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POTENTIAL BOTTOM-UP CONTROL OF BLUE CRAB DISTRIBUTION AT VARIOUS SPATIAL SCALES

Rochelle D. Seitz, Romuald N. Lipcius, William T. Stockhausen, Kristen A. Delano, Michael S. Seebo and Paul D. Gerdes

ABSTRACT

Top-down (i.e., predation), bottom-up (i.e., food availability), and physical factors may influence blue crab (*Callinectes sapidus*) distribution. To assess the role of bottom-up and physical process in blue crab distributions, we concurrently measured density of the blue crab (*Callinectes sapidus*), density of its principal prey, the Baltic clam (*Macoma balthica*), and physical characteristics in mud and sand habitats spanning various spatial scales (1–10 km and 10–50 km) in the York River, Chesapeake Bay. Clam and crab densities were intermediate in mud, low in downriver sand, and high in upriver sand. Clam and crab densities were not correlated in mud, whereas in sand, they were significantly and positively correlated at both the local scale (1 km) and at the broadest spatial scale (10–50 km). Crab density also correlated with salinity at the broad spatial scale. After removing the effect of salinity, crab density remained significantly correlated with clam density. Using a hydrodynamic model for the York River, potential transport of clams from downriver coves was primarily to upriver habitats, but transport of crabs was mainly to downriver seagrass habitats. At the local scale, upriver zones where crab and clams were abundant, crab density was highly correlated ($r^2 = 0.93$) with clam density, but not with salinity, suggesting that the distribution of blue crabs was driven mostly by their primary food item—clams. The collective findings are consistent with the hypotheses that crab density is driven by both food availability and salinity at broad spatial scales (10–50 km), whereas food availability is a primary control at smaller spatial scales (1–10 km). Bottom-up control of upper trophic levels may be distinctive; thus far, in marine and freshwater systems, bottom-up control has not been demonstrated to filter from basal to upper trophic levels. Furthermore, unvegetated habitats where food, such as clams, is abundant may be important in the population dynamics of the blue crab, even in systems where seagrass beds are common.

Although predation is crucial in driving community structure of marine benthos (Paine, 1980; Wilson, 1991; Strong, 1992; Duffy and Hay, 2000), there is growing recognition that food limitation may be as important in some ecosystems (Brett and Goldman, 1996; Micheli, 1999). A combination of predation (i.e., top-down factors) and food limitation (i.e., bottom-up factors) likely influences species distributions in marine, freshwater, and terrestrial habitats, depending on aspects of the local food web (Getz, 1984; Arditi and Ginzburg, 1989; Posey et al., 1995; Menge et al., 1996). At broad spatial scales, bottom-up or physical factors may be more important than top-down factors (Power, 1992; Menge et al., 1997; Seitz and Lipcius, 2001). Additionally, bottom-up factors commonly drive freshwater systems, whereas top-down factors are often more important in marine systems (Menge and Sutherland, 1987; McQueen et al., 1989; Peckarsky et al., 1990; Brett and Goldman, 1996; Brett and Goldman, 1997). Previously, bottom-up control by resources has not been demonstrated to permeate upper trophic levels in marine pelagic systems (Micheli, 1999) or freshwater systems (Brett and Goldman, 1996). However, our study provides evidence for potential bottom-up control of an upper-level omnivore (i.e., the blue crab) by its primary prey (i.e., the Baltic clam).

Distribution of the blue crab (*Callinectes sapidus*) may be affected by predators, food, habitat type or complexity, and physical transport (Lipcius and Hines, 1986; Orth and van Montfrans, 1987; Hines et al., 1990; Perkins-Visser et al., 1996; Pile et al., 1996; Clark et al., 1999a, 1999b). In seagrass habitats, crab densities

are elevated (Orth and van Montfrans, 1987), presumably because of the refuge from predation (Pile et al., 1996) or elevated food (Perkins-Visser et al., 1996). However, in unvegetated habitats, the important features of the habitat for blue crab survival and distribution generally have not been identified (but see Ruiz et al., 1993). Top-down factors (i.e., predation) are not likely to control distribution of large juvenile (>75 mm carapace width [CW]) and adult blue crabs, since these individuals obtain a size refuge from predation (Hines et al., 1990; Moody, 1994). Alternatively, bottom-up factors (i.e., food availability) influence young juveniles in seagrass beds (Perkins-Visser et al., 1996), and may be similarly important in defining the distribution of large juvenile and adult blue crabs in other habitats.

Clams are a primary food source for crabs and might be expected to influence crab distribution. Clams comprise approximately 50% of the blue crab diet in many habitats, whereas conspecifics, polychaetes, amphipods, and other benthic prey are secondary prey items (Laughlin, 1982; Hines et al., 1990; Mansour and Lipcius, 1991; Mansour, 1992). Clam patch density and distance between patches can influence blue crab distribution at the local scale (Clark et al., 1999a, 1999b; Clark et al., 2000; Terwin et al., in review). Given these facets of the crab-clam interaction in Chesapeake Bay, we hypothesized that bottom-up factors might be important in determining crab distribution.

The Baltic clam, *Macoma balthica,* is distributed in muddy and sandy sediments along both coasts of the temperate North Atlantic and Pacific Oceans (Beukema and Meehan, 1985; Martini and Morrison, 1987). This facultative deposit- and suspension-feeding clam typically inhabits soft-sediment habitats from intertidal to deep depths and is abundant in Chesapeake Bay (Dauer et al., 1982a; Holland, 1985; Hines et al., 1990; Seitz, 1996; Schaffner et al., 2001). *Macoma* is a major prey of invertebrates (crabs: Hines et al., 1990; Mansour, 1992) and vertebrates (birds: Horwood and Goss-Custard, 1977; fish: Hines et al., 1990) within estuaries and marsh creeks. Furthermore, the effects of predation on *Macoma* vary substantially as a function of habitat structure and clam density (Eggleston et al., 1992; Seitz et al., 2001), and distance between prey patches (Clark et al., 1999a, 1999b; Clark et al., 2000; Terwin et al., in review).

In Chesapeake Bay, the key predator of whole adult *Macoma* is the blue crab, *Callinectes sapidus* (Hines et al., 1990), although epibenthic predatory fish such as spot (*Leiostomus xanthurus*), croaker (*Micropogonias undulatus*), and hogchoker (*Trinectes maculatus*) may nip clam siphons (Peterson and Skilleter, 1994). Blue crabs, which are dispersed widely along the Atlantic and Gulf coasts of North America, have been abundant throughout the Chesapeake Bay (Williams, 1984; Hines et al., 1987; Hines et al., 1990; Lipcius and Van Engel, 1990; Lipcius and Stockhausen, 2002). Prey availability, predator density, and habitat complexity can influence feeding efficiency and prey capture in blue crabs foraging for bivalves such as *Macoma* (Vernstein, 1977; Blundon and Kennedy, 1982a, 1982b; Arnold, 1984; Lipcius and Hines, 1986; West and Williams, 1986; Hines et al., 1990; Mansour and Lipcius, 1991; Eggleston et al., 1992).

In our study system, the York River in lower Chesapeake Bay (Fig. 1), vegetation (e.g., seagrass) is limited to the lower reaches of the river (Orth et al., 1996). However, blue crabs are common well upriver of Gloucester Point (Lipcius and Van Engel, 1990), where only unvegetated habitats exist, suggesting that habitats besides seagrass are important in defining crab distributions. Moreover, low dissolved oxygen, a potential controlling physical stress, is typically not a problem in shallow water habitats, less than 3 m depth, in Chesapeake Bay (Diaz and Rosenberg, 1995). Accordingly, we quantified densities of crabs and their
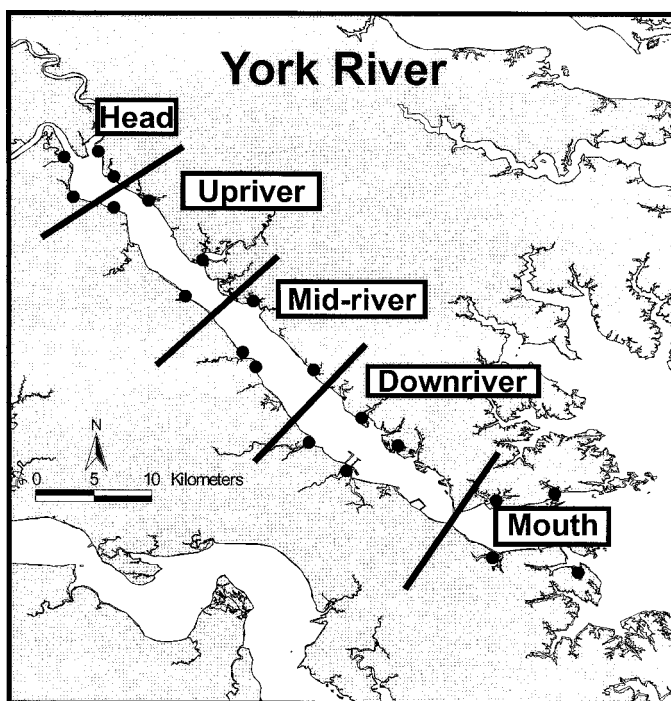
Figure 1. Sampling locations on the York River (Lat N 37°20′, Lon W 76°30′) with the five study zones delineated with solid lines and the circles indicating location of the four sites (two on the north shore and two on the south shore) within each zone. Within each site, we sampled a mud and muddy sand habitat (except in the 'head' zone where a total of three mud and three sand samples were taken).

principal prey, *Macoma balthica,* in the two most common shallow unvegetated habitats and in various geographic zones spanning 50 km along the axis of the York River. Specifically, we aimed to identify those habitats and zones that were superior based on food availability for crabs (i.e., clams). By estimating physical variables and quantifying food, habitat features, associated crab density, and potential hydrodynamic transport, we attempted to disentangle the key variables driving crab distribution.

APPROACH.—Our objectives were to determine what drives crab distribution at broad and local spatial scales in the York River. To do so, we examined (1) physical factors (temperature, salinity, dissolved oxygen [DO]) and nutrients (organic carbon, nitrogen), (2) bottom-up factors (food availability), and (3) physically-mediated factors (hydrodynamic transport), at shallow depths (1–2 m) in the York River. We hypothesized that if crabs drive densities of their primary prey, there would be a significant negative correlation between crab and clam densities. Alternatively, if clams drive crab densities, there would be a significant positive correlation. We recognize that correlations do not prove causality since two correlated factors may be driven by a third independent factor. However, given the strong interaction between crabs and clams in the York River food web (Mansour and Lipcius, 1991; Eggleston et al., 1992; Seitz et al., 2001) and documented behavioral responses of crabs to clam distributions (Clark et al., 1999a, 1999b; Clark et al., 2000; Terwin et al., in review), a positive correlation between prey and predator would be consistent with a hypothesis of bottom-up control.

In the third component of the study, we assessed the fate of crab and clam

postlarvae released downriver and subjected to hydrodynamic transport within the York River. Using a three-dimensional hydrodynamic model that incorporated clam and crab postlarval behavior (Stockhausen and Lipcius, 2003, this issue), we were able to predict potential post-settlement dispersal throughout the York River. We surmised that, because of the vertical migration of postlarvae to surface waters during the nocturnal flood tide, hydrodynamic transport to upriver locations would be high compared to downriver locations. We therefore hypothesized that hydrodynamic transport would also be important in driving clam and crab densities at broad spatial scales.

METHODS

SAMPLING DESIGN.—We subdivided the York River into five zones, (1) mouth, (2) downriver, (3) mid-river, (4) upriver, and (5) river head (Fig. 1). In each zone we selected four sites in 1–2 m water depth that contained both muddy sand (hereafter 'sand') and mud (hereafter 'mud') habitats, except in the uppermost 'river head' zone where only three sites within each habitat were available (i.e., a total of 19 sites for each habitat). In each habitat-site combination, we measured water temperature, salinity, and dissolved oxygen, collected sediment samples for grain-size and carbon-hydrogen-nitrogen (CHN) nutrient analysis, and sampled infaunal clams (using suction sampling) and epibenthic crabs (using otter trawls).

SEDIMENT ANALYSIS.—Sedimentary nutrient content (CHN) was determined by taking 1–2 cm of surface sediment with a 3-cm-diam core at each habitat-site combination in all 5 zones. Sediments were stored in a freezer, defrosted, weighed, dried completely (for 24 h) in an oven at 160°C, ground with an automatic grinder, mechanically homogenized, and combusted at 924°C in a CHN analyzer. Sediment composition (i.e., grain size) was measured through standard grain-size analysis using wet-sieving and pipette analysis (Folk, 1980) of the top 3–5 cm of surface sediment collected with a 3-cm-diam core.

CRAB DENSITY.—We conducted shallow-water trawling (1–2 m depths) from a small 'open skiff'-style vessel with an outboard engine and shallow draft. The sampling was conducted in July and August of 1999 to quantify blue crab density across habitats and within zones at the same sites where clams were sampled (see below). At each habitat-site combination, demersal fishes and crabs were collected during daytime with a 4.9-m semi-balloon otter trawl (3-m wide mouth, 5-cm mesh net body, and 7-mm mesh codend) along a 100 m transect line parallel to shore. Although the estimates of crab density from trawling can be low due to gear avoidance by the predators (trawl efficiency for most predators including large crabs is ~22%; Homer et al., 1980), all sizes of crabs are caught with approximately equal efficiency except for extremely small individuals (not analyzed in this study) which can escape through the mesh (Homer et al., 1980). Crabs in each trawl were counted and measured (carapace width [CW]).

CLAM DENSITY.—Since crab guts contain up to 50% clams by volume (Hines et al., 1990), we targeted the thin-shelled clam, *Macoma balthica,* which is the biomass dominant in the York River (Mansour, 1992). Clam density was quantified through suction sampling (Eggleston et al., 1992) at the trawl sites, using a cylinder of 0.46 m diameter (0.17 m² area) to a depth of 40–50 cm, which effectively samples the deepest-dwelling *Macoma* (Hines and Comtois 1985). At each site in each habitat, two samples were suctioned into a 1-mm mesh bag and subsequently sieved on a 1-mm mesh screen. All bivalves in the sample were identified, counted and shell length (longest dimension, anterior to posterior) was measured with calipers accurate to 0.1 mm. A mean of the two suctions from each habitat-site combination provided an independent value used in statistical analyses.

STATISTICAL ANALYSIS.—Data for crab and clam density, physical variables (temperature, salinity, dissolved oxygen) and nutrients (total organic carbon, total nitrogen) by habitat (sand or mud) and zone (mouth, downriver, mid-river, upriver, and head) were analyzed using two-way ANOVA models with habitat type and zone as fixed factors with 2 and 5 levels, respectively. Data were log-transformed when necessary to meet assumptions of normality and homogeneity of variance (Underwood, 1997; Bartlett's test). Physical and biotic variables that had significant patterns by zone were used in a multiple regression of crab density at the broad scale. When there was a significant zone effect, we performed Student-Newman-Keuls (SNK) tests (Underwood, 1997) to determine which levels of the factor differed.

In addition, for each habitat, crab densities from all 19 sites were correlated with physical variables (temperature, salinity, dissolved oxygen) and with clam densities. Independent variables that were not collinear were used in multiple regression analyses for each habitat. We used linear regression to regress log crab density with other variables, or we used non-linear regression with multiple parameters if this method increased the r^2 and fit of the regression.

Two types of regression analyses were performed with crab and clam densities, (1) those using individual data points from all sites (38 points with both habitats, or 19 points for each habitat), and (2) those using data points derived from a mean of 4 sites in each zone × habitat combination (except only 3 sites were used in the 'head' zone). To define the effects of clam density upon crab density in the absence of salinity, we regressed the residuals from the crab-salinity regression with clam density. Moreover, to ascertain the effects of salinity upon crab density in the absence of the effects of clam density, we regressed the residuals from the crab-clam regression with salinity.

Finally, to look at crab-clam correlations at a small spatial scale, we regressed crab and clam densities from individual sites in both sand and mud habitats within only the two most upriver zones (i.e., 14 data points from 'upriver' and 'head' zones).

HYDRODYNAMIC TRANSPORT.—Transport of clam and crab postlarvae were each simulated using separate runs of the VIMS three-dimensional hydrodynamic model (HEM-3D) (Hamrick, 1992; Sisson et al., 1997). Postlarvae migrate to surface waters during nocturnal flood tides, both in the blue crab (Olmi et al., 1990) and in the Baltic clam (Dauer et al., 1982b; Baker and Mann, 1997). We therefore integrated (1) the VIMS 3-D hydrodynamic model for the York River, (2) a simple behavioral model for clam and crab postlarvae, and (3) a spatial habitat grid for the York River to predict spatially-explicit patterns of postlarval settlement.

We simulated the fate of clam and crab postlarvae released downriver and at the mouth, respectively, to determine if distributions based on hydrodynamic transport could be driving the observed distribution patterns. Clam postlarvae were released from the downriver mud coves at the beginning of a nighttime flood tide. Downriver coves were chosen as the release point since these areas harbor adult Baltic clams (Lipcius and Seitz, unpubl. data). The model subsequently tracked densities of clam postlarvae in the water column and those settling to the benthos over 6 d. In addition to the shallow mud and sand habitats, we also investigated transport to the deep mud channel of the York River. Spatial patterns of benthic density and depth-integrated planktonic density were portrayed for the end of a 6-d model run.

Crab postlarvae were released at the mouth, where they naturally enter the York River system (Orth and van Montfrans, 1987). The model simulated a time-varying settlement rate to the three possible habitats (1) shallow mud, (2) shallow sand, and (3) seagrass, using the 'current' seagrass areal coverage (Stockhausen and Lipcius, 2003, this issue). Deep mud habitats (>2 m) were not made available for crab settlement. The model subsequently tracked the densities of crab postlarvae in the water column and those that settled to the benthos over 6 d (see Stockhausen and Lipcius, 2003, this issue). Spatial patterns of benthic density and depth-integrated planktonic and benthic density were portrayed for the end of 6 d. The results from this model depict initial settlement of crabs, but do not preclude the possibility of crabs later returning to the water column for post-settlement dispersal.

The numerical circulation model incorporated 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 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), the dispersal of clam larvae from proposed seed beds in the James River (Shen et al., 1997), the retention of oyster larvae in the James River (Mann and Evans, 1998), and settlement of blue crab postlarvae as a function of seagrass habitat (Stockhausen and Lipcius, 2003, this issue).

RESULTS

SEDIMENTS AND PHYSICAL FACTORS.—Sediments in mud habitats averaged 77.0% silt and clay fraction, whereas those in sand habitats averaged 13.15%. Food resources for clams (i.e., sedimentary carbon and nitrogen) were significantly greater in mud than sand (Tables 1 and 2). In mud, both sedimentary carbon and nitrogen were highest upriver, though this difference was only significant for nitrogen (Tables 1 and 2). Salinity was the only physical factor that varied significantly by zone (Table 3) and was therefore the only physical factor used as a predictor in subsequent multiple regressions for crab density.

CRAB DENSITY.—Crab density was significantly higher in upriver and head zones than in the other three downriver zones (SNK, $P < 0.05$), and did not differ by habitat type (Fig. 2a; Table 4). Both sand and mud habitats contributed to higher densities upriver (Fig. 2b, c), although the difference between upriver and downriver zones was greater in sand (Fig. 2b) than mud (Fig. 2c).

CLAM DENSITY.—Total clam densities (sand and mud habitats combined) gen-

Table 1. Mean sedimentary organic carbon and nitrogen, and silt & clay grain size (% with standard error in parentheses) by zone for each of two habitats (sand and mud) in the York River.

| Nutrient | Habitat | Zone | | | | |
		Mouth	Downriver	Mid-river	Upriver	Head
Carbon	Sand	0.28 (0.11)	0.30 (0.12)	0.20 (0.09)	0.21 (0.04)	0.32 (0.05)
	Mud	1.93 (0.24)	2.03 (0.31)	1.94 (0.32)	3.03 (0.91)	3.48 (0.10)
Nitrogen	Sand	0.03 (0.01)	0.03 (0.01)	0.02 (0.01)	0.02 (0.003)	0.14 (0.05)
	Mud	0.19 (0.02)	0.21 (0.03)	0.17 (0.03)	0.28 (0.07)	0.52 (0.09)
Silt & clay	Sand	11.39 (4.41)	11.90 (5.76)	11.04 (3.30)	13.12 (3.40)	19.99 (5.96)
	Mud	74.18 (3.76)	83.44 (7.10)	64.86 (2.73)	74.47 (14.30)	91.73 (3.41)

Table 2. Two-way analysis of variance for log-transformed total organic carbon (%) and for log-transformed total nitrogen (%) between habitats (mud and sand) and among five river zones (Mouth, Downriver, Mid-river, Upriver, and Head). Log-transformation was used to equalize variances (Bartlett's test).

Source of variation	df	MS	F	P
Total organic carbon				
Habitat	1	9.30	125.08	**0.0001**
Zone	4	0.06	0.86	0.500
Habitat × zone	4	0.01	0.13	0.970
Error	27	0.07		
Total nitrogen				
Habitat	1	7.93	93.35	**0.0001**
Zone	4	0.43	5.02	**0.004**
Habitat × zone	4	0.06	0.75	0.566
Error	27	0.09		

Table 3. Two-way analysis of variance results for physical variables (temperature, salinity, dissolved oxygen) between habitats (mud and sand) and among five river zones (Mouth, Downriver, Mid-river, Upriver, and Head).

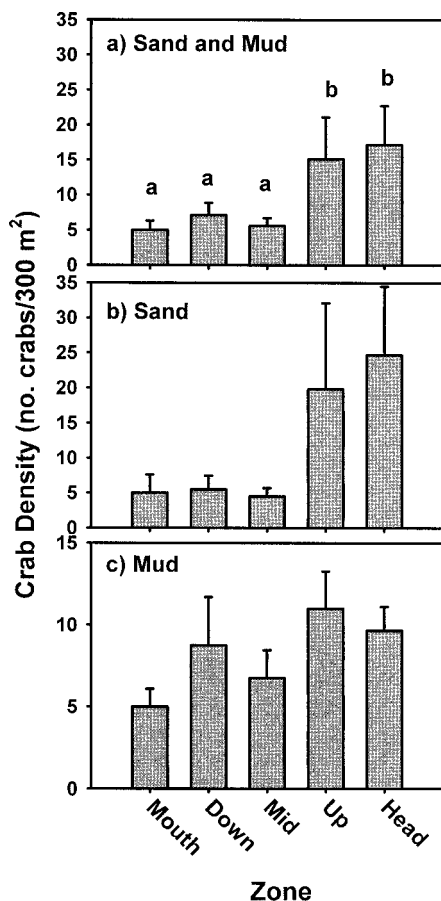| Source of variation	df	MS	F	P
Temperature				
Habitat	1	0.20	0.02	
Zone	4	6.42	0.47	0.899
Habitat × zone	4	0.20	0.02	0.755
Error	28	13.57		0.999
Salinity				
Habitat	1	0.24	0.20	0.655
Zone	4	66.87	56.87	**0.0001**
Habitat × zone	4	0.45	0.38	0.818
Error	28	1.18		
Dissolved oxygen				
Habitat	1	4.94	3.46	0.073
Zone	4	0.66	0.46	0.764
Habitat × zone	4	1.51	1.06	0.395
Error	28	1.42		

Figure 2. Crab density (number of crabs/300 m² plus standard error) by river zone in the York from trawls taken in July and August 1999 from (a) sand and mud habitats combined, (b) sand habitat, and (c) mud habitat. Since there was no significant Habitat × Zone interaction an SNK multiple comparison was run for Sand and Mud habitats combined (a). Bars with different letters are significantly different ($P < 0.05$, SNK). Note that the scale of panel (c) is different from that of (a) and (b). Densities are not corrected for trawl efficiency (~22%).

erally mirrored crab densities (Fig. 3a; Table 5). Clam density differed significantly by zone and habitat, but with a significant zone × habitat interaction effect which precluded general conclusions about the main effects (Table 5). In sand, clam density was significantly higher in the two upriver zones than the three

Table 4. ANOVA for log-transformed crabs/300 m² by habitat (mud and sand) and zone (mouth, downriver, mid-river, upriver, and head). Log-transformed densities were used to equalize variances (Bartlett's test).

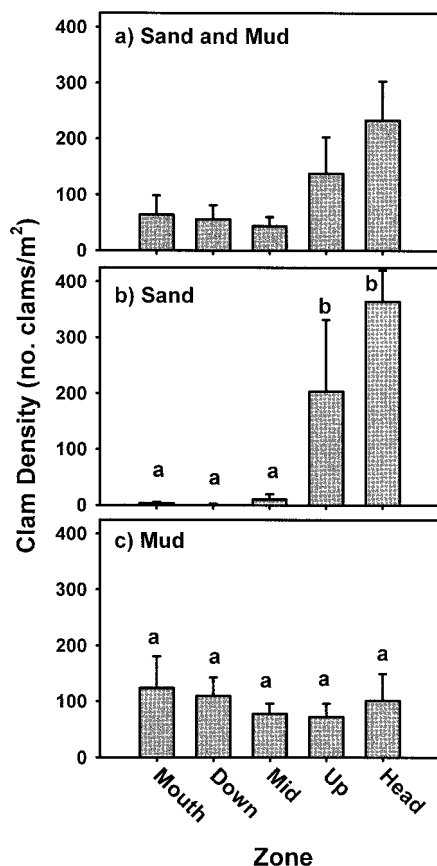| Source of variation	df	MS	F	P
Habitat	1	0.001	0.00	0.952
Zone	4	0.344	3.09	**0.032**
Habitat × zone	4	0.096	0.86	0.500
Error	27	0.111		

Figure 3. Clam density (number of clams/m² plus standard error) by river zone in the York from suction samples taken in July and August 1999 from (a) sand and mud sites combined, (b) sand habitat, and (c) mud habitat. Since there was a significant Habitat × Zone interactions, SNK multiple comparisons were run for both Sand and Mud habitats separately. Bars with different letters are significantly different ($P < 0.05$, SNK).

downriver zones (Fig. 3b; SNK, $P < 0.05$), whereas, in mud, clam density was intermediate and did not vary significantly by zone (Fig. 3c; SNK, $P > 0.05$).

CORRELATION ANALYSIS.—In sand and mud, crab density correlated negatively with salinity, but not with temperature or dissolved oxygen (Table 6). Using all 38 individual data points, crab density also correlated significantly with clam

Table 5. ANOVA for log(x + 1)-transformed clams/m² by habitat (mud and sand) and zone (mouth, downriver, mid-river, upriver, and head). Log-transformed densities were used to equalize variances (Bartlett's test).

Source of variation	df	MS	F	P
Habitat	1	3.986	15.20	**0.001**
Zone	4	1.717	6.55	**0.001**
Habitat × zone	4	2.185	8.34	**0.0005**
Error	28	0.262		

Table 6. Correlation matrix for sand and mud habitats comparing raw crab density/300 m^2 with physical variables (temperature, salinity, dissolved oxygen), and clam density/m^2 (19 data points for each habitat, four from each of 4 zones, and 3 from the 'head' zone). Values in each block are Pearson's correlation on top and *P*-value below. *P*-values < 0.05 are highlighted in bold.

	Crabs/300 m^2	Temp	Salinity	Clams/m^2
Sand				
Temperature	0.168			
	0.491			
Salinity	−0.553	0.122		
	0.014	0.619		
Clams/m^2	0.919	0.076	−0.677	
	0.0005	0.757	**0.0005**	
Dissolved oxygen	0.055	0.498	0.133	0.148
	0.822	**0.030**	0.587	0.546
Mud				
Temperature	0.381			
	0.108			
Salinity	−0.462	0.130		
	0.046	0.596		
Clams/m^2	−0.342	−0.049	0.233	
	0.152	0.843	0.338	
Dissolved oxygen	0.346	0.254	0.006	−0.335
	0.147	0.294	0.980	0.161

density in mud and sand sites combined (Fig. 4a). This relationship was driven by the sand habitat where crab density was significantly correlated with clam density (Fig. 4b; compare Figs. 2b and 3b; Table 6). In mud, where crab and clam densities were intermediate, they were not correlated (Fig. 4c; compare Figs. 2c and 3c; Table 6).

At the broad scale across both habitats, using a mean from each zone in each habitat (10 data points), crab density was correlated with salinity (Fig. 5a; $r^2 = 0.54$, $P = 0.015$). After removing the effect of salinity, crab density correlated highly with clam density (Fig. 5b; $r^2 = 0.60$, $P = 0.008$). When examining clam density first, crab density was significantly correlated with clam density (Fig. 5c; $r^2 = 0.76$, $P = 0.001$). After removing the effect of clam density, crab density was also correlated with salinity (Fig. 5d; $r^2 = 0.45$, $P = 0.034$).

At a local scale (i.e., the two upriver zones), in sand and mud combined (14 sites), salinity did not correlate significantly with crab density (linear regression: $r^2 = 0.14$, $P = 0.181$). However, crab density was highly correlated with clam density (Fig. 6; non-linear regression, $r^2 = 0.93$, $P < 0.0001$).

HYDRODYNAMIC TRANSPORT.—Using our model, when clam postlarvae were released from downriver coves, a high proportion was transported to upriver zones (Figs. 7 and 8). In contrast, the fraction transported to the 'mouth' zone was negligible. Transport to mid-river and downriver shallow sand or deep mud was low to moderate.

For blue crab postlarvae, settlement was greatest at the mouth because of high settlement in seagrass beds (Fig. 9; see Stockhausen and Lipcius, this issue, for details of spatial habitat grid). Settlement mid-river was moderate, and settlement to upriver and head zones was low. These predicted patterns for initial settlement of crab postlarvae do not correspond well with abundances of juvenile and adult crabs detected in the various zones (compare Figs. 2 and 9).
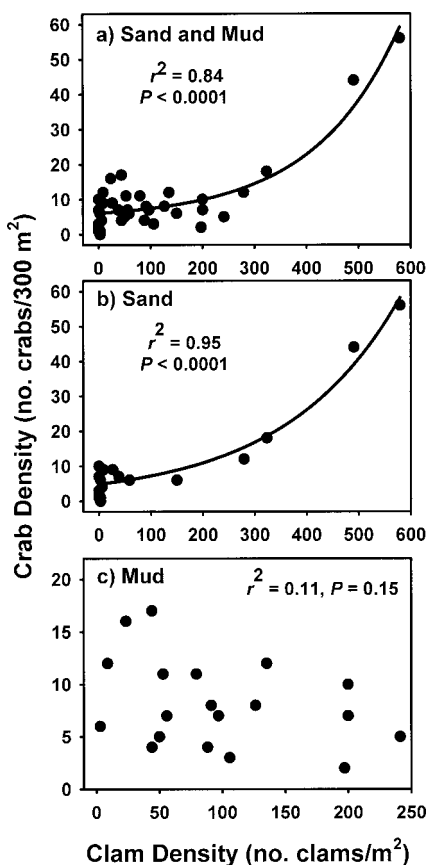
Figure 4.   Scatter plots and regression lines of York River crab and clam densities from: (a) sand and mud habitats in combined, non-linear regression; (b) sand sites alone, non-linear regression; (c) mud sites alone, linear regression. Note that scale in panel (c) is different from that in (a) and (b). Crab densities are not corrected for trawl efficiency.

DISCUSSION

Density of the blue crab (*Callinectes sapidus*) correlated significantly with density of its major prey, the Baltic clam (*Macoma balthica*), both across broad (50 km) and narrower (1–10 km) spatial scales in the York River, Chesapeake Bay. At the broad spatial scale, in addition to correlating with clam density, crab density also correlated with salinity but not with the simulated initial settlement of postlarvae predicted by hydrodynamic transport. Furthermore, after removing the effect of salinity, crab density remained highly correlated with clam density at the broad scale, suggesting that the broad distribution of crabs was dictated primarily by the distribution of clams. At a small spatial scale, where salinity did not differ, crab density remained highly correlated with clam density ($r^2 = 0.93$), suggesting strongly that a bottom-up factor (i.e., food) affected crab distributions at both spatial scales. The collective evidence is consistent with the hypothesis that crab density is driven by both food availability and salinity at broad spatial scales (10–50 km), whereas crab density is primarily controlled by food availability at smaller spatial scales (1–10 km). Hence, unvegetated habitats charac-
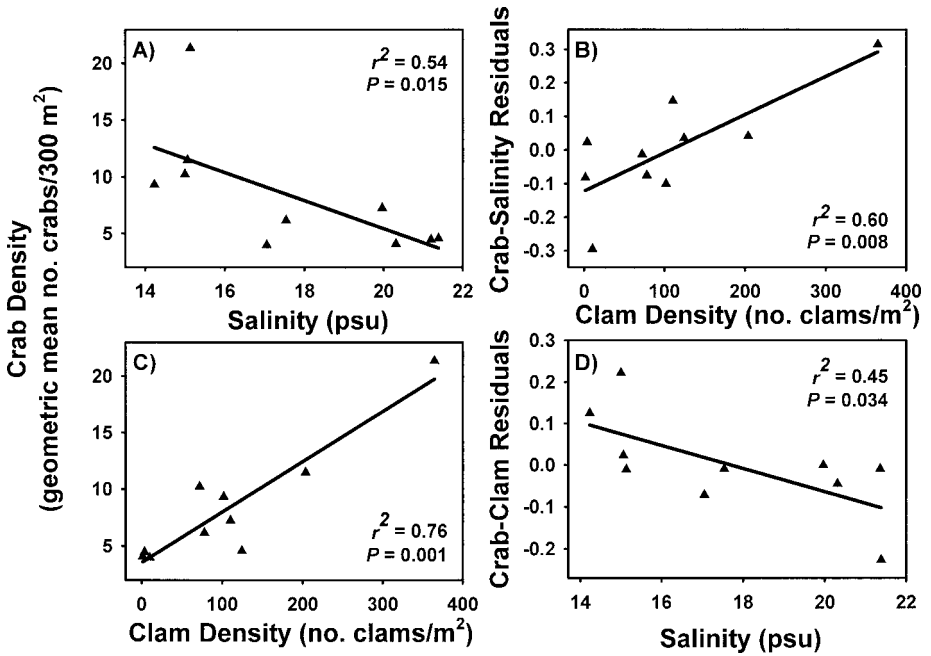
Figure 5. Broad-scale regressions derived from ten data points, each a mean from four sites in each habitat type (sand or mud) in each of the five river zones. (A) Crab density (geometric mean no. crabs/300 m^2) versus salinity (psu); regression equation $y = 1.96 - 0.062x$. (B) Residuals from the crab-salinity regression versus clam density (no. crabs m^2); regression equation $y = -0.122 + 0.001x$. (C) Crab density (geometric mean no. crabs/300 m^2) versus clam density (no. clams/m^2); regression equation $y = 0.652 + 0.002x$. (D) Residuals from the crab-clam regression versus salinity; regression equation $y = 0.492 - 0.028x$.
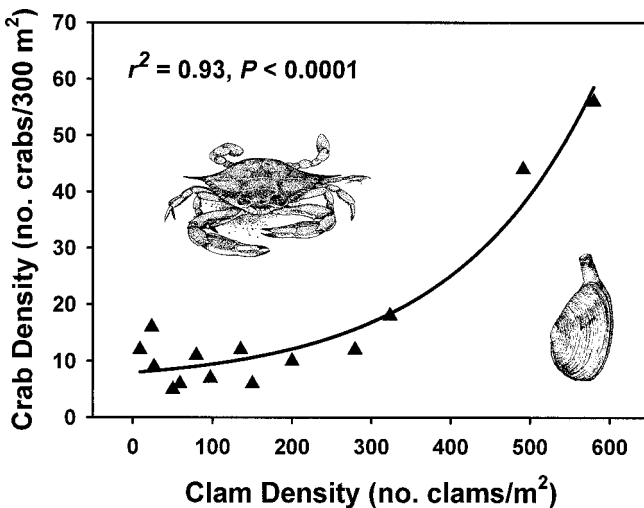

Figure 6. Scatter plot of raw crab and clam densities from sand and mud habitats (14 points) at the local scale from 'upriver' and 'head' zones (non-linear regression: $y = 5.99 + 1.98 \cdot e^{0.006x}$). *Callinectes sapidus* and the thin-shelled clam *Mya arenaria* are depicted.
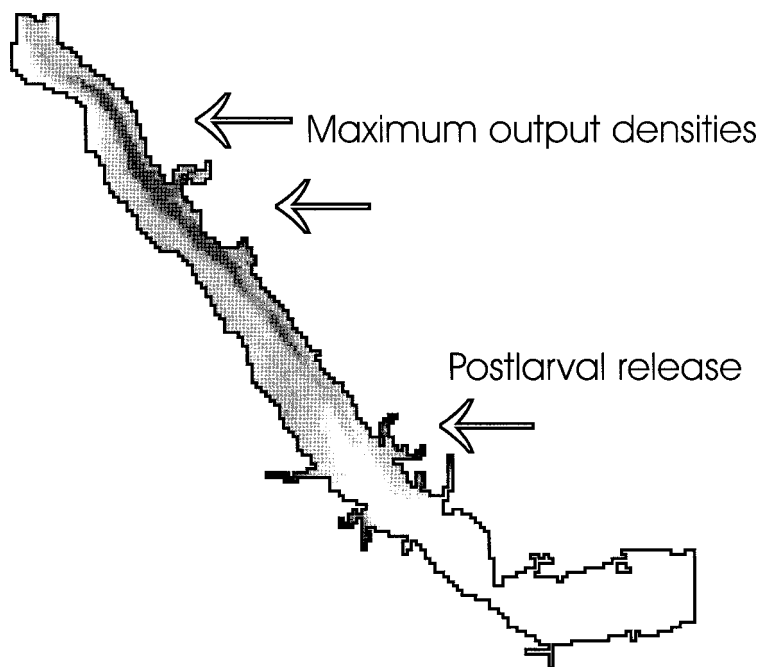
Figure 7.   Model output of hydrodynamic transport of clam postlarvae in the York River after pos-tlarvae were released in downriver coves and allowed 6 d in the plankton. Densities are integrated over the water column and benthos. Dark shading indicates high densities. Arrow for ''Postlarval release'' is pointing to the seven downriver coves where postlarvae were released. Arrows for ''Max-imum output densities'' indicate areas of dark shading upriver where maximum clam densities were predicted after 6 d in the plankton.

terized by high clam density may be critical in the population dynamics of the blue crab.

Top-down control of large juvenile and adult blue crabs is not likely, since these individuals obtain a size refuge from predation (Hines et al., 1990; Moody, 1994). Small juvenile crabs (<50 mm carapace width) may be consumed by some predatory fishes such as striped bass and red drum (J. Van Montfrans, unpubl. data), as well as conspecifics (Mansour, 1992).

Crab distribution patterns in sand and mud habitats were consistent with the hypothesis that crab density is driven mostly by clam density rather than by other factors. For example, crab densities were highest at the sites in sand where clam densities were highest. In mud, where clam densities were intermediate, crab densities also remained intermediate. This demonstration of bottom-up control of blue crabs is notable, since previous investigations failed to demonstrate bottom-up control of upper-trophic-level species (Micheli, 1999; Brett and Goldman, 1996).

Predators such as the blue crab select prey patches to maximize fitness or energy intake (Pyke, 1984; Stephens and Krebs, 1986), within the constraints of predator interference (Mansour and Lipcius, 1991), habitat features (Lipcius and Hines, 1986; Eggleston et al., 1992; Seitz et al., 2001), predation risk, and predator behavior (Micheli, 1997; Sih et al., 1998; Clark et al., 1999a). In our system, crab predators were apparently attracted to patches or zones where prey were concen-trated (e.g., sand habitats upriver).
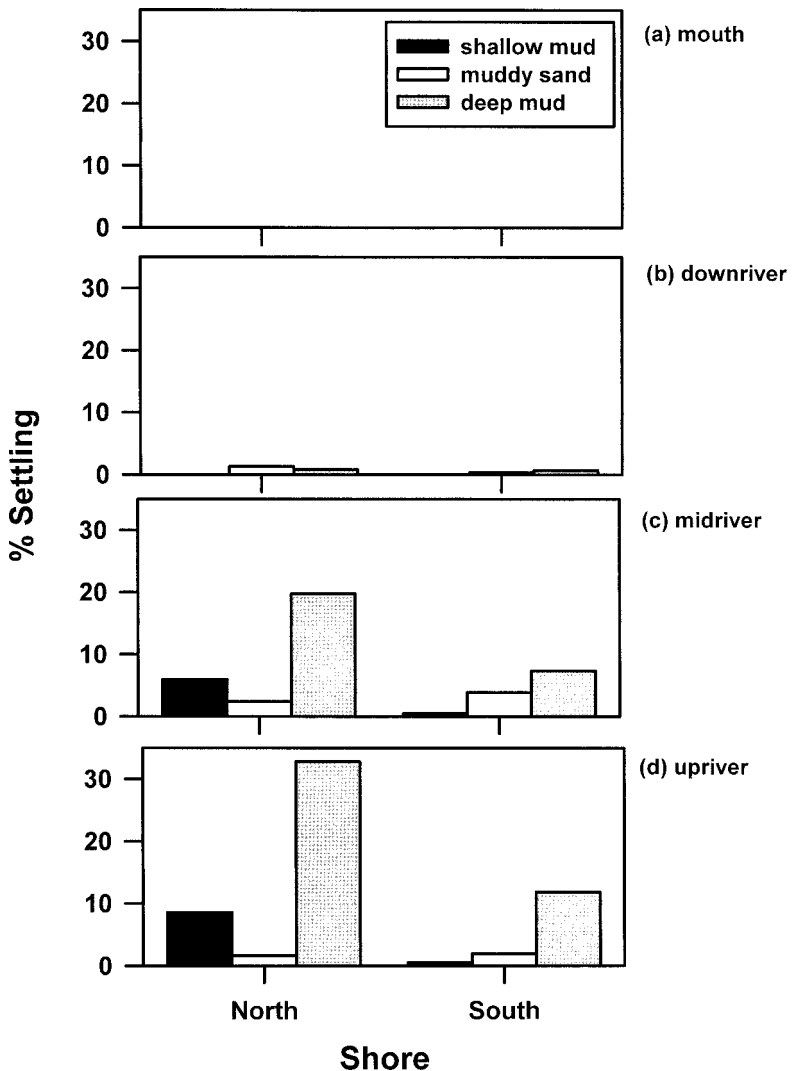
Figure 8. Hydrodynamic transport model estimates of percent settlement of clam postlarvae into various river zones (a) mouth, (b) downriver, (c) mid-river, and (d) upriver, on either the north or south shore of the river (estimated from model run depicted in Fig. 7). Postlarvae were released from the 7 largest downriver coves, allowed 6 d in the plankton, and after 6 d, were assumed to settle in the zones in which they persisted.

Since crab and clam densities were positively rather than negatively correlated, a hypothesis of top-down control of clams was not supported. We therefore suggest that clam distribution dictates crab distribution, rather than crabs controlling clams through predation. Clams persisted at high densities even in areas where crabs were abundant (i.e., upriver). Predation on clams may be limited in this system because of (1) agonistic interactions between crabs at high predator densities (Mansour and Lipcius, 1991), or (2) prey swamping of predators in the productive turbidity maximum zone (Seitz and Lipcius, 2001). At the local scale, crabs aggregate on clam patches (Clark et al., 1999a, 1999b), although their ability
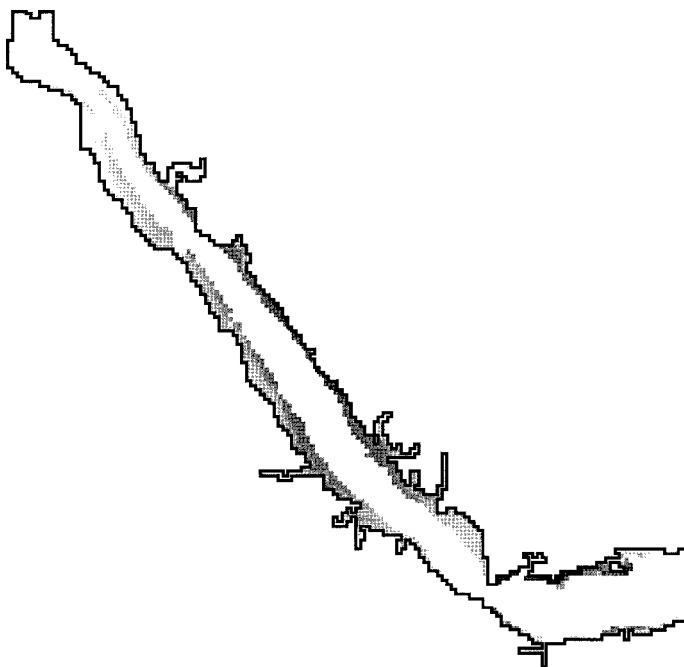
Figure 9. Model output of hydrodynamic transport of crab postlarvae in the York River after post-larvae were released at the mouth and allowed 6 d in the plankton. Densities are integrated over the water column and benthos. Dark shading indicates high densities. Settlement was restricted to areas <2 m depth.

to find patches and remain on them is influenced by both the density of conspecifics on patches and the distance between patches (Terwin et al., in review). Foraging success of blue crabs was reduced at high densities both in the lab (Mansour and Lipcius, 1991) and field (Clark et al., 1999b) because of aggressive interactions and mutual interference by conspecifics. Such aggressive interactions may afford a relative refuge from predation for clams in dense aggregations (i.e., in upriver sand habitats in the York River).

The correlations between clams and crabs were mainly driven by processes in the sand habitat. Whereas mud harbored intermediate densities of clams regardless of location in the river, sand harbored low densities of clams at downriver locations and high densities at upiver locations. Clam postlarvae can actively select settlement habitats (Sorlin, 1988; Beukema, 1993) as can crabs (Orth and van Montfrans, 1987; Olmi et al., 1990; van Montfrans et al., 1990), and zones of highest food quality (i.e., high carbon and nitrogen) were upriver. Apparently, at the broadest spatial scale (10–50 km) clams were either distributed upriver by hydrodynamic forces and remained there because of favorable conditions (i.e., plentiful food), or clams in downriver habitats continued post-settlement migration upriver until a favorable habitat was found (i.e., upriver or in mud coves downriver). In simulations, crab postlarvae were mainly distributed downriver, but potentially could continue post-settlement dispersal to a more suitable habitat (i.e., upriver). Hydrodynamic transport of clams to upriver habitats was high, but initial transport of crab postlarvae upriver was extremely low.

Previous authors have examined the blue crab-clam relationship in association with habitat and clam density. For example, predation on *Macoma* in both sand

and mud habitats in the lab (Eggleston et al., 1992) and the field (Seitz et al., 2001) is density dependent (i.e., there is a low-density refuge from predation). The mechanism underlying a low-density refuge from predation is the relatively lower encounter rate and feeding efficiency of blue crabs at low prey densities (Lipcius and Hines, 1986; Mansour and Lipcius, 1991; Eggleston et al., 1992; Micheli, 1997). Blue crabs search for prey by probing the sediment with the tips of their walking legs. Thus, we would predict that the predator would move to more profitable patches as prey become scarce or difficult to detect (e.g., Clark et al., 1999a, 1999b). Such a low-density refuge is likely maintained even at high predator densities due to mutual interference between predators (Ens and Goss-Custard, 1984; Mansour and Lipcius, 1991; Micheli, 1997). In our system, mutual interference among predators may likewise explain the persistence of elevated clam densities amid high predator densities upriver.

There was a trend of increased clam densities with elevated sedimentary carbon, although clam densities did not significantly correlate with sedimentary carbon at small spatial scales. Thus, we suggest possible bottom-up control of clam densities, as observed in previous studies (Seitz, 1996; Seitz and Lipcius, in press). In addition to sedimentary carbon, planktonic food availability (i.e., chlorophyll *a* [chl *a*]) might also be important, since *Macoma* can filter feed as well as deposit feed (Skilleter and Peterson, 1994; Lin and Hines, 1994; de Goeij and Luttink-huizen, 1998). *Macoma* deposit feed when sedimentary food is plentiful, and suspension feed when food is readily available in the water column or when there is an absence of food on the sediment surface (Hummel, 1985; Ólaffson, 1986; Kamermans et al., 1992).

Although chl *a* was not measured in our study, it was previously measured along a transect from the mouth to the head of the York River (J. Maa, unpubl. data). The concentration of chl *a* in bottom water was lower downriver near the mouth (~8 ug/L in October 1996) than near the head of the river at West Point (~28 ug/L in October 1996). Consequently, planktonic food availability for *Macoma* in the York River appears to parallel sedimentary carbon availability with generally greater concentrations upriver. Hence, the elevated clam densities upriver may have been a consequence of high water column chl *a* or sedimentary C and N in upriver habitats.

The enhanced density and biomass of clams in the upriver zone may be caused by physical processes in association with the turbidity maximum of this partially mixed estuary. The turbidity maximum in the York River extends from the 'head' zone down through the 'upriver' zone (see Fig. 1) (Schaffner et al., 2001). Typically, turbidity maxima are characterized by water-borne sediment concentrations $10–100\times$ greater than those farther downstream (Nichols and Biggs, 1985). Turbidity maximum zones trap fine sediments and enhance food availability for deposit feeders, such as the clams in our system. Augmented densities of clams in the turbidity maximum zone may have subsequently led to elevated crab densities.

Though this study was conducted in shallow water in one tributary of Chesapeake Bay, the observed crab and clam densities are similar to deeper habitats and other tributaries such that conclusions for the York River may be applicable to other tributaries and systems. For instance, in deeper areas of the York and Rappahannock rivers (i.e., mud channels), crab and clam densities were elevated in upriver zones compared with downriver zones (Lipcius and Van Engel, 1990; Mansour, 1992; Seitz, 1996; Schaffner et al., 2001). Thus, large tributaries with geography and hydrography similar to that of the York River may show comparable crab-clam correlations and bottom-up control.

An alternative hypothesis to explain the differential distribution of clams is that

predation on clams reduced their densities downriver; this hypothesis was previously investigated and rejected (Seitz and Lipcius, 2001). In the York River, proportional mortality of transplanted clams was significantly greater upriver, in the high-density clam habitat, than downriver. This pattern held across three experimental trials through the summer of 1995 (Seitz and Lipcius, 2001), and thus does not explain higher clam densities upriver. In the present study, the two zones that varied in clam density were separated by approximately 50 km, and crabs could not readily migrate between the two zones (Mansour, 1992; Hines et al., 1995). Crabs apparently congregated where their main food source (i.e., clams; Hines et al., 1990) was in greatest abundance, yet their predation in that zone was not extreme enough to drive clams to low densities (Seitz and Lipcius, 2001).

Similarly, crab density in the smaller-scale Rhode River (5 km length) was elevated in a high-clam-density habitat compared with a low-clam-density habitat, although foraging efficiency was reduced in the former habitat. In the smaller-scale Rhode River system, predators had higher foraging efficiency in the low-clam-density habitat and could easily migrate between habitats differing in clam density (Seitz and Lipcius, 2001). Because of the small scale of the river, predators could more easily benefit from reduced aggressive interactions with conspecifics in a low-clam-density habitat than they could in a larger-scale system where their access to such habitats may be limited. Thus, regardless of spatial scale, in unvegetated habitats, crab density is positively correlated with clam density, but the resultant effect on the benthic community may differ depending on a crab's accessibility to other habitats.

While the value of seagrass beds for juvenile blue crabs is recognized (Orth and van Montfrans, 1987; Olmi et al., 1990; Perkins-Visser et al., 1996; Pile et al., 1996), the role of unvegetated habitats, particularly habitats such as those in the upriver zones of the York where food resources are plentiful, needs further attention. The high crab densities in upriver unvegetated habitats suggests that these habitats play a key role in blue crab population dynamics. These habitats are numerous throughout Chesapeake Bay and are often characterized by abundant food (Mansour, 1992; Seitz, 1996; Seitz and Lipcius, 2001). We suggest that, in addition to well-studied habitats (i.e., seagrass beds), those habitats with plentiful food (i.e., habitats with high clam densities) and elevated crab densities should also be considered essential and be targeted for protection in conservation efforts.

Literature Cited

Arditi, R. and L. R. Ginzburg. 1989. Coupling in predator-prey dynamics: ratio-dependence. J. Theor. Biol. 139: 311–326.

Arnold, S. K. 1984. The effects of prey size, predator size and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* Rathbun, on the hard clam, *Mercenaria mercenaria* (Linne). J. Exp. Mar. Biol. Ecol. 80: 207–219.

Baker, P. K. and R. Mann. 1997. The post-larval phase of bivalve mollusks: a review of functional

ecology and new records of post-larval drifting in Chesapeake Bay bivalves. Bull. Mar. Sci. 61: 409–430.

Beukema, J. J. 1993. Successive changes in distribution patterns as an adaptive strategy in the bivalve *Macoma balthica* (L.) In the Wadden Sea. Helgol. Meersunter. 47: 287–304.

———— and B. W. Meehan. 1985. Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica.* Mar. Biol. 90: 27–33.

Blundon, J. A. and V. S. Kennedy. 1982a. Mechanical and behavioral aspects of blue crab, *Callinectes sapidus* (Rathbun), predation on Chesapeake Bay bivalves. J. Exp. Mar. Biol. Ecol. 56: 47–65.

———— and ————. 1982b. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. J. Exp. Mar. Biol. Ecol. 56: 67–81.

Brett, M. R. and C. R. Goldman. 1996. A meta-analysis of the freshwater trophic cascade. Proc. Nat. Acad. Sci. USA 93: 7723–7726.

———— and ————. 1997. Consumer versus resource control in freshwater pelagic food webs. Science 275: 384–386.

Clark, M. E., T. G. Wolcott, D. L. Wolcott and A. H. Hines. 1999a. Intraspecific interference among foraging blue crabs *Callinectes sapidus*: interactive effects of predator density and prey patch distribution. Mar. Ecol. Prog. Ser. 178: 69–78.

————, ————, ———— and ————. 1999b. Foraging and agonistic activity co-occur in free-ranging blue crabs (*Callinectes sapidus*): observations of animals by ultrasonic telemetry. J. Exp. Mar. Biol. Ecol. 233: 143–160.

————, ————, ———— and ————. 2000. Foraging behavior of an estuarine predator, the blue crab *Callinectes sapidus* in a patchy environment. Ecography 23: 21–31.

Dauer, D. M., R. M. Ewing, G. H. Tourtellotte, W. T. Harlan, J. W. Sourbeer and H. R. Barker, Jr. 1982a. Predation, resource limitation and the structure of benthic infaunal communities of the lower Chesapeake Bay. Intern. Rev. der ges Hydrobiol. 67: 477–489.

————, R. M. Ewing, J. W. Sourbeer, W. T. Harlan and T. L. Stokes, Jr. 1982b. Nocturnal movements of the macrobenthos of the Lafayette River, Virginia. Intern. Rev. der ges. Hydrobiol. 67: 761–775.

de Goeij, P. and P. Luttikhuizen. 1998. Deep-burying reduces growth in intertidal bivalves: field and mesocosm experiments with *Macoma balthica.* J. Exp. Mar. Biol. Ecol. 228: 327–337.

Diaz, R. J. and R. Rosenberg. 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanog. Mar. Biol. Ann. Rev. 33: 245–303.

Duffy, E. J. and M. E. Hay. 2000. Ecology and evolution of marine consumer-prey interactions. Pages 131–157 *in* M. D. Bertness, M. E. Hay and S. D. Gaines, eds. Marine community ecology. Sinauer Associates.

Eggleston, D. B., R. N. Lipcius and A. H. Hines. 1992. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. Mar. Ecol. Prog. Ser. 85: 55–68.

Ens, B. J. and J. D. Goss-Custard. 1984. Interference among oystercatchers, *Haematopus ostralegus,* feeding on mussels, *Mytilus edulis,* on the Exe Estuary. J. Anim. Ecol. 53: 217–231.

Folk, R. L. 1980. Petrology of sedimentary rocks. Hemphill Publishing Co., Austin, Texas, U.S.A. 182 p.

Garrison, L. P. 1997. The influence of physical transport and nutritional stress on the zooea of estuarine crabs. Ph.D. dissertation, School of Marine Science, The College of William and Mary, Gloucester Point, Virginia. U.S.A.

Getz, W. M. 1984. Population dynamics: a *per capita* resource approach. J. Theor. Biol. 108: 623–643.

Hamrick, J. M. 1992. A three-dimensional environmental fluid dynamics computer code: theoretical and computational aspects. SRAMSOE no. 317, VIMS, Gloucester Point, Virginia. 63 p.

————. 1996. User's manual for the environmental fluid dynamics code. SRAMSOE no. 331, VIMS, Gloucester Point, Virginia. 223 p.

Hines, A. H. and K. Comtois. 1985. Vertical distribution of estuarine infauna in sediments of central Chesapeake Bay. Estuaries 8: 251–261.

————, A. M. Haddon and L. A. Wiechert. 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. Mar. Ecol. Prog. Ser. 67: 105–126.

————, A. M. Haddon, J. J. Miklas, L. A. Wiechert and A. M. Haddon. 1987. Estuarine invertebrates and fish: sampling design and constraints for long-term measurements of population dynamics. Pages 140–164 *in* T. P. Boyle, ed. New approaches to monitoring aquatic ecosystems. ASTM STP 940, American Society of Testing and Materials, Philadelphia, Pennsylvania, U.S.A.

————, T. G. Wolcott, E. González-Gurriarán, J. L. González-Gurriarán and J. Friere. 1995. Movement patterns and migrations in crabs: telemetry studies of juvenile and adult behavior in *Callinectes sapidus* and *Maja squinado.* Journal of the Marine Biological Association, U.K. 75: 27–42.

Holland, A. F. 1985. Long-term variation in macrobenthos in the mesohaline region of Chesapeake Bay. Estuaries 8: 93–113.

Homer, M., J. H. Mihursky and P. Jones. 1980. Quantitative approaches towards characterizing estuarine fish populations and communities. Pages 39–99 *in* American Fisheries Society—The Potomac Chapter. Proceedings of the fourth annual meeting.

Horwood, J. W. and J. D. Goss-Custard. 1977. Predation by the oystercatcher, *Haematopus ostralegus* (L.), in relation to the cockle, *Cerastoderma edule* (L.), fishery in the Burry Inlet, South Wales. J. Appl. Ecol. 14: 139–158.

Hummel, H. 1985. Food intake of *Macoma balthica* (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea. Neth. J. Sea Res. 19: 52–76.

Kamermans, P., H. W. van der Veer, L. Karczmarski and G. W. Doeglas. 1992. Competition in deposit- and suspension-feeding bivalves: experiments in controlled outdoor environments. J. Exp. Mar. Bio. Ecol. 162: 113–135.

Laughlin, R. A. 1982. Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary, Florida. Bull. Mar. Sci. 32: 807–822.

Lin, J. and A. H. Hines. 1994. Effects of suspended food availability on the feeding mode and burial depth of the Baltic clam, *Macoma balthica*. Oikos 69: 28–36.

Lipcius, R. N. and A. H. Hines. 1986. Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. Ecology 67: 1361–1371.

————— and W. T. Stockhausen. 2002. Concurrent decline of spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. Mar. Ecol. Prog. Ser. 226: 45–61.

————— and W. A. Van Engel. 1990. Blue crab population dynamics in Chesapeake Bay: variation in abundance (York River, 1972–1988) and stock-recruit functions. Bull. Mar. Sci. 46: 180–194.

Mann, R. and D. A. Evans. 1998. Estimation of oyster, *Crassostrea virginica*, standing stock, larval production and advective loss in relation to observed recruitment in the James River, VA. J. Shellfish Res. 17: 239–253.

Mansour, R. A. 1992. Foraging ecology of the blue crab, *Callinectes sapidus* Rathbun, in lower Chesapeake Bay. Dissertation, The College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, Virginia, U.S.A.

————— and R. N. Lipcius. 1991. Density-dependent foraging and mutual interference in blue crabs preying upon infaunal clams. Mar. Ecol. Prog. Ser. 72: 239–246.

Martini, I. P. and R. I. G. Morrison. 1987. Regional distribution of *Macoma balthica* and *Hydrobia minuta* on the subarctic coasts of Hudson Bay and James Bay, Ontario, Canada. Est. Coast. Shelf Sci. 24: 47–68.

McQueen, D. J., M. R. S. Johannes, J. R. Post, T. J. Steward and D. R. S. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecol. Monogr. 59: 289–309.

Menge, B. A. and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. Trends Ecol. Evol. 5: 52–57.

————— and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am. Nat. 130: 730–757.

—————, B. Daley and P. A. Wheeler. 1996. Control of interaction strength in marine benthic communities. Pages 258–274 *in* G. A. Polis and K. O. Winemiller, eds. Food webs: integration of pattern and dynamics. Chapman and Hall, Chap. 25.

—————, —————, ————— and P. T. Strub. 1997. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. Limnol. Oceanog. 42: 57–66.

Micheli, F. 1997. Effects of predator foraging behavior on patterns of prey mortality in marine soft bottoms. Ecol. Monogr. 67: 203–224.

—————. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. Science 285: 1396–1398.

Moody, K. E. 1994. Predation on juvenile blue crabs, *Callinectes sapidus* Rathbun, in lower Chesapeake Bay: patterns, predators, and potential impacts. Ph.D. dissertation, The College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, Virginia, U.S.A.

Nichols, M. M. and R. B. Biggs. 1985. Estuaries. Pages 77–186 *in* R. A. Davis, ed. Coastal sedimentary processes. Springer-Verlag, New York, New York.

Ólafsson, E. B. 1986. Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica*: a field experiment. J. Anim. Ecol. 55: 517–526.

Olmi, E. J., J. van Montfrans, R. N. Lipcius, R. J. Orth and P. W. Sadler. 1990. Variation in planktonic availability and settlement of blue crab megalopae in the York River, Virginia. Bull. Mar. Sci. 46: 230–243.

Orth, R. J. and J. van Montfrans. 1987. Utilization of seagrass meadow and tidal marsh creek by blue crabs, *Callinectes sapidus*. I. Seasonal and annual variation in abundance with emphasis on post-settlement juveniles. Mar. Ecol. Prog. Ser. 41: 283–283–294.

————, J. van Montfrans, R. N. Lipcius and K. S. Metcalf. 1996. Utilization of seagrass habitat by the blue crab, callinectes sapidus Rathbun, in Chesapeake Bay: a review. Pages 213–244 *in* J. Kuo, R. C. Phillips, D. I Walker and H. Kirkman, eds. Seagrass biology: proceedings of an international workshop. Western Australian Museum, Perth, Australia.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. J. Animal Ecol. 49: 667–685.

Peckarsky, B. L., S. C. Horn and B. Statzner. 1990. Stonefly predation along a hydraulic gradient: a field test of the harsh-benign hypothesis. Freshwater Biol. 24: 181–191.

Perkins-Visser, E., T. G. Wolcott and D. L. Wolcott. 1996. Nursery role of seagrass beds: Enhanced growth of juvenile blue crabs (*Callinectes sapidus* Rathbun). J. Exp. Mar. Biol. Ecol. 198: 155–173.

Peterson, C. H. and G. A. Skilleter. 1994. Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica,* flow environment, and siphon-cropping fishes. Oecologia 100: 256–267.

Pile, A. J., R. N. Lipcius, J. van Montfrans and R. J. Orth. 1996. Density dependent settler : recruit : juvenile relationships in blue crabs: mechanisms and effects of a tropical storm. Ecol. Monogr. 66: 277–300.

Posey, M. C. Powell, L. Cahoon and D. Lindquist. 1995. Top down vs. bottom up control of benthic community composition on an intertidal tideflat. J. Exp. Mar. Biol. Ecol. 185: 19–31.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73: 733–746.

Pyke, G. H. 1984. Optimal foraging theory: a critical review. Ann. Rev. Ecol. Syst. 15: 523–575.

Ruiz, G. M., A. H. Hines and M. H. Posey. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Mar. Ecol. Prog. Ser. 99: 1–16.

Schaffner, L. C., T. M. Dellapenna, E. K. Hinchey, C. T. Fridrichs, M. T. Neubauer, M. E. Smith and S. A. Kuehl. 2001. Physical energy regimes, seabed dynamics and organism-sediment interactions along an estuarine gradient. Pp. 161–182 *in* J. Y. Aller, S. A. Woodin and R. C. Aller, eds. Organism-sediment interactions. University of South Carolina Press, Columbia, South Carolina.

Seitz, R. D. 1996. The role of epibenthic predators in structuring marine soft-bottom communities along an estuarine gradient. Ph.D. dissertation, The College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, Virginia, U.S.A.

———— and R. N. Lipcius. 2001. Variation in top-down and bottom-up control of marine bivalves at differing spatial scales. ICES J. Mar. Sci. 58: 689–699.

————, R. D., R. N. Lipcius, A. H. Hines and D. B. Eggleston. 2001. Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. Ecology 82(9): 2435–2451.

Shen, J., J. D. Boon and G. M. Sisson. 1997. Hydrodynamic model Hem-3D: clam larval dispersions, James River. VIMS report to Virginia Marine Resources Commission, Plans and Statistics Dept., Virginia Institute of Marine Science, Gloucester Point, Virginia. 14 p.

Sih, A., G. Englund and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends Ecol. Evol. 13: 350–355.

Sisson, G. M., J. Shen, S.-C. Kim, J. D. Boon and A. Y. Kuo. 1997. VIMS three-dimensional hydrodynamic-eutrophication model (HEM-3D): application of the hydrodynamic model to the York River system. SRAMSOE no. 341, VIMS, Gloucester Point, Virginia. 64 p.

Skilleter, G. A. and C. H. Peterson. 1994. Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica* and interactions between competition and siphon cropping. Oecologia 100: 268–278.

Sorlin, T. 1988. Floating behaviour in the tellinid bivalve *Macoma balthica* (L.). Oecologia 77: 273–277.

Stephens, D. W. and J. R. Krebs, eds. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey, U.S.A.

Stockhausen, W. T. and R. N. Lipcius. 2003. Impact of seagrass loss and restoration on spatial patterns of settlement by blue crab postlarvae and young juveniles in Chesapeake Bay: a modeling approach. Bull. Mar. Sci. 71. This volume.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73: 747–754.

Terwin, J. R., A. H. Hines and S. F. Thrush. In Review. Scale matters: the spatial distribution of prey patches affects predation rates in an estuarine benthic community. J. Exp. Mar. Biol. Ecol.

Underwood, A. J. 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, U.K.

van Montfrans, J., C. A. Peery and R. J. Orth. 1990. Daily, monthly and annual settlement patterns by *Callinectes sapidus* and *Neopanope sayi* megalopae on artificial collectors deployed in York River, Virginia 1985–1988. Bull. Mar. Sci. 46: 214–229.

Virnstein, R. W. 1977. The importance of predation by blue crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58: 1199–1217.

West, D. L. and A. H. Williams. 1986. Predation by *Callinectes sapidus* (Rathbun) within *Spartina alterniflora* (Loisel) marshes. J. Exp. Mar. Biol. Ecol. 100: 75–95.

Williams, A. B. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C., U.S.A.

Wilson, W. H. 1991. Competition and predation in marine soft-sediment communities. Ann. Rev. Ecol. Syst. 21: 221–241.

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