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SIMULATED EFFECTS OF SEAGRASS LOSS AND RESTORATION ON SETTLEMENT AND RECRUITMENT OF BLUE CRAB POSTLARVAE AND JUVENILES IN THE YORK RIVER, CHESAPEAKE BAY

William T. Stockhausen and Romuald N. Lipcius

ABSTRACT

Seagrass meadows provide important settlement habitat, food and refuge for postlarvae and young juveniles of the blue crab, *Callinectes sapidus*. In the York River, Chesapeake Bay, areal cover and distribution of seagrass beds has declined historically. Beds which existed 12–25 km upriver from the mouth disappeared and have not recovered. A model for planktonic postlarval behavior, coupled with a 3-dimensional hydrodynamic transport model for the York River, was used to investigate potential effects of the decline in seagrass abundance, and hypothetical restoration, on blue crab settlement and recruitment to the benthos, both in seagrass and to unvegetated bottom. Effects of habitat loss were investigated in model simulations using two historic patterns of seagrass cover (ca. 1965 and ca. 1996), five patterns with intermediate loss of cover, and three settlement rates. Declines of crab settlement in seagrass (<40%) and total settlement (<25%) were not as great as the reduction in seagrass cover (70%). Although settlement was higher when seagrass cover was greater, a “settlement shadow” created by seagrass near the river mouth reduced settlement in historic upstream seagrass beds and ameliorated effects associated with the loss of those beds. Increases in recruitment associated with restored seagrass beds differed significantly with restoration location, such that seagrass restoration in some locations enhanced recruitment substantially more than equivalent restoration in other locations, due to spatial variation in transport processes. Thus, landscape-level spatial patterns of existing and lost seagrass habitat across the landscape interact with transport processes and postlarval behavior to determine settlement and recruitment, and should be considered when evaluating population impacts of habitat loss or restoration.

For benthic invertebrates with complex life histories (sensu Thorson, 1950), the transition from the late pelagic to the early benthic life-history stages, involving settlement from the water column to the benthos and metamorphosis from a larval or postlarval form to a benthic form, is a critical period. The fraction of individuals in a cohort which successfully make this transition reflects complex interactions among a number of physical and biological factors, including (1) physical transport by currents, (2) behavioral responses to environmental cues, (3) timing of development, and (4) differential mortality rates. Many mobile, macrobenthic species favor particular habitats among those available within the landscape during settlement and afterward as early benthic nursery grounds; examples include abalone (*Haliotis rubra*, McShane, 1992), whelks (*Concholepas concholepas*, Moreno et al., 1993), lobsters (*Homarus americanus*, Wahle and Steneck, 1991; *Panulirus argus*, Marx and Herrnkind, 1985) and crabs (*Callinectes sapidus*, Welch et al., 1997). Preferred settlement and nursery habitats may satisfy immediate nutritional or physical requirements (e.g., shelter) for metamorphosis or they may enhance post-settlement survival or growth. For these species, the size, geometry and location of preferred habitats in the landscape may also play an important role in determining benthic recruitment; thus, the “value” of a particular habitat patch may depend on its characteristics relative to the landscape.

For species which exhibit habitat preference, loss or degradation of preferred

settlement habitats through anthropogenic or natural causes may create or exacerbate demographic bottlenecks (Caddy, 1986; Wahle and Steneck, 1991). Conversely, the restoration of lost or degraded settlement habitats may relieve existing bottlenecks. However, if habitat value varies spatially, then equal amounts of habitat loss or restoration will have different population-level impacts when that loss or restoration occurs in different locations.

In the Chesapeake Bay, U.S.A., seagrass beds—principally eelgrass (*Zostera marina*) and widgeon grass (*Ruppia maritima* L. sensu lato)—are a “preferred” habitat of the blue crab, *Callinectes sapidus* Rathbun, particularly during settlement and for young benthic juveniles (Orth and van Montfrans, 1987). Megalopae, the final pelagic life-history stage, prefer eelgrass over unvegetated mud bottom or live oysters as settlement habitat prior to metamorphosis to the first benthic juvenile instar (van Montfrans et al., this issue), and settle in these habitats in relation to their planktonic availability (Lipcius et al., 1990). Subsequent growth is faster, and predation risk is lower, for the first several juvenile instars in seagrass habitats compared with unvegetated bottom (Olimi and Lipcius, 1991; Perkins-Visser et al., 1996; Pile et al., 1996; Moksnes et al., 1997). Upon reaching the ninth instar, juvenile blue crabs achieve a relative size refuge from predation (Pile et al., 1996) and subsequently disperse from seagrass beds to forage widely over all submerged habitats in the Bay. Crabs less than 25 mm carapace width overwinter in seagrass beds (Orth and van Montfrans, 1987; Montane et al., 1995) while larger crabs utilize seagrass beds during molting and mating to reduce predation risk (Ryer et al., 1990).

In the 1960s and 1970s, seagrasses and other species of submerged aquatic vegetation (SAV) in Chesapeake Bay experienced a dramatic and unprecedented decline in total abundance and geographic range, reaching minimum abundance in the 1980s (Orth and Moore, 1983; Orth and Moore, 1984). Deteriorating water quality associated with anthropogenic inputs of nutrients and sediments was identified as a major factor contributing to the decline (Kemp et al., 1983). Although there has been some recovery over the past 15 years (Moore et al., 1998), many previously vegetated areas remain bare, including riverine and mid-bay areas where eelgrass and widgeon grass were once abundant (Orth and Moore, 1984). In the York River prior to the decline, eelgrass beds extended from the river mouth to approximately 15 km upriver from Gloucester Point (Fig. 1). By 1972, the area upriver from Gloucester Point was devoid of eelgrass; it remains so today. From Gloucester Point to the river mouth, seagrass beds experienced substantial declines in the early 1970s, but have partially recovered due to expansion from remnant patches, successful transplant experiments, and seed recruitment from downriver vegetated areas (Batiuk et al., 1992).

The decline in seagrass cover correlated with declines in catch per unit effort (CPUE) in the Virginia blue crab hard-shell fishery (Anderson, 1989). Further, there is a significant, positive relationship between SAV cover and the abundance of juvenile crabs in the York River (Lipcius, unpubl.). Hence, SAV cover may determine the production of juvenile blue crabs through its effect on survival and growth of juveniles in the nursery grounds.

In this study, we address the potential impact of seagrass loss and restoration on blue crab settlement and benthic recruitment using a modeling approach. Here, we define benthic recruits as juvenile crabs which attain the ninth instar, at which they achieve a relative size refuge from predation and disperse from seagrass nursery habitats (Pile et al., 1996). We use a simple model for late-stage postlarval behavior coupled with a 3-dimensional hydrodynamic transport model for the York River to simulate spatial patterns of postlarval dispersal and settlement in

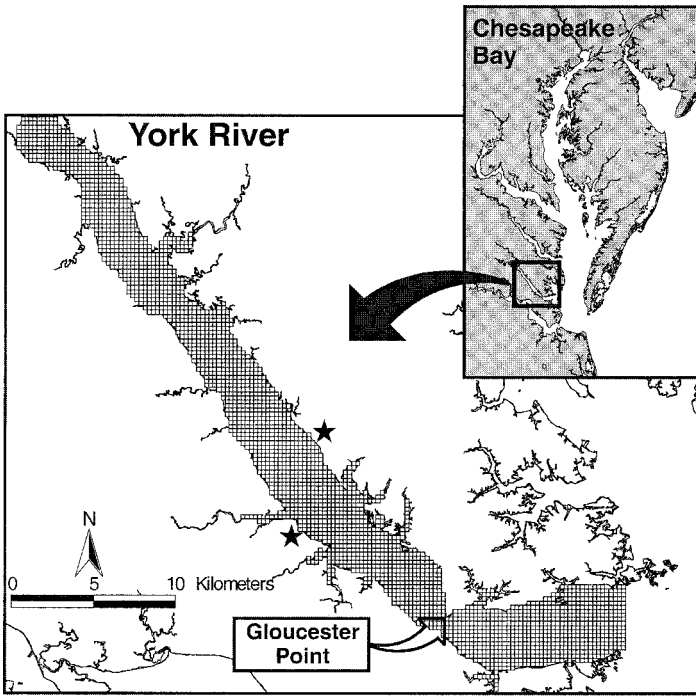


Figure 1. The York River, Virginia, overlaid with the horizontal, cartesian portion of the computational grid for the HEM-3D York River model application. The computational grid extends upriver into the two York River tributaries, the Mattaponi and Pamunkey, and ends at the fall line in each tributary. Horizontal cell dimensions in the cartesian portion of the grid are 250 m by 250 m. Vertical cell dimensions represent one-eighth of the local total depth (i.e., the model uses a “stretched” vertical coordinate). Currently, seagrass beds extend upriver to Gloucester Point. Historically, seagrass beds extended upriver to Clay Bank (★) on the north shore and Cheatham Annex (★) on the south shore of the river.

the river for different configurations of seagrass habitat. We examine the change in blue crab settlement and benthic recruitment due to the loss of seagrass habitat in the York River. Additionally, we use the model to consider whether restoration of seagrass to formerly vegetated areas, when considered in the context of enhancing postlarval settlement and benthic recruitment, should be prioritized on the basis of landscape-scale location.

METHODS

COMBINED MODEL FORMULATION.—We combined (1) a numerical model for 3-dimensional estuarine circulation and material transport in the York River (Fig. 1), (2) a simple behavioral model for late-stage postlarvae, and (3) a spatial pattern for settlement habitat in the York River to predict spatially-explicit patterns of postlarval settlement. A “pulse” of postlarvae was injected into the model near the river mouth (Fig. 2) at the beginning of a nighttime flood tide. The model subsequently tracked the densities of postlarvae in the water column and those that settled to the benthos over 6 d. Spatial patterns of benthic density and depth-integrated planktonic density were output at 1 h intervals.

HYDRODYNAMIC TRANSPORT MODEL.—The numerical circulation model incorporates the hydrodynamic and scalar transport components of the HEM-3D hydrodynamic-eutrophication model (Hamrick, 1992; Hamrick, 1996; Sisson et al., 1997). The HEM-3D model has been used in similar contexts to investigate: (1) the effect of vertical migration behavior on the spatial distribution of brachyuran crab larvae hatched in upriver tidal creeks of the York River (Garrison, 1997); (2) the dispersal of clam larvae from proposed seed beds in the James River (Shen et al., 1997); and, (3) the retention of oyster larvae in the James River (Mann and Evans, 1998).

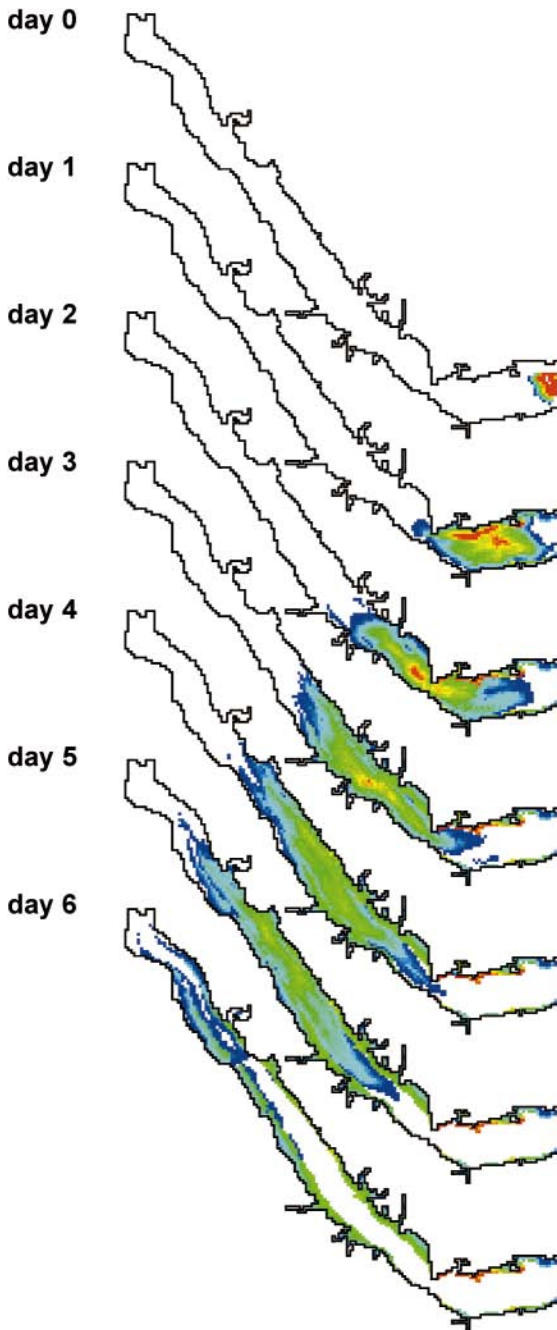


Figure 2. Density of postlarvae in the water column (depth-integrated) and on the benthos during the Current settlement habitat/Fast settlement scenario model run. Units are arbitrary, shading scale is logarithmic: blue shading indicates low values (1–10), green shading indicates intermediate values (10–500), red shading indicates highest values (>500).

Table 1. Values for postlarval behavioral model parameters. Swimming occurs on nighttime flood tides, sinking occurs on all ebb tides and daytime flood tides. Three behavioral scenarios are referenced to settlement rates in seagrass beds (indicated by superscripts in the table): (a) Fast, (b) Time-Varying, and (c) Slow. In the Time-Varying scenario, the settlement rate in seagrass is 0.05 mm s^{-1} initially, then changes to 1.0 mm s^{-1} on day 4. For each scenario, settlement rates on shallow, unvegetated bottom are 1/20 that in seagrass beds. No settlement occurs on deep bottom.

Parameter	Value	Units
Vertical migration characteristics		
Swimming rate	2	cm s^{-1}
Sinking rate	2	cm s^{-1}
Habitat specific settlement characteristics		
Per capita settlement rate in seagrass (ν_{SG})	$1.0^a, 0.05-1.0^b, 0.05^b$	mm s^{-1}
ν_{unveg}/ν_{SG}	0.05	(none)
ν_{deep}/ν_{SG}	0	(none)

The hydrodynamic component of the HEM-3D model uses a multi-parameter, finite-difference representation for intra-tidal estuarine flow and material transport in three dimensions (Hamrick, 1992; Hamrick, 1996). The model combines a stretched (i.e., "sigma") vertical coordinate system with a curvilinear-orthogonal horizontal coordinate system to solve vertically-hydrostatic, free-surface, variable-density, and turbulent-averaged equations of fluid motion (Hamrick, 1992; Hamrick, 1996). The numerical scheme incorporates an internal-external mode-splitting approach to separate the internal baroclinic mode from the external barotropic mode (Hamrick, 1992; Hamrick, 1996). This solution is coupled with transport equations for turbulent kinetic energy, turbulent length scale, salinity, and temperature (Hamrick, 1992; Hamrick, 1996). The scalar transport model uses a second-order accurate positive-definite advective transport algorithm (Smolarkiewicz and Clark, 1986; Smolarkiewicz and Grabowski, 1990) for solution of the Eulerian transport equations for a dissolved substance (Hamrick, 1992).

The computational grid for this application (Fig. 1) consisted of (1) a 3-dimensional cartesian grid with $250 \text{ m} \times 250 \text{ m}$ horizontal cell sizes in the York River mainstem from the river mouth to West Point, (2) a 2-dimensional (vertical), curvilinear grid extending to the "head of tide" in the Mattaponi and Pamunkey tributaries, and (3) a set of 1-dimensional marsh cells used for water storage in the tributary sections (Sisson et al., 1997). The model is physically forced by 1) seven constituents (M2, S2, N2, K1, M4, O1, M6) for tidal height at the river mouth, 2) freshwater discharge at the upper reach of each tributary, 3) salinity and temperature fields at the river mouth, and 4) synoptic, time-varying winds. In 1997, this application underwent extensive calibration using environmental data for the period May–September, 1989 and it accurately reflected tidal range, tidal phase, current velocity, and salinity within the model domain during this time period (Sisson et al., 1997).

Amplitude and phase for tidal constituents used in the model were determined by Fourier analysis of time series of tidal height at Gloucester Point, then adjusted to the river mouth (Sisson et al., 1997). Freshwater discharge rate for each tributary was fixed temporally, based on a 10-year average of the USGS-measured daily discharge rate during the month of September. Preliminary model runs (Stockhausen, unpubl.) indicated that changes in hydrodynamic forcing factors like wind and freshwater discharge increased small-scale variability, but did not alter large-scale patterns of settlement. Consequently, we used a single set of parameters for the hydrodynamic component of the model for all model runs.

POSTLARVAL BEHAVIORAL MODEL.—In our simple behavioral model, postlarvae exhibited three responses to environmental cues which modified their distribution in the water column beyond that of passive dispersal: (1) vertical migration in response to diurnal and tidal cues, (2) temporary settlement to the bottom, and (3) permanent settlement to the bottom. Postlarvae in the water column could swim up to the surface or sink to the bottom (Table 1), depending on whether model time corresponded to day or night and whether the tidal stage was ebb or flood. Here, we assumed that postlarvae rose to the surface only on nighttime flood tides, and otherwise remained near the bottom (Olmi, 1994). Second, postlarvae which sank during ebb tides temporarily settled on the bottom until the tide changed, thus avoiding transport downstream. Temporary settlement to the substrate in deep water explains the temporary disappearance of postlarvae from the water column on ebb tides (Olmi, 1994). In shallow water, postlarvae at the bottom could settle to the benthos and permanently leave the water column. The rate of permanent settlement depended on benthic habitat type, and thus varied spatially. Once settlement occurred, return to the water column was precluded.

For this study, we defined three benthic habitat types: (1) deep, (2) shallow unvegetated, and (3)

seagrass bed. We did not differentiate seagrass beds according to physical features such as shoot density, and we assumed that (1) seagrass was the preferred settlement habitat and (2) settlement did not occur in deeper areas. We further defined three settlement rates which likely bracket natural rates: (1) Fast, (2) Time-Varying, and (3) Slow (Table 1). For these behavioral scenarios, per capita settlement rate in seagrass beds was 20 times greater than on shallow, unvegetated bottom.

Model cells were classified according to bottom type. Cells at depths greater than 2 m were classified as "deep," the remaining cells as "shallow." No settlement occurred in deep cells. Shallow cells were classified as unvegetated or seagrass, as discussed below.

MODEL STUDIES: SEAGRASS LOSS.—To examine potential changes in settlement and recruitment caused by the loss in settlement habitat, we used published maps to define two settlement habitat scenarios, one corresponding to the present pattern of seagrass cover in the York River and one corresponding to the historic pattern prior to the disappearance of beds upriver (Fig. 3). We used the spatial pattern of seagrass in 1996 (Orth et al., 1997) to create the "Current" settlement habitat scenario (Fig. 3a). Shallow grid cells which overlapped mapped seagrass beds were classified as "seagrass" and the remaining shallow cells were classified as "shallow unvegetated." We created the "Historic" settlement habitat scenario (Fig. 3b) based on descriptions of the historic extent of seagrass in the river (Batiuk et al., 1992; Orth et al., 1994; Robert J. Orth, pers. comm.). The Current scenario represents a 70% decrease in areal coverage of seagrass relative to the Historic scenario.

We created model simulations using each combination of habitat scenario and behavioral scenario. For each simulation, we determined the fraction of postlarvae which remained in the water column, the fraction which settled in seagrass, and the fraction which settled on shallow, unvegetated bottom by model termination. We also determined the spatial pattern of settlement at landscape scales by quantifying the fraction of postlarvae which had settled in both habitats by model termination for each river zone/shore combination (Fig. 3).

Survival and growth of young juveniles is substantially higher in seagrass than on unvegetated bottom (e.g., Perkins-Visser et al., 1996; Pile et al., 1996). To estimate the effects of seagrass loss on benthic recruitment—i.e., recruitment to later juvenile stages—we assumed that postlarvae settling on shallow, unvegetated bottom did not survive and that growth and survival within seagrass was independent of bed size, shape and location. We further assumed that postlarvae remaining in the water column perished. Under these assumptions, recruitment in the nursery grounds was simply proportional to settlement in seagrass alone. Thus, to assess the impact of seagrass loss on recruitment, we compared the fraction of postlarvae which settled in seagrass alone under the various habitat scenarios.

MODEL STUDIES: SEAGRASS RESTORATION.—Restoration of seagrass beds to formerly vegetated areas within the Chesapeake Bay is one of the priorities identified in the Chesapeake Bay Agreement (Chesapeake Executive Council, 1989). However, the location of restored beds, relative to the overall landscape, may affect their value as settlement and nursery habitats for the blue crab. To examine this issue, we used the Current settlement habitat scenario as a baseline from which to evaluate the impact of restoration location on blue crab settlement within seagrass nursery habitats in the York River.

We addressed the effect of habitat restoration location on blue crab settlement and recruitment using two fixed location factors, (1) river zone (mouth, downriver, midriver, upriver) and (2) shore (north, south), in a full-factorial experimental design. Because seagrass beds were historically found only within the mouth and downriver zones of the York River, we limited restoration to within these two levels of river zone (Fig. 3). To create a single restoration scenario for a given combination of factor levels, we converted the benthic type of four randomly-selected "shallow, unvegetated" grid cells in the Current scenario to "seagrass." For each combination of river zone and shore factor levels, we created 10 replicate restoration scenarios, yielding 40 model cases per experiment. We repeated the entire experiment for the Fast and Slow behavioral scenarios to bracket likely settlement rates.

We analyzed experimental results for each behavioral scenario using a two-way, fixed-factor analysis of variance model with river zone and shore as factors. We focused on changes in benthic recruitment (functionally equivalent to changes in settlement in seagrass, see above) due to seagrass restoration; thus, for each model run, we first computed the percentage of postlarvae which settled in seagrass prior to model termination and then computed the difference between this value and the corresponding value for the baseline case with no restoration to obtain ΔP , the increase in the percentage of postlarvae settling in seagrass due to the restored habitat. In both experiments, values of ΔP were \log_{10} -transformed prior to analysis to meet assumptions of homogeneity of variance. When the interaction effect between river zone and shore was significant, we used Tukey's method of multiple comparisons (Underwood, 1997; MINITAB, 1997) to discern significant differences between factor levels.

RESULTS

SEAGRASS LOSS.—For each of the behavioral scenarios, total settlement (i.e., the fraction of postlarvae settling in either seagrass or shallow, unvegetated bottom) and settlement in seagrass alone were greater in simulations using the His-

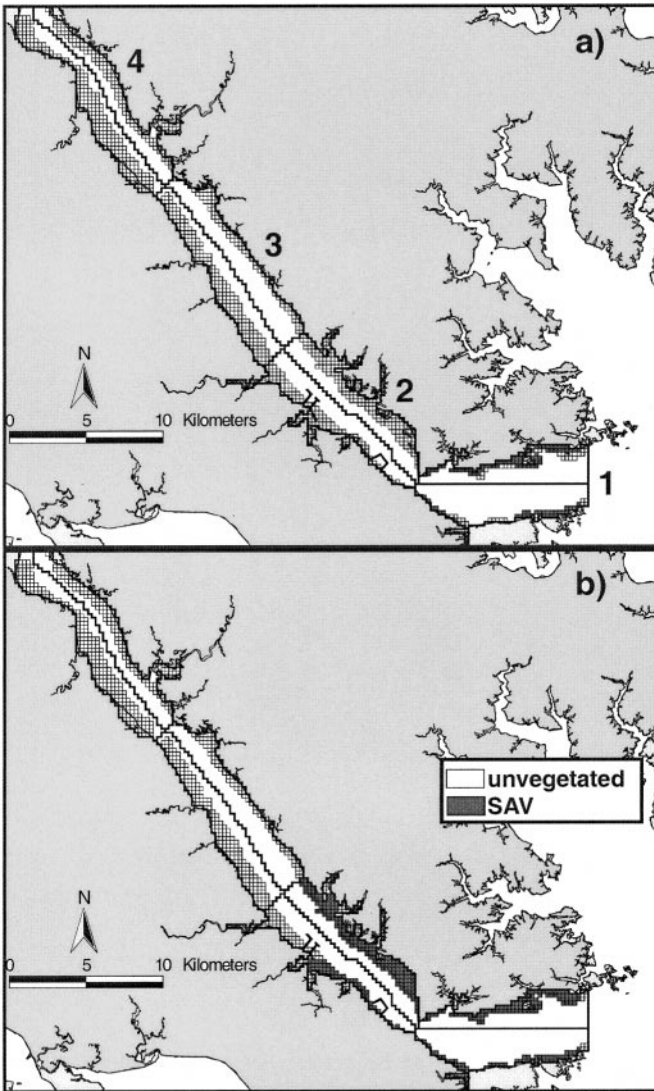


Figure 3. Model grid cells by benthic habitat type (shaded: seagrass bed, unshaded: shallow, unvegetated) for the two settlement habitat scenarios: (a) “Current” and (b) “Historic.” Cells characterized as “deep” (where settlement could not occur) are not shown. The Current scenario represents a 70% reduction in seagrass areal cover from the Historic scenario. Also indicated are the areas (north, south) shore x (1) mouth, (2) downriver, (3) mid-river, (4) upriver} zone) used in subsequent analyses.

toric habitat scenario than corresponding ones using the Current scenario (Fig. 4a, b), while the opposite was true for settlement on shallow, unvegetated bottom (Fig. 4c). The relative reduction in total settlement associated with the 70% decline in seagrass abundance from the Historic to Current habitat scenarios was small ($<10\%$ for the Fast and Time-Varying behavioral scenarios, Fig. 5) to moderate (25% for the Slow scenario, Fig. 5). The relative reduction in settlement in seagrass was much greater, 40–45%, and varied less among the behavioral scenarios (Fig. 5).

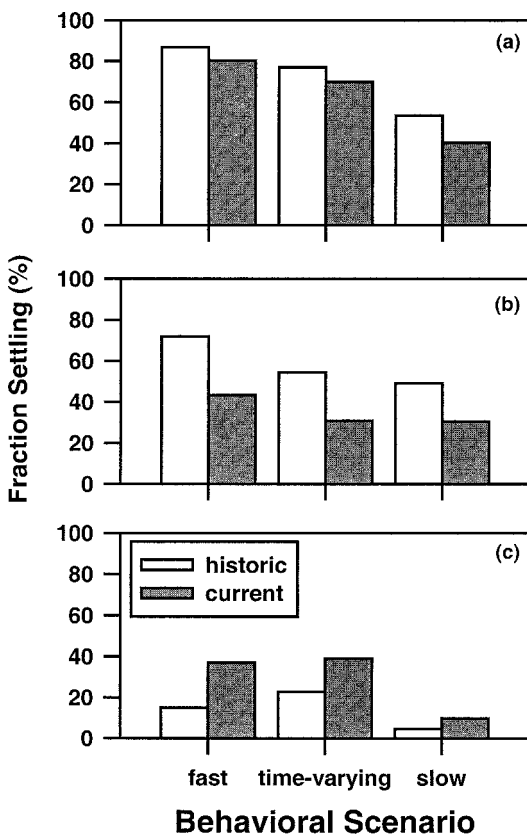


Figure 4. Comparison of settlement for the Historic (unshaded bars) and Current (shaded bars) habitat scenarios under each behavioral scenario. The graphs indicate the percentage of postlarvae which settled: (a) in both shallow benthic habitats, (b) in seagrass, and (c) on unvegetated bottom.

Spatial patterns in settlement differed by model scenario (Fig. 6), although these were qualitatively similar for all three behavioral scenarios. Total settlement was highest in the mouth river zone and generally decreased with distance upriver. Settlement was higher on the northern shore than on the southern shore, though the difference decreased upriver (Fig. 6). Whereas total settlement within the mouth river zone was similar under both habitat scenarios for a given behavioral

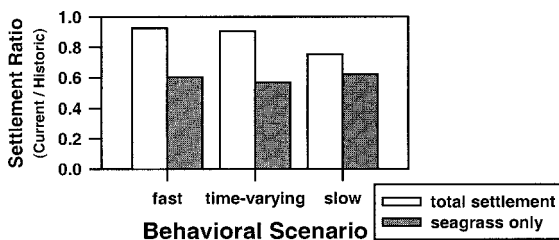


Figure 5. Reduction in settlement accompanying the 70% decline in seagrass cover from Historic to Current habitat scenario under the three behavioral scenarios. Unshaded bars represent the ratio of total settlement for the Current scenario to that for the Historic scenario under the behavioral scenario indicated on the x-axis. Shaded bars represent the corresponding ratio for settlement in seagrass.

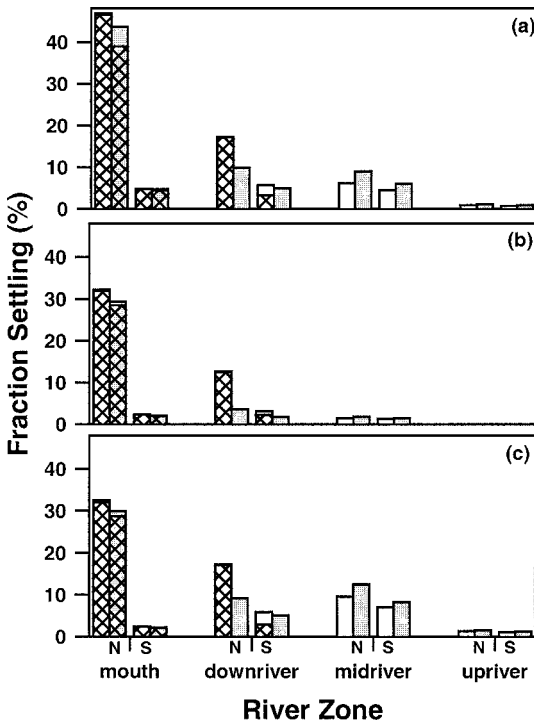


Figure 6. Comparison of settlement under the Historic (unshaded bars) and Current (shaded bars) habitat scenarios by habitat type and river zone for the three behavioral scenarios: (a) Fast, (b) Slow and (c) Time-Varying settlement. Each bar represents the percentage of postlarvae which settled in both shallow habitats by model termination (day 6) within the river zone indicated on the x-axis. For each bar, settlement is broken down by benthic habitat type: seagrass beds (crosshatching) and shallow, unvegetated bottom (solid).

scenario, settlement in seagrass on the northern shore was lower in the Current scenario relative to the Historic scenario. In the downriver zone, total settlement was higher on both shores in the Historic scenario. In this zone, settlement under the Historic scenario occurred primarily in seagrass. Seagrass was absent from this zone in the Current habitat scenario; consequently, settlement occurred only on unvegetated bottom. In the mid-river and upriver zones, settlement was higher on both shores in the Current scenario.

SEAGRASS RESTORATION.—“Restoring” seagrass in four randomly-selected unvegetated grid cells in the Current habitat scenario increased benthic recruitment (=settlement in seagrass) in all 80 restoration cases, regardless of restoration zone or behavioral scenario. However, mean increases in settlement in seagrass varied significantly among restoration zones (Fig. 7, Tables 2, 3). When postlarvae settled quickly overall (Fig. 7a), there was a significant interaction between river zone and shore on settlement (Table 2). The positive effect of restoration on the south shore at the river mouth was significantly smaller than that associated with restoring seagrass in the other three areas, which did not differ significantly (Table 2). When postlarvae settled slowly (Fig. 7b), the main effects of river zone and shore were significant, but the interaction term was not (Table 3). Significantly higher increases in settlement in seagrass were associated with restoration on the

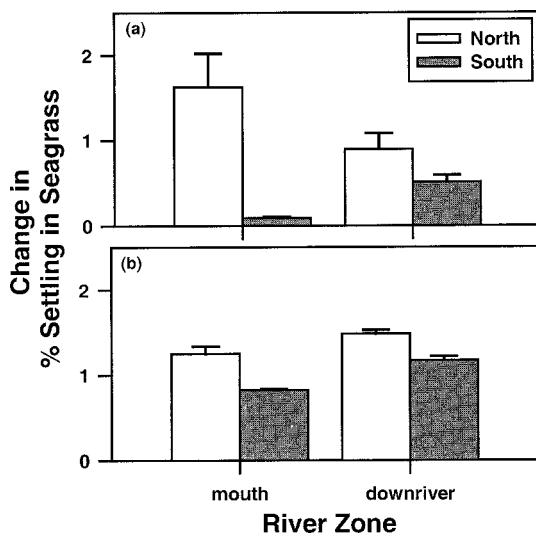


Figure 7. Seagrass restoration results for the (a) Fast and (b) Slow settlement scenarios. For each model run, the benthic habitat type of four randomly-selected shallow, unvegetated grid cells within the Current habitat scenario was changed to seagrass. Ten replicate model runs were performed per shore/zone factor level combination. Vertical bars represent the mean increase, relative to that for the baseline Current settlement habitat scenario, in the percentage of postlarvae settling in seagrass after "restoration" of seagrass beds within the indicated levels of river zone and shore. Error bars indicate standard errors.

north shore than on the south shore, and in the downriver zone than near the river mouth (Table 3).

DISCUSSION

To our knowledge, this study is unique in examining the role of the spatial configuration of habitat patches relative to transport processes and postlarval behavior in determining habitat value for the blue crab. Previous modeling studies which examined transport processes in relation to blue crab recruitment focused principally on mechanisms enhancing the reinvasion of estuarine nursery grounds from offshore larval pools (e.g., Johnson and Hess, 1990; Garvine et al., 1997). Those studies addressed processes on temporal scales of days to weeks and spatial scales of 10s–100s of kilometers. Settlement was not explicitly modeled, nor were habitat preferences or the spatial arrangement of settlement habitat. In this study,

Table 2. Effects of seagrass restoration by river zone and shore on \log_{10} -transformed percentage of postlarvae settling in seagrass (i.e., $\log_{10}(\Delta P)$, see text) under the fast settlement scenario. The increase in settlement was significantly lower when seagrass was restored on the south shore at the river mouth than when seagrass was restored at the other three locations (north shore/river mouth, north shore/downriver, south shore/downriver), while these did not differ significantly (Tukey's Test, $\alpha = 0.05$).

Source of variation	df	MS	F
River zone	1	0.9272	7.15*
Shore	1	4.2065	32.42***
Interaction	1	1.8412	14.19***
Error	36	0.1297	

* $P < 0.05$, *** $P < 0.001$

Table 3. Effects of seagrass restoration by river zone and shore on the \log_{10} -transformed change in percentage of postlarvae settling in seagrass (i.e., $\log_{10}(\Delta P)$, see text) under the slow settlement scenario. The increase in settlement was significantly higher when seagrass was restored on the north shore than on the south shore, and downriver than near the river mouth.

Source of variation	df	MS	F
River zone	1	0.1365	35.24***
Shore	1	0.1912	49.37***
Interaction	1	0.0117	3.01 ^{ns}
Error	36	0.0039	

^{ns} $P > 0.05$, *** $P < 0.001$

we emphasized processes at temporal and spatial scales an order of magnitude smaller than previous studies (i.e., minutes to days and 0.1–10s km), and explicitly incorporated habitat preference and the spatial arrangement of habitat in a coupled transport/behavior model for postlarvae to address the potential effects of loss and restoration of settlement habitat for the blue crab.

SEAGRASS LOSS.—Our simulations indicate that a 70% reduction in seagrass cover in the York River reduced blue crab settlement in seagrass and unvegetated bottom only slightly to moderately (10–25%), depending on whether settlement rates were fast or slow. However, because crabs which settle in shallow, unvegetated habitats survive at low rates (Perkins-Visser et al., 1996; Pile et al., 1996), the impact of seagrass loss on blue crab recruitment was likely greater than that reflected by settlement in seagrass and unvegetated bottom. Using settlement in seagrass alone as indicative of recruitment to the juvenile stage, our simulations indicate that recruitment was reduced 40–45% by a 70% loss of seagrass habitat. Although this reduction in recruitment represents a substantial impact on the blue crab population, it also indicates that seagrass cover alone does not explain the dependence of either settlement or recruitment on seagrass habitat. Rather, the spatial pattern of seagrass cover and decline also play a key role.

Settlement at different spatial locations was a function of (1) the local per capita settlement rate, (2) the local concentration of settlement-competent postlarvae, and (3) the amount of time the postlarvae are retained locally. The pattern of settlement habitat across the landscape determined (1) and influenced (2) through the creation of a “settlement shadow” whereby downriver areas “intercepted” postlarvae, and thus reduced the available pool of settlers for upriver areas. In contrast, local hydrodynamic conditions and postlarval behavior influenced (3).

In the York River, the remaining seagrass beds are ideally located to ameliorate effects on settlement and recruitment associated with the historic decline in seagrass abundance. Existing seagrass beds are near the river mouth, while formerly vegetated areas (which remain unvegetated to date) were upriver from Gloucester Point and therefore in the settlement shadow of the downriver beds. Further, the constriction of the river at Gloucester Point restricts exchange on flood tides between the mouth and upriver regions, thus retarding the progress of postlarvae upriver and retaining them longer in the area of existing seagrass. Hence, we conclude that the settlement shadow caused by settlement of blue crab postlarvae in the mouth region has ameliorated the impact of seagrass decline in the upriver regions.

SEAGRASS RESTORATION.—Our simulations indicated that the spatial location of restored seagrass beds significantly affected the value of those beds for blue crab settlement and recruitment. The channel bathymetry and constriction at Gloucester Point influence hydrodynamic current patterns such that restoring seagrass beds

on the south shore near the mouth of the river would likely not enhance recruitment. Conversely, restoring seagrass beds on the north shore, both near the mouth and in the downriver zone, would most likely enhance blue crab settlement and recruitment.

MODEL SIMPLIFICATIONS.—In the interest of simplicity and tractability, we ignored several complicating factors, including: (1) postlarval mortality in the water column, (2) density dependence in per capita settlement rates, (3) variations in habitat quality within settlement habitats, (4) alternative settlement habitats, and (5) variable hydrodynamic forcing factors, such as wind, which influence current patterns. Including mortality for postlarvae in the plankton would further emphasize the shadow effect created by seagrass beds near the river mouth and discount the importance of beds further upriver, since some fraction of the postlarvae transported upriver would die prior to settling. Including density-dependent settlement rates (e.g., assigning a carrying capacity to settlement habitats) would have the opposite effect in times of high settlement. The shadow effect of seagrass beds near the river mouth would be reduced once they were saturated. Further, the settlement pattern of a “pulse” of postlarvae would depend not only on its magnitude (i.e., a small pulse might not activate density-dependent mechanisms in any beds, while a large one might overwhelm the carrying capacity of all beds), but also on the history of prior pulses within a settlement season. Variations in habitat quality within seagrass beds would tend to emphasize the importance of spatial location of seagrass habitat loss, while the existence of alternative settlement habitats with nursery value would tend to de-emphasize it. Finally, preliminary model runs (Stockhausen, unpubl.) indicated that changes in hydrodynamic forcing factors like wind and freshwater discharge increased small-scale variability, but did not alter large-scale patterns of settlement (e.g., little settlement on the south shore near the river mouth).

IMPLICATIONS FOR HABITAT LOSS AND RESTORATION.—Landscape-level patterns of loss or restoration of essential habitats may not have important demographic consequences for the population when the movement of individuals is not constrained across the landscape by physical or behavioral factors. In contrast, our findings suggest that effects of the loss or restoration of seagrass habitats in the York River on blue crab settlement and recruitment depend considerably on past and present patterns of seagrass beds within the landscape. Moreover, a key spatial phenomenon is the settlement shadow effect created by downriver settlement habitats on upriver habitats. The shadow effect will be important where the degree of movement differs spatially (e.g., cross-shore and alongshore), and individuals pass available settlement habitats in an ordered manner, such as in long, narrow rivers, estuaries, fjords, or canyons. Conversely, the shadow effect will be less important where the scales of movement are similar in different directions and individuals disperse randomly.

Finally, our findings have major implications for restoration efforts directed at seagrass and other submerged aquatic vegetation (SAV) habitats in Chesapeake Bay (Chesapeake Executive Council, 1989). Our findings indicate that the value and, therefore, effectiveness of restored habitat in augmenting blue crab recruitment depend substantially on the location of those habitats. Hence, restoration efforts should be guided by estimates of the value of specific habitats based on organismal behavior, habitat location, quantity and quality, and transport processes.

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