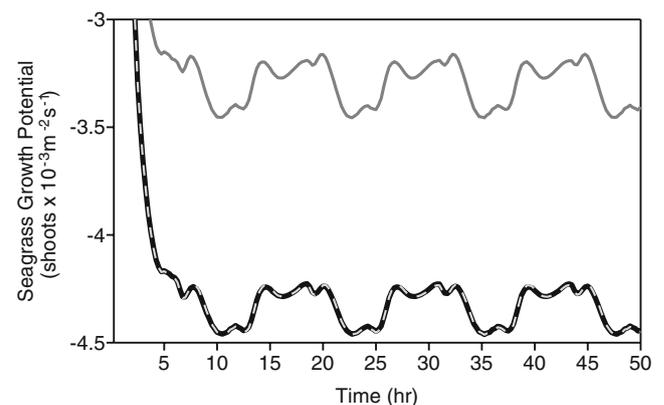


Fig. 6 Spatially averaged seagrass growth potential vs. time for conditions with 0.1 m waves and no oysters (“Seagrass” simulation, black line), oysters separated from seagrass bed by 10 m (“Adjacent oyster bed” simulation, light gray dashed line), or oysters in the center of the seagrass bed (“Co-located oyster bed” simulation, dark gray line). See Table 1 for information on simulation parameterization

in the same area and concluded that a tenfold increase in oysters in Chesapeake Bay above levels present in the 1990s would reduce phytoplankton concentrations, increase water clarity, and increase seagrass abundance in tributaries. Their three-dimensional model of the entire Chesapeake Bay was designed to assess Bay-wide conditions; it did not have high enough spatial resolution to separate the location of oysters and seagrass in the nearshore environment. We focused on a much smaller scale, and our model results suggest that oyster filtration may not benefit seagrass in the <1.5-m deep nearshore region during wind events when waves induce sediment resuspension. It also suggests that small increases in local oyster abundance likely would have little demonstrable effect on turbidity in an open system like Chesapeake Bay, where particles are continually being imported from adjacent water masses. This highlights the difficulty of trying to achieve measurable long-term ecosystem benefits through small-scale oyster reef restoration. As noted previously (Newell and Ott 1999; Newell et al. 2005; Cerco and Noel 2007), although there are many ecosystem benefits from oyster restoration, it is unrealistic to expect that these benefits will be quantifiable at specific locations until oysters are sufficiently abundant for their feeding activity to affect tributary-scale processes.

Summary

Although the SWOLS model simplifies many complexities of the natural seagrass system, it does allow assessment of the complex and spatially dependent interactions between waves, seagrasses, tidal currents, submerged structures, and suspension-feeding organisms. Along-shore breakwaters in the model were only effective in improving seagrass growth potential, via reduced sediment resuspension, in high wave situations; cross-shore groins, conversely, were most beneficial under low wave conditions. In addition, the spatial separation of oysters and seagrass coupled with tidal advection prevented oyster filtration from having a direct beneficial effect on seagrass growth. These results indicate that there is no simple solution to improve light levels over seagrass beds. Site-specific solutions, which may be informed by adapting the SWOLS model to individual sites, are necessary, especially when taking into account additional environmental alterations caused by coastal structures.

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References

- Barko, J.W. and M. Smart. 1983. Effects of organic matter additions to sediment on the growth of aquatic plants. *Journal of Ecology* 71: 161–175. doi:10.2307/2259969.
- Barko, J.W. and M. Smart. 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. *Ecology* 67: 1328–1340. doi:10.2307/1938689.
- Batiuk, R.A., J.J. Orth, K.A. Moore, W.C. Stevenson, L.W. Staver, V. Carter, N. Rybicki, R.E. Hickman, S. Kollar, S. Bieber and P. Heasley. 1992. Submerged aquatic vegetation habitat requirements and restoration targets: a technical synthesis. USEPA-CBP 68-WO-0043
- Cerco, C.F., and M.R. Noel. 2005. Assessing a ten-fold increase in the Chesapeake Bay native oyster population. A Report to the EPA Chesapeake Bay Program. July, 2005
- Cerco, C.F. and M.R. Noel. 2007. Can oyster restoration reverse cultural eutrophication in Chesapeake Bay? *Estuaries and Coasts* 30(2): 331–343.
- Chen, S.-N., L.P. Sanford, E.W. Koch, F. Shi, and E.W. North. 2007. A nearshore model to investigate the effects of seagrass bed geometry on wave attenuation and suspended sediment transport. *Estuaries and Coasts* 20(2): 296–310.
- Dame, R.F., R.G. Zingmark, and E. Haskin. 1984. Oyster reefs as processors of estuarine materials. *Journal of Experimental Marine Biology and Ecology* 83: 239–247. doi:10.1016/S0022-0981(84)80003-9.
- Dennison, W.C., R.J. Orth, K.A. Moore, J.C. Stevenson, V. Carter, S. Kollar, P.W. Bergstrom, and R.A. Batiuk. 1993. Assessing water quality with submersed aquatic vegetation. *BioScience* 43: 86–94. doi:10.2307/1311969.
- Duarte, C.M. 1991. Seagrass depth limits. *Aquatic Botany* 40: 363–377. doi:10.1016/0304-3770(91)90081-F.
- Eckman, J.E. 1983. Hydrodynamic processes affecting benthic recruitment. *Limnology and Oceanography* 28: 241–257.
- Ekebjærg, L. and P. Justesen. 1991. An explicit scheme for advection-diffusion modelling in two dimensions. *Computer Methods in Applied Mechanics and Engineering* 88(3): 287–297. doi:10.1016/0045-7825(91)90091-J.
- Fonseca, M.S. and J.S. Fisher. 1986. A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Marine Ecology Progress Series* 29: 15–22. doi:10.3354/meps029015.
- Fonseca, M.S. and J.A. Cahalan. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. *Estuarine, Coastal and Shelf Science* 35: 565–576. doi:10.1016/S0272-7714(05)80039-3.
- Gallegos, C.L. 2001. Calculating optical water quality targets to restore and protect submersed aquatic vegetation: overcoming problems in partitioning the diffuse attenuation coefficient for photosynthetically active radiation. *Estuaries* 24(3): 381–297. doi:10.2307/1353240.
- Green, E.P. and F.T. Short. 2003. *World atlas of seagrasses*. Berkeley, California: University of California Press.
- Idestam-Almqvist, J. and L. Kautsky. 1995. Plastic responses in morphology of *Potamogeton pectinatus* to sediment and above-sediment conditions at two sites in the northern Baltic proper. *Aquatic Botany* 52: 205–216. doi:10.1016/0304-3770(95)00499-8.
- Jones, J.I., J.W. Eaton, and K. Hardwick. 2000. The influence of periphyton on boundary layer conditions: pH microelectrode

- investigation. *Aquatic Botany* 67: 191–206. doi:10.1016/S0304-3770(00)00089-9.
- Jordan, S. 1987. Sedimentation and remineralization associated with biodeposition by the American oyster *Crassostrea virginica* (Gmelin). Ph.D. Dissertation, University of Maryland, College Park, Maryland.
- Kaihatu, J.M., F. Shi, J.T. Kirby, and I.A. Svendsen. 2002. Incorporation of random wave effects into a quasi-3D nearshore circulation model. Proceedings of the 28th International Conference on Coastal Engineering, Cardiff, July 7–12, 2002. 747–759.
- Kemp, W.M., W.R. Boynton, R.R. Twilley, J.C. Stevenson, and J.C. Means. 1983. The decline of submerged vascular plants in upper Chesapeake Bay: Summary of results concerning possible causes. *Marine Technology Society Journal* 17: 78–89.
- Kirby, J.T., R.A. Dalrymple, and F. Shi. 2005. Combined refraction/diffraction model REF/DIF S, Version 1.3. Documentation and user's manual. Research Report, Center for Applied Coastal Research, University of Delaware. Newark, Delaware.
- Koch, E.W. 2001. Beyond light: Physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* 24: 1–17. doi:10.2307/1352808.
- Koch, E.W., J. Ackerman, M. van Keulen, and J. Verduin. 2006. Fluid dynamics in seagrass ecology: from molecules to ecosystems. In *Seagrasses: Biology, ecology and conservation*, ed. A.W.D. Larkum, R.J. Orth, and C.M. Duarte, 193–225. New York: Springer.
- Koch, E.W., M.S. Fonseca, L. Karrh, and A. Malhotra. 2008. Wave exposure: and additional parameter for identification of suitable SAV restoration sites. Final Report to NOAA Chesapeake Bay Program, 38 pp.
- Lalli, C.M. and T.R. Parsons. 1997. *Biological oceanography: An introduction*, 2nd ed, 314. Oxford: Butterworth-Heinemann.
- Langland, M. and T. Cronin (eds). 2003. *A summary report of sediment processes in Chesapeake Bay and watershed, water-resources investigations report 03-4123*. New Cumberland, Pennsylvania: U.S. Geological Survey.
- Lubbers, L., W.R. Boynton, and W.M. Kemp. 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. *Marine Ecology Progress Series* 65: 1–14. doi:10.3354/meps065001.
- Martin, D., F. Bertasi, M.A. Colangelo, M. de Vries, M. Frost, S.J. Hawkins, E. Macpherson, P.S. Moschella, M.P. Satta, R.C. Thompson, and V.U. Ceccherelli. 2005. Ecological impact of coastal defence structures on sediment and mobile fauna: Evaluating and forecasting consequences of unavoidable modifications of native habitats. *Coastal Engineering* 52: 1027–1051. doi:10.1016/j.coastaleng.2005.09.006.
- Newell, R.I.E. and C.J. Langdon. 1996. Mechanisms and physiology of larval and adult feeding. In *The eastern oyster; Crassostrea virginica, chapter 5*, ed. V.S. Kennedy, R.I.E. Newell, and A. Eble, 185–230. College Park: Maryland Sea Grant Publication.
- Newell, R.I.E., J.C. Cornwell, and M.S. Owens. 2002. Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: A laboratory study. *Limnology and Oceanography* 47(5): 1367–1379.
- Newell, R.I.E., T.R. Fisher, R.R. Holyoke, and J.C. Cornwell. 2005. Influence of eastern oysters on nitrogen and phosphorus regeneration in Chesapeake Bay, USA. In *The comparative roles of suspension feeders in ecosystems. NATO Science Series: IV—earth and environmental sciences*, ed. R. Dame and S. Olenin, 93–120. Netherlands: Springer.
- Newell, R.I.E. and J. Ott. 1999. Macro-benthic communities and eutrophication. In *Ecosystems at the land-sea margin: Drainage basin to coastal sea*, ed. T.C. Malone, A. Malej, L.W. Harding Jr., N. Smolaka, and R.E. Turner, 265–293. American Geophysical Union: Coastal and Estuarine Studies.
- Newell, R.I.E. and E.W. Koch. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries* 27(5): 793–806. doi:10.1007/BF02912041.
- Orth, R.J. and K.A. Moore. 1983. Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. *Science, New Series* 222(4619): 51–53.
- Orth, R.J. and J. van Montfrans. 1987. Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*: Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Marine Ecology Progress Series* 41: 283–294. doi:10.3354/meps041283.
- Peterson, C.H. 1986. Enhancement of *Mercenaria mercenaria* densities in seagrass beds: Is pattern fixed during settlement season or altered by subsequent differential survival? *Limnology and Oceanography* 31: 200–205.
- Rybicki, N.B., H.L. Jenter, V. Carter, R.A. Baltzer, and M. Turtora. 1997. Observations of tidal flux between a submersed aquatic plant stand and the adjacent channel in the Potomac River near Washington, D.C. *Limnology and Oceanography* 42(2): 307–317.
- Sanford, L.P., S.E. Suttles, and J.P. Halka. 2001. Reconsidering the physics of the Chesapeake Bay estuarine turbidity maximum. *Estuaries* 24: 655–669. doi:10.2307/1352874.
- Shi, F., J.T. Kirby, and D. Hanes. 2007. An efficient mode-splitting method for a curvilinear nearshore circulation model. *Coastal Engineering* 54: 811–824. doi:10.1016/j.coastaleng.2007.05.009.
- Shi, F., I.A. Svendsen, J.T. Kirby, and J.M. Smith. 2003. A curvilinear version of a quasi-3D nearshore circulation model. *Coastal Engineering* 49(1–2): 99–124. doi:10.1016/S0378-3839(03)00049-8.
- Short, F.T. and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23: 17–27.
- Shumway, S.E. 1996. Natural environmental factors. In *The eastern oyster; Crassostrea virginica*, ed. V.S. Kennedy, R.I.E. Newell, and A. Eble, 467–513. College Park: Maryland Sea Grant Publication.
- Smith, G.F., D.G. Bruce, E.B. Roach, A. Hansen, R.I.E. Newell, and A.M. McManus. 2005. Habitat conditions of mesohaline oyster bars in the Maryland Chesapeake Bay: An assessment of 40 years of oyster management. *North American Journal of Fisheries Management* 25: 1569–1590. doi:10.1577/M04-058.1.
- Svendsen, I. A., K. Haas, and Q. Zhao. 2004. Quasi-3D Nearshore Circulation Model SHORECIRC: Version 2.0. Research Report, Center for Applied Coastal Research, University of Delaware. Newark, Delaware.
- Ward, L.G., W.M. Kemp, and W.R. Boynton. 1984. The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Marine Geology* 59: 85–103. doi:10.1016/0025-3227(84)90089-6.
- Wright, L.D. 1995. *Morphodynamics of inner continental shelves*. Boca Raton, Florida: CRC.
- Zyserman, J.A. and H.K. Johnson. 2002. Modelling morphological processes in the vicinity of shore-parallel breakwaters. *Coastal Engineering* 45: 261–284. doi:10.1016/S0378-3839(02)00037-6.