

# Ontogenetic changes in habitat use by postlarvae and young juveniles of the blue crab

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**ABSTRACT:** Changing habitat requirements are evident during the developmental cycles of many species. In this field investigation, we attempted to distinguish between depth (shallow vs deep), habitat structure (seagrass species), and study site as factors influencing the distribution and abundance of postlarvae and juvenile blue crabs *Callinectes sapidus* in the Chesapeake Bay. Deep ( $\geq 70$  cm mean low water [MLW]) and shallow ( $\leq 50$  cm MLW) suction samples in monospecific *Zostera marina* and *Ruppia maritima* beds were taken in the York River, a tributary of the Chesapeake Bay. Our studies revealed ontogenetic changes in habitat use, which suggested that blue crabs are influenced differently by physical and biological factors even during the earliest life stages. Postlarvae through 3rd instar distributions were not related to seagrass species, but their densities increased with distance upriver (regression,  $p < 0.004$ ,  $n = 36$ , postlarvae:  $r^2 = 0.173$ , 1st instars:  $r^2 = 0.308$ , 2nd–3rd instars:  $r^2 = 0.231$ ). This suggests that the smallest instar distributions are related to larval supply and physical forces, such as currents and winds, which determine water-column transport. In contrast, 4th and greater instars were significantly more abundant in *Ruppia* than in *Zostera* (ANOVA,  $df = 1$ ,  $p < 0.05$ ), possibly because of the high shoot density of *Ruppia* beds. Habitat use by 4th and greater instars may be related to seasonal changes in seagrass shoot density. Water depth did not influence the distribution of any crab stage. We suggest that habitat selection and differential mortality among habitats influence larger instar distributions more strongly than they influence the distribution of postlarvae and the earliest instars of *C. sapidus*.

**KEY WORDS:** Blue crabs · *Callinectes sapidus* · Ontogenetic changes · Habitat structure · Habitat use · Settlement · Recruitment · Shallow-water refuge · Seagrass beds

## INTRODUCTION

Distributions of marine organisms are often mediated by habitat complexity (Roughgarden et al. 1988, Olmi et al. 1990, Eggleston & Armstrong 1995), which is defined by structural aspects of the environment, such as rock, heterogeneous sediments, oyster reefs, worm tubes, macroalgae and emergent or submersed vegetation (Marinelli & Coull 1987, Day & Lawton 1988, Wilson et al. 1990, Heck & Crowder 1991, Schneider & Mann 1991a, Love & Bailey 1992). High organism abundances in complex habitats may be due to flow-induced transport (Eckman 1983, Eckman & Nowell 1984, Butman 1987), reduced predation (decapod crustaceans, Heck & Thoman 1981; spiny lobster, Herrinck & Butler 1986, Lipcius et al. 19998; queen conch, Ray & Stoner 1995; amphipods, Ryer 1987; Atlantic cod,

Tupper & Boutilier 1995), abundant living space, and food availability (snails, Bronmark 1985; amphipods, Hacker & Steneck 1990; juvenile spiny lobster, Herrinck & Butler 1986; epifaunal invertebrates, Schneider & Mann 1991b; juvenile blue crab, Perkins-Visser et al. 1996).

Water depth can also affect species distributions. In simple, unstructured areas, many organisms take refuge in shallow water (Ruiz et al. 1993), where their predators (e.g. larger finfish or invertebrates) are less abundant. These primary predators may avoid shallow water because of their susceptibility to avian and mammalian predators higher in the food web, because of decreased foraging ability, or because of fluctuating temperature and oxygen levels (Ruiz et al. 1993, Loneragan et al. 1994, Dittel et al. 1995, Lonzarich & Quinn 1995, Platell & Potter 1996). Alternatively, high food abundances can attract both prey and predators into shallow water in some systems (Miltner et al. 1995).

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Interactions between depth and habitat complexity occur in some habitats. Plant species composition, leaf morphology, and the abundances of woody debris, shells and rooted submersed aquatic plants often change with depth (den Hartog 1977, Duarte 1991, Platell & Potter 1996). In seagrass beds, habitat complexity and depth collectively influence species distributions. The high density and diversity of fauna associated with seagrass beds (Orth 1977, Orth et al. 1984, Heck et al. 1995) can vary within and between seagrass species (Schneider & Mann 1991b). Measures of habitat complexity, such as plant biomass, blade density, leaf surface area, plant architecture, and plant species composition, may explain these patterns (Stoner 1980, 1983, Orth et al. 1984, Stoner & Lewis 1985, Virnstein & Howard 1987, Orth 1992, Lipcius et al. 1998). Seagrass beds also slow currents and enhance deposition of fine sediments and passive plankters. This effect varies with plant morphology, bed shape, size and height of different seagrass species (Kikuchi & Peres 1977, Fonseca & Fisher 1986) and may influence larval distributions (Orth 1992).

Given the many facets of habitat complexity and the limitations of space, food, or refugia in the marine environment, the distributions of many organisms shift during development. An obvious example is an organism, such as the blue crab, progressing from a planktonic to a benthic existence (Olm et al. 1990). Such ontogenetic changes in habitat use can result from changing nutritional needs, competition, and predation. During development, the spiny lobster *Panulirus argus* shifts from plankton to macroalgae to crevices, and finally ventures into open spaces when it is large enough to deter predators (Childress & Herrnkind 1994). In a laboratory experiment, small and medium Jonah crabs chose cobble substrate over sand more frequently and burrowed deeper than large crabs, compensating for their increased vulnerability to predation (Richards 1992). This investigation reveals subtle changes in the habitat use of blue crabs during the rapid growth of the earliest life stages.

In the Chesapeake Bay, 2 seagrass species with distinct morphologies and spatial distributions dominate shoal areas (< 2 m at mean low water [MLW]): widgeon grass *Ruppia maritima* (hereafter *Ruppia*) and eelgrass *Zostera marina* (hereafter *Zostera*). Vegetative *Zostera* has wide, straplike blades; reproductive *Zostera*, appearing from April to June in the Chesapeake Bay, has longer, branched shoots, each with several spathes (den Hartog 1970, Orth & Moore 1986). In contrast, vegetative *Ruppia* has short, threadlike shoots. Reproductive *Ruppia*, growing mainly from July through September, has highly branched, threadlike shoots, which can reach over a meter in length. *Ruppia* commonly grows in monospecific stands in shallow

water (approx. < 0.3 m MLW). At intermediate depths (approx. 0.3 to 0.6 m MLW), *Zostera* and *Ruppia* co-occur, while in deep water (approx. > 0.6 m MLW), generally only *Zostera* is abundant (Orth & Moore 1988).

Seagrass beds in the lower Chesapeake Bay are an important nursery habitat for the blue crab *Callinectes sapidus* (Orth & van Montfrans 1987, Orth et al. 1996, Pile et al. 1996). After larval development on the continental shelf (Epifanio 1988), blue crab postlarvae reinvade the Chesapeake Bay and settle in seagrass beds, where growth through several juvenile stages occurs. The effectiveness of a seagrass bed as a refuge is a function of crab density (Perkins-Visser et al. 1996, Moksnes et al. 1997), crab size (Pile et al. 1996) and seagrass characteristics (Heck & Thoman 1981, Williams et al. 1990, Schulman 1996). Postlarval settlement occurs episodically from July to November, with pulses associated with the full and new moons (van Montfrans et al. 1990, 1995).

Floral species composition and water depth are fundamental and ubiquitous features of the seagrass habitat, and likely influence survival, feeding and habitat preferences of blue crab postlarvae and young juveniles. Previous studies have not distinguished the effects of water depth and seagrass species on blue crab distributions, despite studies indicating that juveniles of epibenthic species should be more abundant in shallow (Ruiz et al. 1993), complex seagrass habitats (Humphries 1996). Also, blue crabs at different stages of growth could be influenced differently by physical and biological forces, even during the earliest stages of development. Hence, the objective of this study was to determine the effect of seagrass species and water depth on blue crab distributions, and examine ontogenetic changes in these distributions with respect to seagrass species and depth.

## STUDY SITES

This investigation took place during the summers of 1994 and 1995, in the lower York River, within beds of *Ruppia* and *Zostera* (Fig. 1). Seagrasses were especially abundant along the north shore, from the river mouth to Gloucester Point. On the south shore, seagrasses were only abundant at the mouth. There were 2 types of seagrass beds: (1) monospecific *Zostera* beds in shallow and deep water (20 to 100 cm MLW), and (2) *Ruppia/Zostera* beds, in which monospecific *Ruppia* in the shallows ( $\leq 50$  cm MLW) graded into monospecific *Zostera* at deeper depths ( $\geq 70$  cm MLW). Only monospecific areas within *Ruppia/Zostera* beds were sampled (Fig. 2). Mixed beds were excluded from sampling.



In 1994, reproductive and vegetative *Ruppia* were present during sampling. Reproductive *Zostera* defoliated prior to sampling in both 1994 and 1995, as did reproductive *Ruppia* in 1995. In 1994, water temperature ranged between 21 and 28°C. Salinity ranged between 12 and 22‰. On the north shore, *Ruppia* beds were in water depths from 15 to 48 cm MLW, and *Zostera* beds from 47 to 85 cm MLW. On the south shore, *Ruppia* beds were in water depths from 20 to 34 cm MLW, and *Zostera* beds from 25 to 59 cm MLW. In 1995, sediments at the study sites were generally 80 to 90% sand and 10 to 20% silt and clays. Water temperature ranged between 20 and 25°C. Salinity ranged between 20 and 25‰. Blue crab postlarvae recruit to the York River from mid-July to November (van Montfrans et al. 1990, 1995), where they settle in seagrass beds and grow through the early juvenile instars (Lipcius et al. 1990, Olmi et al. 1990, Orth et al. 1996).

## MATERIALS AND METHODS

In 1994, we tested the hypothesis that early-stage blue crabs were evenly distributed between adjacent *Ruppia* and *Zostera* beds. A grid (100 × 100 m) was established near the York River mouth on each shore: Guinea Marsh (north) and Goodwin Island (south)

(Fig. 1). Each grid enclosed approximately equal proportions of *Ruppia* in the shallows and *Zostera* in deeper areas. Mixed grassbeds in the center of the grids were excluded from sampling. Prior to sampling, grids were marked at 10 m intervals, resulting in 100 quadrats, each 10 × 10 m. On each sampling date, 20 quadrats were randomly selected from each grid: 10 each in *Zostera* and *Ruppia* areas.

As in previous summers, blue crab postlarval abundance was monitored in the York River with nightly plankton samples and artificial settlement substrates (van Montfrans et al. 1995). Our sampling was initiated on 26 July, 20 August, 23 August, 21 September, and 23 September, after postlarval pulses were detected. On all dates, samples were taken on each shore. Because of patchy seagrass beds and epiphyte growth, samples on the north shore in July were excluded from this study. Crabs were sampled with a suction dredge (Orth & van Montfrans 1987) in each randomly selected grid unit. A 0.05 m<sup>2</sup> drop cylinder was placed over the grass, and crabs were suctioned into a mesh bag for 30 s. Spine to spine carapace width (CW) of each crab was measured with calipers to the nearest mm. In each selected grid, a 0.02 m<sup>2</sup> core was used to sample above-ground standing seagrass crop. Above-ground wet weight and dry weight were determined for vegetative and reproductive *Ruppia* and vegetative

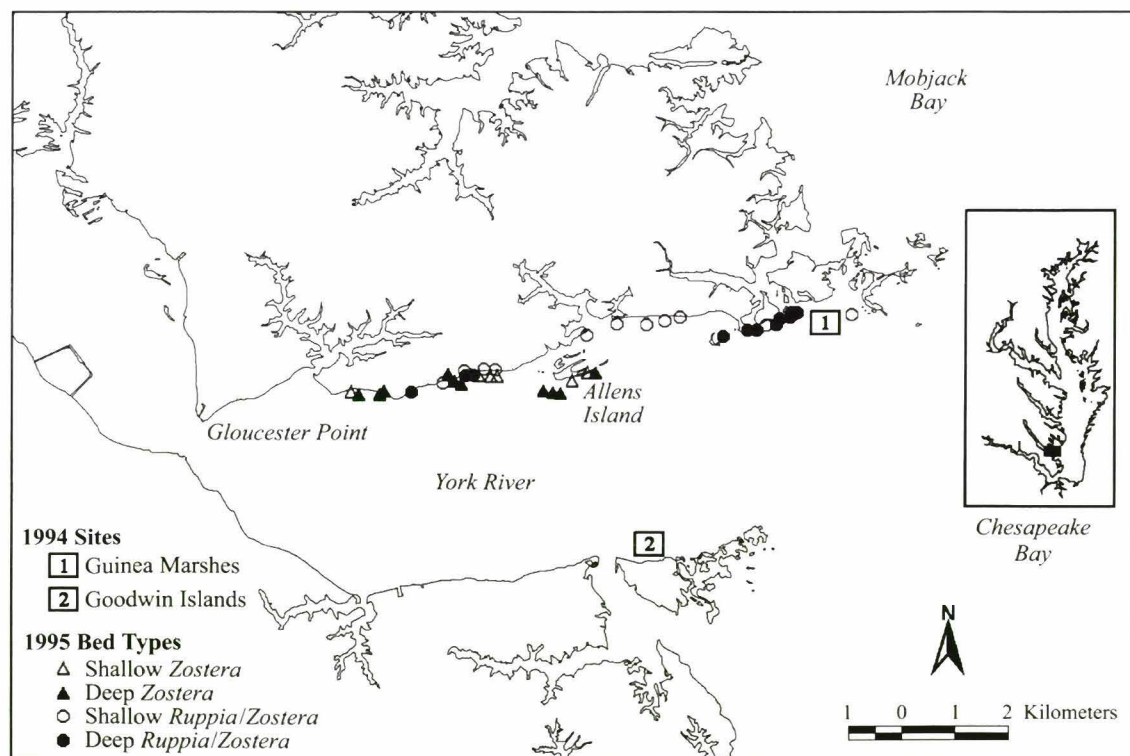


Fig. 1. Map of study area showing 1994 and 1995 sampling sites in seagrass beds in the York River, Virginia

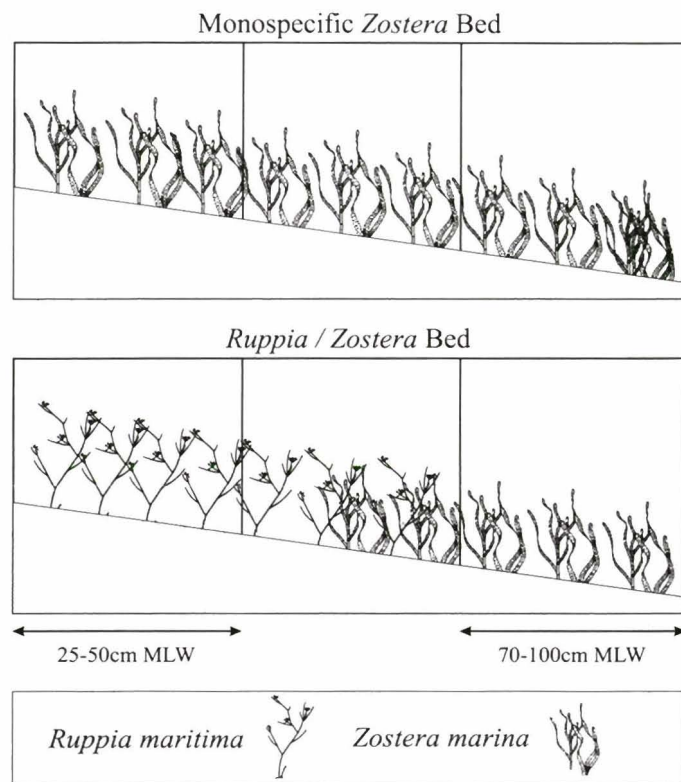


Fig. 2. Types of grassbeds found in the York River during the study period. Samples were taken at shallow and deep depths in monospecific grassbeds. Mixed areas, at intermediate depths, were excluded from sampling

*Zostera* collected in core samples. For wet weights, above-ground material was separated from roots and rhizomes, and then weighed to the nearest 0.0001 g on an electric balance. Plants were then dried at 75°C for at least 48 h, and then reweighed to determine dry weights. Temperature, water depth and salinity were measured for each plant and crab sample.

Blue crabs were grouped into 3 size classes: postlarvae and 1st instars (<3.1 mm CW), 2nd to 5th instars (3.1 to 9.1 mm CW), and larger juveniles (>9.1 mm CW) (Pile et al. 1996). Crabs could not be grouped into finer divisions because of low crab densities. The effect of size class on the odds of settling in *Ruppia* over *Zostera* was evaluated using logistic regression (Agresti 1990). We assumed that within a size class, each crab was an independent replicate, and binary responses were between *Ruppia* and *Zostera* habitats. The assumption of independence for each crab was justified by the general lack of aggregation, determined by a goodness-of-fit test to a Poisson series (for each crab size class, in July, August and September, in *Ruppia* or *Zostera*, on the north or south shore) (Elliott 1971). Most areas contained randomly distributed crabs according to this test ( $Q = 0.975$ ,  $df = 8, 9$ , or  $19$ ,  $p > 0.05$ ) (Pearson & Hartley 1966). A contagious distri-

bution was only found in August, for 2nd to 5th instars on the south shore (*Ruppia*:  $Q = 0.975$ ,  $df = 19$ ,  $p < 0.05$ ; *Zostera*:  $Q = 0.975$ ,  $df = 19$ ,  $p < 0.05$ ), and in September, for postlarvae to 1st instars on the north shore in *Ruppia* beds ( $Q = 0.975$ ,  $df = 19$ ,  $p < 0.05$ ).

The predicted  $p$  of a crab occurring in *Ruppia* was obtained from the logistic function derived from the logistic regression. The predicted  $p$  for crab occurrence in *Zostera* was  $1 - p$ . On the north and the south shore, the probability of occurrence of each crab was compared between *Ruppia* and *Zostera* through time. Crab densities in *Ruppia* and *Zostera* were significantly different if a 95% confidence interval generated from the asymptotic standard error excluded a probability of 0.5, which denotes even proportions of crabs in each treatment (Agresti 1990).

The 1994 results indicated that seagrass species, depth, or site were influencing crab distributions, but we could not distinguish between these effects since grass species covaried with water depth. In 1995, because of unusually extreme summer leaf defoliation, grassbeds were too sparse on the south shore to continue inquiries into the shore effect. Therefore, in 1995, we attempted to distinguish effects of seagrass species and depth on juvenile blue crab distributions and examine ontogenetic changes in habitat use on the north shore. As described previously, bed types were classified into monospecific *Zostera* beds and *Ruppia*/*Zostera* beds (with monospecific *Ruppia* in the shallows adjacent to monospecific *Zostera* in deeper water) (Fig. 2). Deep (70 to 100 cm MLW) and shallow (25 to 50 cm MLW) sites were randomly selected in *Zostera* beds and in *Ruppia*/*Zostera* beds, resulting in 4 treatments: deep and shallow *Zostera* beds, and deep and shallow *Ruppia*/*Zostera* beds (Fig. 1). The shallow *Ruppia*/*Zostera* treatment only contained *Ruppia*, whereas the remaining 3 treatments only contained *Zostera*. Mixed beds were excluded from sampling. Randomly selected sites were marked with stakes prior to sampling, which was initiated after peaks in postlarval settlement were detected with plankton samples and settlement substrates (J. van Montfrans unpubl. data). Four suction samples were taken at randomly selected sites in each treatment on each of 3 consecutive days: 8 to 10 October, using a 1.67 m<sup>2</sup> sampling ring. The ring was deployed next to the field marker, and the enclosed contents were suctioned for 6 min, followed by 3 min of dipnetting. This method has an 88% efficiency in crab capture in seagrass beds (Orth & van Montfrans 1987). Before sampling crabs, plant biomass cores (0.02 m<sup>2</sup>) were taken inside each sampling ring to determine above-ground



dry weight, shoot density and canopy height of vegetative *Ruppia* and vegetative *Zostera*. Sediment cores were taken with all samples and frozen for later analysis. Temperature, salinity, and depth were also recorded.

Blue crabs were grouped into 6 size classes for analyses: postlarvae, 1st instars (<3.1 mm CW), 2nd to 3rd instars (3.1 to 5.9 mm), 4th to 7th instars (6.0 to 12.6 mm), 8th to 9th instars (12.7 to 16.0 mm) and greater than 9th instars (>16.0 mm) (Pile et al. 1996). Samples were analyzed by ANCOVA (dependent variable: crab density; independent variables: bed type and depth; blocked factor: date; covariates: grass dry weight, shoot density, log of shoot density, canopy height, distance upriver). Data were tested for homogeneity of variances and log-transformed when necessary. Linear regressions were conducted when covariates were significant (Zar 1984). Plant dry weight and shoot density were similarly tested as dependent variables by bed type and depth.

## RESULTS

### Seagrass and algal composition 1994

Although sampling grids were established in mono-specific stands of the respective seagrass beds, some samples contained small amounts of the other grass species. Also, vegetation in some samples was covered by red algae, e.g. *Ceramium* spp. (E. Bailey pers. comm.), which was especially difficult to remove from the fine *Ruppia* shoots. Red algae made up a large proportion of many *Ruppia* samples. Red algae also grew on *Zostera*, but was easy to remove. Thus, comparisons of seagrass biomass are made tentatively. *Ruppia* dry weight averaged  $15.3 \text{ g m}^{-2}$ . *Zostera* dry weight averaged  $12.2 \text{ g m}^{-2}$ . In *Ruppia*-dominated beds, *Ruppia* biomass decreased through time on both shores, and *Zostera* decreased on the south shore. In *Zostera*-dominated beds, *Zostera* did not appear to change over time (Fig. 3). Algal biomass was not quantified.

### Differential habitat utilization

In 1994, on the south shore, all crab stages were evenly distributed between *Zostera* and *Ruppia*, with 1 exception (Fig. 4). In August, crabs greater than the 5th instar were significantly more abundant in *Ruppia* than in *Zostera* ( $p < 0.05$ ).

On the north shore, all crab stages were significantly more abundant in *Ruppia* than in *Zostera* ( $p < 0.05$ ), except in August, when postlarvae and 1st instars were evenly distributed between *Ruppia* and *Zostera* (Fig. 4).

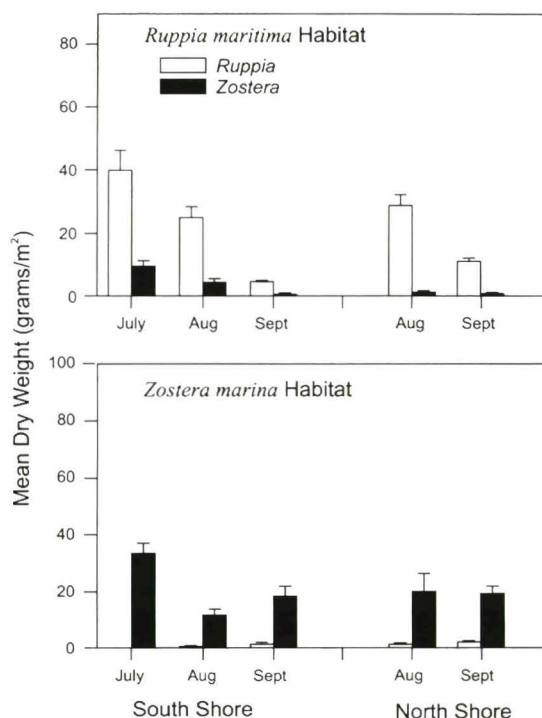


Fig. 3. Mean grass dry weights in *Ruppia* and *Zostera* habitats on the north and south shores of the York River in 1994. Standard error bars are shown

### Seagrass and algal composition 1995

Seagrass dry weight and shoot density varied by bed type and depth (Table 1, Fig. 5). *Ruppia* dry weight averaged  $20.1 \text{ g m}^{-2}$  (shallow *Ruppia/Zostera*), and *Zostera* dry weight averaged  $7.8 \text{ g m}^{-2}$  (deep *Ruppia/Zostera*, deep and shallow *Zostera* beds). Shoot density averaged 3062 shoots  $\text{m}^{-2}$  for *Ruppia* and 220 shoots  $\text{m}^{-2}$  for *Zostera*. Grass dry weight was significantly greater in shallow *Ruppia* beds than in shallow or deep *Zostera* beds. Grass dry weight also was significantly greater in deep than in shallow *Zostera* beds. There were significantly more shoots in shallow *Ruppia* beds than in deep or shallow *Zostera* beds (Table 2, Fig. 5). There was no noticeable epiphyte growth on vegetation in 1995.

### Ontogenetic differences in habitat use

Postlarvae through 3rd instars showed similar results by bed type, depth, and distance upriver (Table 3, Figs. 6 & 7). Crab densities averaged  $2.0 \text{ m}^{-2}$  (postlarvae),  $6.8 \text{ m}^{-2}$  (1st instars), and  $3.4 \text{ m}^{-2}$  (2nd to 3rd instars). Postlarvae, 1st instar, and 2nd to 3rd instar abundances did not vary by bed type or depth, and were not influenced by grass dry weight or shoot den-

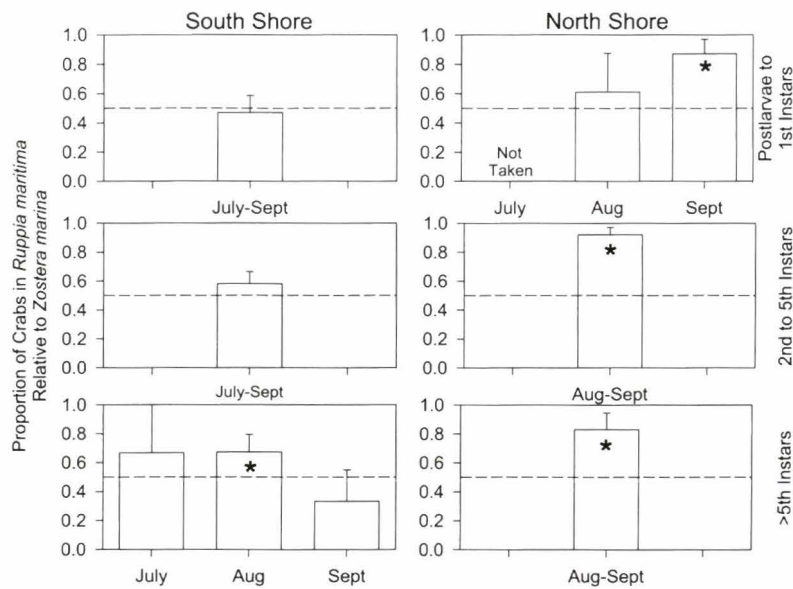


Fig. 4. Comparison of observed crab densities between *Ruppia* and *Zostera* on the north or south shore of the York River in 1994. Crabs are evenly distributed between *Ruppia* and *Zostera* if standard error bar overlaps line drawn at 0.5. If proportions exceed 0.5, crab densities are higher in *Ruppia*. If proportions are below 0.5, crab densities are higher in *Zostera*. \*Significant differences between crab densities in *Ruppia* and *Zostera* ( $p < 0.05$ ). When there is no significant change through time, crab proportions are collapsed across time and represented by a single bar

sity (Table 3, Fig. 6). In contrast, abundances of the earliest stages increased significantly with distance upriver (Table 3, Fig. 7), though with high variance.

Seagrass species strongly influenced distributions of crabs greater than the 3rd instar, with highest crab abundances in *Ruppia* habitats (Table 3, Fig. 6). Specifically, 4th to 7th instars were significantly more abundant in shallow *Ruppia* than in all other habitats (*Zostera*) (Table 4). In *Ruppia/Zostera* beds, 8th to 9th instar abundance was significantly higher in shallow *Ruppia* than in deep *Zostera* habitats (Table 4). 9th instars and greater were significantly more abundant

in *Ruppia/Zostera* beds than in monospecific *Zostera* beds regardless of depth (Table 3), and highest abundances occurred in *Ruppia* beds. Depth appears to be unimportant in vegetated habitats since it was nonsignificant in monospecific *Zostera* beds, and only significant in *Ruppia/Zostera* beds, where it was tied to seagrass species. The covariates grass dry weight, shoot density, log-transformed shoot density, and distance upriver, were nonsignificant for crabs greater than the 3rd instar (Table 3).

Although the covariate shoot density was nonsignificant in all tests, late stage crab densities reflect this distinguishing seagrass characteristic (see above). In general, highest abundances of 4th instars and greater occurred in shallow *Ruppia* beds which had the highest shoot densities. *Ruppia* shoot densities, which ranged between 700 and 4800 shoots  $m^{-2}$ , were correlated with the number of 4th to 7th instars (regression,  $r^2 = 0.303$ ,  $p = 0.064$ ) (Fig. 8). Shoot density in *Zostera* beds, which ranged from 50 to 550 shoots  $m^{-2}$ , was not significantly related to crab abundance.

## DISCUSSION

Habitat use by blue crabs changes ontogenetically in seagrass beds and unvegetated habitats (Orth & van Montfrans 1987). In our study, postlarvae and earliest instar distributions were related to site rather than seagrass species or water depth in shallow habitats (i.e.  $< 2$  m depth). In contrast, 4th and greater instar distributions were related to seagrass species, whereas water depth was not influential.

Table 1. ANOVA results with total dry weight or shoot density per  $1.67 m^2$  as the dependent variable, bed type (B) and water depth (D) as fixed factors, and date as a blocking factor. \* $p < 0.05$ , \*\*\*\* $p < 0.0001$ ; ns:  $p > 0.05$

|                  | Factor       | df | SS     | MS      | F         |
|------------------|--------------|----|--------|---------|-----------|
| Total dry weight | Bed type     | 1  | 0.0814 | 0.0977  | 4.43*     |
|                  | Depth        | 1  | 0.0154 | <0.0001 | <0.01 ns  |
|                  | B $\times$ D | 1  | 0.082  | 0.0812  | 3.68 ns   |
|                  | Date         | 2  | 0.0426 | 0.0213  | 0.97 ns   |
| Shoot density    | Bed type     | 1  | 6664.2 | 5160.9  | 20.19**** |
|                  | Depth        | 1  | 9602.5 | 4395.6  | 20.6****  |
|                  | B $\times$ D | 1  | 5499.5 | 5238.9  | 24.55**** |
|                  | Date         | 2  | 638.7  | 319.4   | 1.5 ns    |



Table 2. Tukey's test for significant interaction effects between depth and bed type in ANOVA (Table 1). R-Z: *Ruppia/Zostera* beds; Z-Z: monospecific *Zostera* beds. To be conservative, we used  $p < 0.1$  as the criterion for performing multiple comparison tests. Parentheses enclose mean dry weight and shoot density of each treatment combination

|               | Category | Factor   | Level          |                   | Tukey's difference <sup>a</sup> |
|---------------|----------|----------|----------------|-------------------|---------------------------------|
| Dry weight    | Bed type | Depth    | Deep<br>(0.18) | Shallow<br>(0.40) | 0.218**                         |
|               |          |          | Deep<br>(0.17) | Shallow<br>(0.11) | 0.059**                         |
|               | Depth    | Bed type | Z-Z<br>(0.11)  | R-Z<br>(0.40)     | 0.287**                         |
|               |          |          | R-Z<br>(0.18)  | Z-Z<br>(0.17)     | 0.010 ns                        |
|               |          | Bed type | R-Z<br>(0.18)  | Z-Z<br>(0.17)     | 0.010 ns                        |
| Shoot density | Bed type | Depth    | Deep<br>(1.64) | Shallow<br>(2.79) | 1.161**                         |
|               |          |          | Deep<br>(1.66) | Shallow<br>(1.63) | 0.037 ns                        |
|               | Depth    | Bed type | Z-Z<br>(1.63)  | R-Z<br>(2.79)     | 1.161**                         |
|               |          |          | R-Z<br>(1.64)  | Z-Z<br>(1.66)     | 0.020 ns                        |
|               |          | Bed type | R-Z<br>(1.64)  | Z-Z<br>(1.66)     | 0.020 ns                        |

<sup>a</sup>Tested against  $D_{0.05}$  or  $D_{0.01}$ , calculated as  $Dx = \text{error mean square} / (1/n_a + 1/n_b)^{1/2} \cdot (q)$ ,  $n$  varies with treatment (6, 10 or 12),  $df = 30$ ,  $q_{30,0.05} = 2.89$ ,  $q_{30,0.01} = 3.89$ . \*\* $p < 0.01$ , ns:  $p > 0.05$

### Influence of site on postlarvae and earliest instar distributions

Postlarvae detect and respond to chemical cues from *Zostera* and estuarine water (Forward et al. 1994) and can swim up to  $12.6 \text{ cm s}^{-1}$  (Luckenbach & Orth 1992). Hence, they could hypothetically select between different seagrass habitats at low to moderate current speeds. In our study, however, earliest instar abundances (postlarvae through 3rd instars) differed between grass species (i.e. *Ruppia* and *Zostera*) in only 1 instance. Generally, earliest instars (postlarvae through 3rd instars) were not significantly influenced by bed type or depth, but differed significantly by site, increasing with distance upriver. This finding suggests that physical forces, rather than microhabitat characteristics, strongly influence early instar distributions. For instance, postlarvae apparently use onshore winds and currents to reinvade estuaries (Goodrich et al. 1989, Olmi 1994). Our findings are therefore consistent with the hypothesis that fine-scale habitat selection by blue crab postlarvae does not occur during water column transport, and that early stage distributions are mainly a function of larval supply and transport.

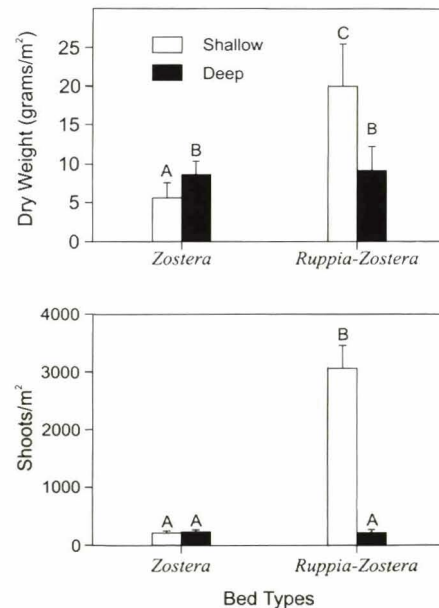
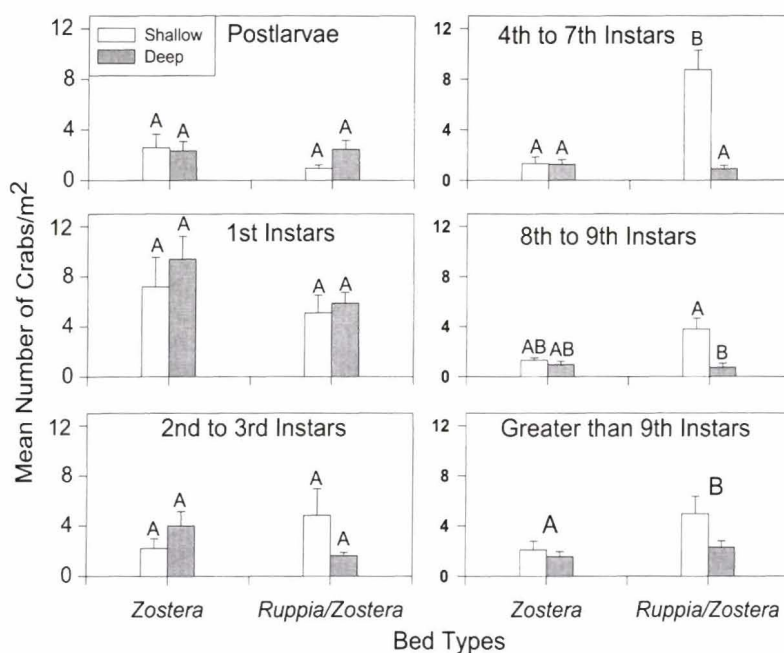


Fig. 5. Seagrass dry weight and shoot density at different depths and bed types in 1995. In *Ruppia-Zostera* beds, values are for *Ruppia* in the shallows and for *Zostera* in the deeper locations. Letters depict significant differences calculated from Tukey's test ( $p < 0.05$ ); bars sharing the same letters indicate nonsignificance

Table 3. ANCOVA results by stage, with crab density per 1.67 m<sup>2</sup> as the dependent variable, bed type and water depth as fixed factors, and date as a blocking factor. Distance upriver, grass dry weight, number of grass shoots, and canopy height were tested as covariates. Distance upriver was the only significant covariate. Nonsignificant covariates ( $p > 0.05$ ) were removed from the models and results are not shown. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.005$ , \*\*\*\* $p < 0.0001$ ; ns:  $p > 0.05$

|                              | Factor           | df | SS    | MS    | F         |
|------------------------------|------------------|----|-------|-------|-----------|
| Postlarvae                   | Bed type         | 1  | 13.69 | 10.76 | 1.09 ns   |
|                              | Depth            | 1  | 10.78 | 9.14  | 0.93 ns   |
|                              | B × D            | 1  | 9.57  | 9.72  | 0.99 ns   |
|                              | Date             | 2  | 2.92  | 1.46  | 0.15 ns   |
|                              | Distance upriver | 1  | 61.7  | 60.59 | 6.14*     |
| 1st instars                  | Bed type         | 1  | 0.14  | 1.39  | 0.03 ns   |
|                              | Depth            | 1  | 72.0  | 100.3 | 2.29 ns   |
|                              | B × D            | 1  | 8.01  | 0.01  | <0.01 ns  |
|                              | Date             | 2  | 366.4 | 183.2 | 4.18*     |
|                              | Distance upriver | 1  | 572.0 | 362.3 | 8.26**    |
| 2nd–3rd instars <sup>a</sup> | Bed type         | 1  | 0.61  | 0.42  | 0.75 ns   |
|                              | Depth            | 1  | 0.13  | 0.44  | 0.78 ns   |
|                              | B × D            | 1  | 0.95  | 0.74  | 1.31 ns   |
|                              | Date             | 2  | 1.28  | 0.64  | 1.14 ns   |
|                              | Distance upriver | 1  | 5.26  | 3.52  | 6.26*     |
| 4th–7th instars <sup>a</sup> | Bed type         | 1  | 1.19  | 0.98  | 11.92***  |
|                              | Depth            | 1  | 1.77  | 0.95  | 11.50***  |
|                              | B × D            | 1  | 1.5   | 1.39  | 16.90**** |
|                              | Date             | 2  | 0.15  | 0.08  | 0.91 ns   |
|                              | Distance upriver | 1  | 5.26  | 3.52  | 6.26*     |
| 8th–9th instars <sup>a</sup> | Bed type         | 1  | 0.11  | 0.04  | 0.49 ns   |
|                              | Depth            | 1  | 1.08  | 0.73  | 8.07**    |
|                              | B × D            | 1  | 0.31  | 0.28  | 3.12 ns   |
|                              | Date             | 2  | 0.07  | 0.04  | 0.40 ns   |
|                              | Distance upriver | 1  | 5.26  | 3.52  | 6.26*     |
| > 9th instars <sup>a</sup>   | Bed type         | 1  | 0.56  | 0.57  | 6.11*     |
|                              | Depth            | 1  | 0.26  | 0.21  | 2.23 ns   |
|                              | B × D            | 1  | 0.09  | 0.14  | 1.53 ns   |
|                              | Date             | 2  | 0.29  | 0.15  | 1.58 ns   |
|                              | Distance upriver | 1  | 5.26  | 3.52  | 6.26*     |

<sup>a</sup>Data were log transformed



One explanation for the lack of micro-habitat selection by early instars is cannibalism by larger conspecifics, which are abundant in shallow *Ruppia* beds. Similarly, in oyster shell habitats, early cohorts of the Dungeness crab *Cancer magister* reduced the density of subsequent cohorts through cannibalism or competition (Fernandez et al. 1993, Eggleston & Armstrong 1995). Crab density patterns may have also reflected a postlarval pulse moving up the York River: sam-

Fig. 6. Mean number of crabs by depth and bed type in 1995. In *Ruppia/Zostera* beds, values are for *Ruppia* in the shallows and for *Zostera* in the deeper locations. Standard error bars are shown. Letters depict significant differences calculated from ANCOVA and Tukey's test ( $p < 0.05$ ): bars sharing the same letters indicate nonsignificance



Table 4. Tukey's test for significant interaction effects between depth and bed type in ANCOVA (Table 3). R-Z: *Ruppia/Zostera* beds; Z-Z: monospecific *Zostera* beds. To be conservative, we used  $p < 0.1$  as the criterion for performing multiple comparison tests. Parentheses enclose mean densities of each treatment combination. \*\* $p < 0.01$ , ns:  $p > 0.05$

|                 | Category | Factor   | Level          |                   | Tukey's difference <sup>a</sup> |
|-----------------|----------|----------|----------------|-------------------|---------------------------------|
| 4th–7th instars | Bed type |          |                |                   |                                 |
|                 | R-Z      | Depth    | Deep<br>(0.33) | Shallow<br>(1.12) | 0.790**                         |
|                 | Z-Z      | Depth    | Deep<br>(0.40) | Shallow<br>(0.41) | 0.009 ns                        |
|                 | Depth    |          |                |                   |                                 |
|                 | Shallow  | Bed type | Z-Z<br>(0.41)  | R-Z<br>(1.12)     | 0.711**                         |
| 8th–9th instars | Deep     | Bed type | R-Z<br>(0.33)  | Z-Z<br>(0.40)     | 0.070 ns                        |
|                 | Bed type |          |                |                   |                                 |
|                 | R-Z      | Depth    | Deep<br>(0.24) | Shallow<br>(0.76) | 0.521**                         |
|                 | Z-Z      | Depth    | Deep<br>(0.35) | Shallow<br>(0.49) | 0.141 ns                        |
|                 | Depth    |          |                |                   |                                 |
|                 | Shallow  | Bed type | Z-Z<br>(0.49)  | R-Z<br>(0.76)     | 0.267 ns                        |
|                 | Deep     | Bed type | R-Z<br>(0.24)  | Z-Z<br>(0.35)     | 0.113 ns                        |
|                 |          |          |                |                   |                                 |
|                 |          |          |                |                   |                                 |
|                 |          |          |                |                   |                                 |

<sup>a</sup>Tested against  $D_{0.05}$  or  $D_{0.01}$ , calculated as  $Dx = \text{error mean square} / (1/n_a + 1/n_b)^{1/2} \cdot (q)$ ,  $n$  varies with treatment (6, 10 or 12),  $df = 30$ ,  $q_{30, 0.05} = 2.89$ ,  $q_{30, 0.01} = 3.89$

pling was initiated when high numbers of postlarvae were collected in nighttime plankton samples upriver, where the highest densities of postlarvae through 3rd instars were also caught in suction samples.

### Influence of plant species on later instar distributions

Abundance of later instars (>3rd instar) did not differ by site along the river axis, but later instars were generally more abundant in *Ruppia* than *Zostera*. This distribution was related to seagrass species and not depth, since crabs were evenly distributed between shallow and deep *Zostera* beds, and may have resulted from habitat selection (Bell & Westoby 1986), differential predation (Pile et al. 1996), or food availability.

Predation can play a major role in the abundance of certain instar stages but may be influenced by certain vegetational characteristics (e.g. shoot density) or prey characteristics (e.g. size) (Heck & Thoman 1981, Pile et al. 1996, Schulman 1996). In 1995, *Ruppia* shoot densities were higher than those of *Zostera*, and 4th to 7th instar abundances were positively correlated with *Ruppia* shoot density. Although Pile et al. (1996) showed that 5th to 7th instars gain a relative refuge from predation because of their size, their greater abundance in vegetation may reflect that these are the

instars (i.e. sizes) that are balancing the relative values of vegetational refuge versus size refuge from predation.

The relationship between *Ruppia* beds, shoot density, and the densities of crabs greater than the 7th instar, however, was not as clear. Within *Ruppia/Zostera* beds, 8th to 9th instars were more abundant in *Ruppia* than in *Zostera* areas. Generally, juveniles greater than the 9th instar were more abundant in *Ruppia/Zostera* beds than in *Zostera* beds. However, these crab densities were not significantly related to shoot densities. The relationship between shoot density and crab density may break down when crabs reach the 8th instar, possibly because size-refuge from predation at these instar stages influences survival more than vegetational characteristics (Pile et al. 1996).

*Ruppia* and *Zostera* shoot densities change seasonally and in response to varying weather conditions (Orth & Moore 1986). The summer of 1995 was unusually hot, with air temperatures above 32°C for over 20 consecutive days prior to sampling. *Zostera* defoliated considerably during this heat wave. Changes in seagrass density may lead to changes in habitat use by blue crabs: juvenile blue crabs may be more abundant in *Zostera* beds prior to yearly summer defoliation. In a recent study, blue crab postlarvae settled in higher

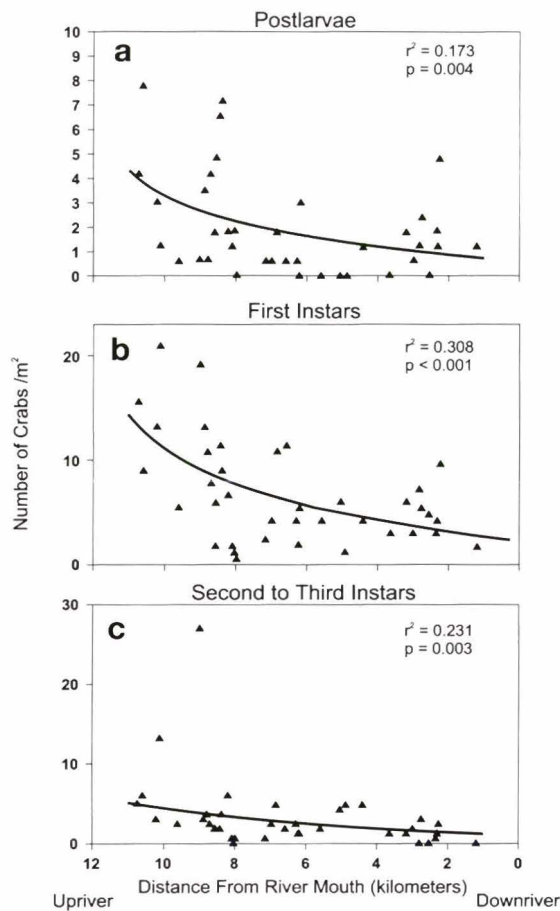


Fig. 7. Correlation between distance along the York River and number of postlarvae, first instars, and second to third instars in 1995. (▲) Individual samples. Linearly transformed regression equations: (a) postlarvae =  $14.73 - 3.47\log(\text{distance upriver})$  (regression,  $r^2 = 0.173$ ,  $p = 0.004$ ). (b) 1st instars =  $47.78 - 11.14\log(\text{distance upriver})$  (regression,  $r^2 = 0.308$ ,  $p < 0.001$ ). (c)  $\ln(2\text{nd to } 3\text{rd instars}) = 1.78 - 0.000144(\text{distance upriver})$  (regression,  $r^2 = 0.231$ ,  $p = 0.003$ )

abundances on *Spartina alterniflora* than on *R. maritima* or *Juncus roemarianus* in August; in September, more postlarvae settled on *Ruppia* (Morgan et al. 1996). *Ruppia* may be a more important habitat during the late summer after *Zostera* defoliates. Similarly, vegetation die-back caused an increase in prawn abundance but a decrease in fish abundance in an Australian estuary (Halliday 1995).

#### Nonsignificance of water depth

In contrast to findings with other invertebrates (Ruiz et al. 1993, Platell & Potter 1996), water depth did not determine abundance of any juvenile crab size classes. In this study, the effect of seagrass species may have

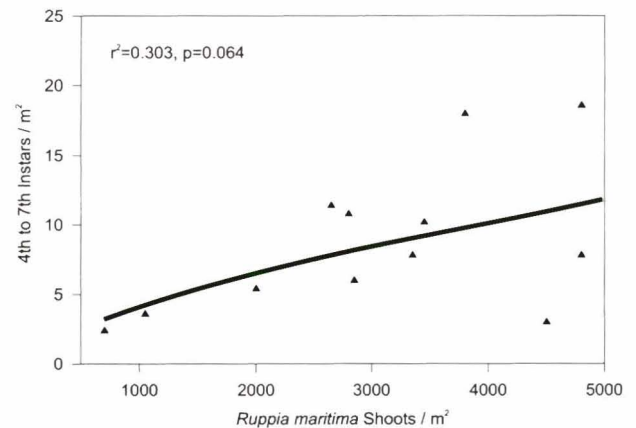


Fig. 8. Correlation between number of 4th to 7th instars and the number of *Ruppia* shoots in 1995. (▲) Individual samples. Linearly transformed regression equation:  $\log(4\text{th to } 7\text{th instars}) = -0.233 + 0.652\log(\text{shoot number})$  (regression,  $r^2 = 0.303$ ,  $p = 0.064$ )

overshadowed the effect of depth as a refuge. In a similar study, benthic invertebrates, including the polychaetes *Ceratonereis aequisetis* and *Capitella capitata*, and the gastropod *Hydrococcus brazieri* were significantly more abundant in shallow water (<1.0 m) than in deep water (2.0 to 2.5 m). *Ruppia megacarpa* was also significantly more dense in shallow water and may have influenced species distributions by providing refuge and nutrition (Platell & Potter 1996).

We propose the following model for the distribution of postlarvae and young juveniles of the blue crab in the York River. The abundance of postlarvae through 3rd instars in a particular habitat is strongly influenced by larval supply and physical forces such as currents and winds, which could result in differential distribution along a river axis. Crabs greater than the 3rd instar are more strongly influenced by microhabitat features (e.g. seagrass species and density). Thus, the intensity and character of habitat selection by juvenile blue crabs appear to vary ontogenetically.

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