

The Influence of Location, Seagrass Species and Water Depth on the
Settlement and Distribution of Early Stage Blue Crabs

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In Partial Fulfillment of
the Requirements for the Degree of
Master of Arts

by
Renee A. Pardieck
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APPROVAL SHEET

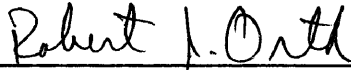
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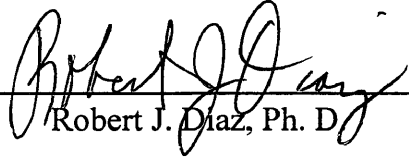


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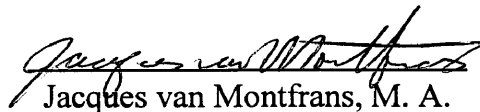
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Dedication

This thesis is dedicated to my family, Mom, Dad, Matt, Ben and Rachel.

Also to my good friends, Celia, Alessandra, Ing Wei, and Tong.

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Abstract

Habitat structure, related to seagrass species and water depth, and physical forces, such as currents and winds, can substantially influence organism distributions. Deep and shallow suction samples in monospecific *Zostera marina* and *Ruppia maritima* beds in the York River, VA, indicate that site and seagrass species influence settlement and distribution of early stage *Callinectes sapidus* (postlarvae through ninth instars). In 1994, early stage blue crabs were significantly more abundant in *R. maritima* than in *Z. marina* on the north shore, while crabs were evenly distributed between seagrass species on the south shore. In 1995, postlarvae through 3rd instars were not related to bed type or depth, but were significantly correlated with distance upriver. Later crab instars (>3rd instar), however, were more abundant in *R. maritima* beds, which had significantly higher shoot densities than *Zostera marina* beds. The effect of water depth on all crab stages was nonsignificant. Fourth to seventh instars were also positively correlated with *R. maritima* shoot densities ($p = 0.064$). Habitat use by early stage blue crabs may be related to changes in seagrass shoot density, which occur each summer, resulting in the domination of different seagrass species at different times of the year. An ontogenetic shift in habitat use was found for the earliest blue crab stages: smallest instars were significantly related to site in both 1994 and 1995, which suggests that larval supply and physical forces, such as currents and winds, influence initial crab distributions. Abundance of later instars was significantly related to seagrass

species, possibly because of differences in shoot density, which indicates the importance of habitat selection and differential mortality.

**The Influence of Location, Seagrass Species and Water Depth on the
Settlement and Distribution of Early Stage Blue Crabs**

Introduction

Distributions of marine organisms with a pelagic larval phase can be strongly influenced by larval supply and behavior, and post-settlement mortality and migration, processes which are often mediated by habitat complexity (Eggleston and Armstrong 1995; Olmi *et al.* 1990; Roughgarden *et al.* 1988). Habitat complexity is characterized by biotic and abiotic structural characteristics of the environment, such as rock, heterogeneous sediments, oyster reefs, worm tubes, macroalgae and emergent or submersed vegetation (Day and Lawton 1988; Heck and Crowder 1991; Love and Bailey 1992; Marinelli and Coull 1987; Schneider and Mann 1991b; Wilson *et al.* 1990). Complex habitats can affect water flow by altering the structure of the boundary layer, especially the shear velocity (u^*) and the roughness height (z_o) (Eckman 1983; Eckman and Nowell 1984). Changes in the flow regime can influence settlement patterns since most pelagic larvae have slow swimming speeds relative to bottom currents (Butman 1987). Furthermore, many organisms are more abundant in complex habitats because of reduced predation (decapod crustaceans, Heck and Thoman 1981; spiny lobster, Herrnkind and Butler 1986; queen conch, Ray and Stoner 1995; amphipods, Ryer 1987; Atlantic cod, Tupper and Boutilier 1995), abundant living space, and high nutrition (snails, Bronmark 1985; amphipods, Hacker and Steneck 1990; juvenile spiny lobster, Herrnkind and Butler 1986; epifaunal invertebrates, Schneider and Mann 1991a).

Water depth is another important feature of the environment which can

affect species distributions by altering relative rates of predation and offering varying degrees of nutrition. In simple, unstructured areas, many organisms take refuge in shallow water (Ruiz *et al.* 1993): larger aquatic predators are less abundant in shallow water, which is associated with avian and mammalian predation, decreased foraging ability, and fluctuating temperature and oxygen levels (Dittel *et al.* 1995; Loneragan *et al.* 1994; Lonzarich and Quinn 1995; Platell and Potter 1996; Ruiz *et al.* 1993). Alternatively, high food abundances can attract predators and prey into shallow water (Miltner *et al.* 1995). Interactions between depth and habitat complexity occur in some habitats. For instance, the abundance of woody and shell debris often changes with depth. Also, rooted submersed aquatic plants grow over a wide range of depths, exhibiting a variety of bed complexities and leaf morphologies (den Hartog 1970; Duarte 1991; Platell and Potter 1996). In seagrass beds, habitat complexity and depth collectively influence species distributions. Seagrasses support a high density and diversity of fauna (Heck *et al.* 1995; Orth 1992). Organism densities can vary within and between seagrass species (Schneider and Mann 1991a). Measures of habitat complexity, such as plant biomass, blade density, leaf surface area, plant architecture, and plant species composition, may explain these patterns (Orth *et al.* 1984; Orth 1992; Stoner 1980, 1983; Stoner and Lewis 1985; Virnstein and Howard 1987; Worthington *et al.* 1992). Seagrass beds also slow currents and enhance deposition of fine sediments, an effect which varies with plant morphology, bed shape, size and height of different seagrass species (Fonseca and Fisher 1986; Kikuchi and Peres 1977) and which also may influence larval

distributions (Orth 1992).

In the Chesapeake Bay, two seagrass species with distinct morphologies and spatial distributions dominate shoal areas (< 2 meters MLW): *Ruppia maritima* and *Zostera marina*. Vegetative *Z. marina* has wide, straplike blades; reproductive *Z. marina*, appearing from April to June in the Chesapeake Bay, has longer, branched shoots with several spathes (den Hartog 1970; Orth and Moore 1986). In contrast, vegetative *R. maritima* has short, threadlike shoots. Reproductive *R. maritima*, growing mainly from July through September, has highly branched, threadlike shoots, which can reach over a meter in length. *Ruppia maritima* commonly grows in monospecific stands in shallow water (approximately < 0.3 m MLW). At intermediate depths (approximately 0.3-0.6 m MLW), *Z. marina* and *R. maritima* co-occur, while in deep water (approximately > 0.6 m MLW), generally only *Z. marina* is abundant (Orth and Moore 1988). Occasionally, monospecific *Z. marina* exists in shallow water and *R. maritima* exists in deeper water (R. Orth, unpublished data).

Seagrass beds in the lower Chesapeake Bay are the primary nursery habitat for blue crabs, *Callinectes sapidus*, which constitute an important commercial fishery in this region (Orth and van Montfrans 1987; Pile *et al.* 1996). *Callinectes sapidus* settle in seagrass beds during the postlarval stage, the reinvasive stage which moves into the Chesapeake Bay from the continental shelf. Settlement occurs from July to November and is generally episodic, with pulses around the full and new moons (van Montfrans *et al.* 1990, 1995). The refugial quality of seagrass beds changes in

effectiveness with crab density, crab size (Pile *et al.* 1996) and shoot density (Heck and Thoman 1981; J. Schulman, unpublished data; Williams *et al.* 1990).

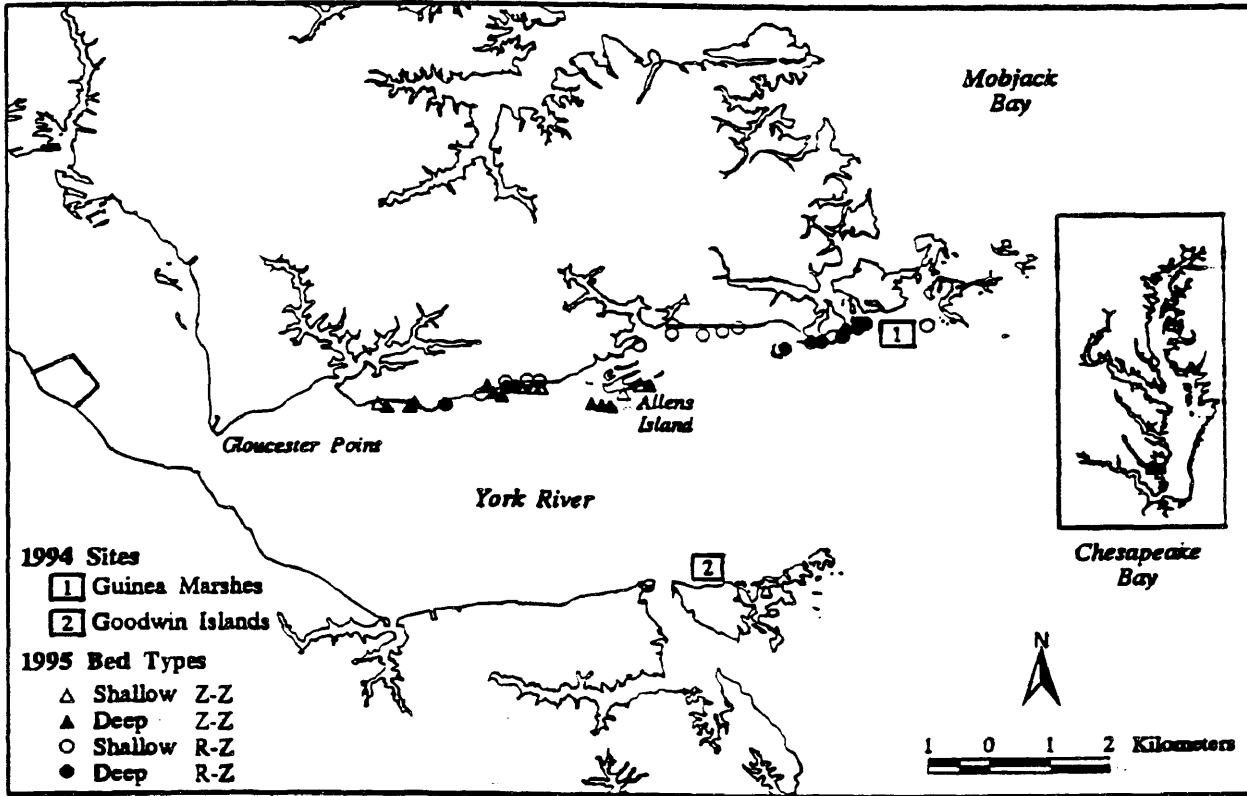
Distributions of early stage blue crabs may be influenced by seagrass species or water depth through many processes, which include differential predation and nutrition, larval supply, habitat selection, and hydrodynamics. Previous studies have not examined the effect of depth and seagrass species on blue crab distributions, although recent work suggests that some small species may be more abundant in shallow, complex seagrass habitats (Humphries 1996; Pile, unpublished data). The objective of this study was to determine the effect of seagrass species and water depth on early stage blue crab settlement, distribution and abundance. Data from both 1994 and 1995 also revealed the importance of location in the York River.

Study Sites

In 1994 and 1995, the relationships between early stage blue crab densities, seagrass species and water depth were examined in the lower York River, where *Ruppia maritima* and *Zostera marina* co-occur (Fig. 1). Seagrasses are especially abundant on the north shore, from the river mouth to Gloucester Point. Generally, shallow, monospecific *R. maritima* beds grade into deep, monospecific *Z. marina* beds. At some sites, especially upstream of Allen's Island, monospecific *Z. marina* occurs in both shallow and deep water (20-100 cm MLW). In 1994, reproductive and vegetative *R. maritima* were present during sampling. Reproductive *Z. marina* had

defoliated prior to sampling in both 1994 and 1995. Reproductive *R. maritima* had defoliated prior to sampling in 1995. Blue crab postlarvae recruit to the York River from mid-July to November (van Montfrans *et al.* 1990, 1995). Postlarvae settle in seagrass beds in the York River, where early instars are also abundant (Lipcius *et al.* 1990; Olmi *et al.* 1990; Orth and van Montfrans 1987).

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



Materials and Methods

In July, 1994, the distribution and abundance of early stage blue crabs were compared between adjacent *Ruppia maritima* and *Zostera marina* beds. Two grids (100m x 100m) were established near the York River mouth, on the north and the south shore: Guinea Marsh and Goodwin Island, respectively (Figure 1). Each grid enclosed approximately equal proportions of shallow, monospecific *Ruppia maritima* beds and deep, monospecific *Z. marina* beds. Prior to sampling, grids were marked at 10 meter intervals, resulting in one hundred 10m X 10m quadrats. For each sampling date, twenty quadrats were randomly selected from each grid: ten units in *Z. marina* areas and ten units in *R. maritima* areas.

Throughout the summer, blue crab postlarval abundance in the York River was monitored with nightly plankton samples and settlement substrates (R. Lipcius, unpublished data). Sampling was initiated after large postlarvae pulses were detected. Samples were taken at the northern and southern sites on July 26, August 20, August 23, September 21, and September 23 (Figure 2). Samples taken at the northern site, on July 26, were excluded because seagrass beds were patchy and fouled, and the northern site was moved for later sampling. On each sampling date, a suction sample (Orth and van Montfrans 1987) was taken haphazardly in each selected grid unit, resulting in ten samples in *R. maritima*, and ten samples in *Z. marina* at each site. A 0.05 m² drop cylinder was placed over the grass, and crabs were collected via suctioning into a mesh bag for 30 seconds. Next to each suction

sample, a sample was taken of aboveground standing seagrass crop, using a 0.02 m² core. Depth and time of each sample were recorded. Temperature and salinity were measured at each site. All samples were returned to the lab and frozen for later analyses. Blue crabs were sorted and enumerated from each sample, and spine to spine carapace widths were measured with calipers to the nearest mm.

Aboveground wet weight and dry weight were determined for vegetative *R. maritima*, reproductive *R. maritima* and vegetative *Z. marina* collected in core samples. Plants were separated into seagrass types. For wet weights, aboveground 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 hours, and then reweighed for dry weights.

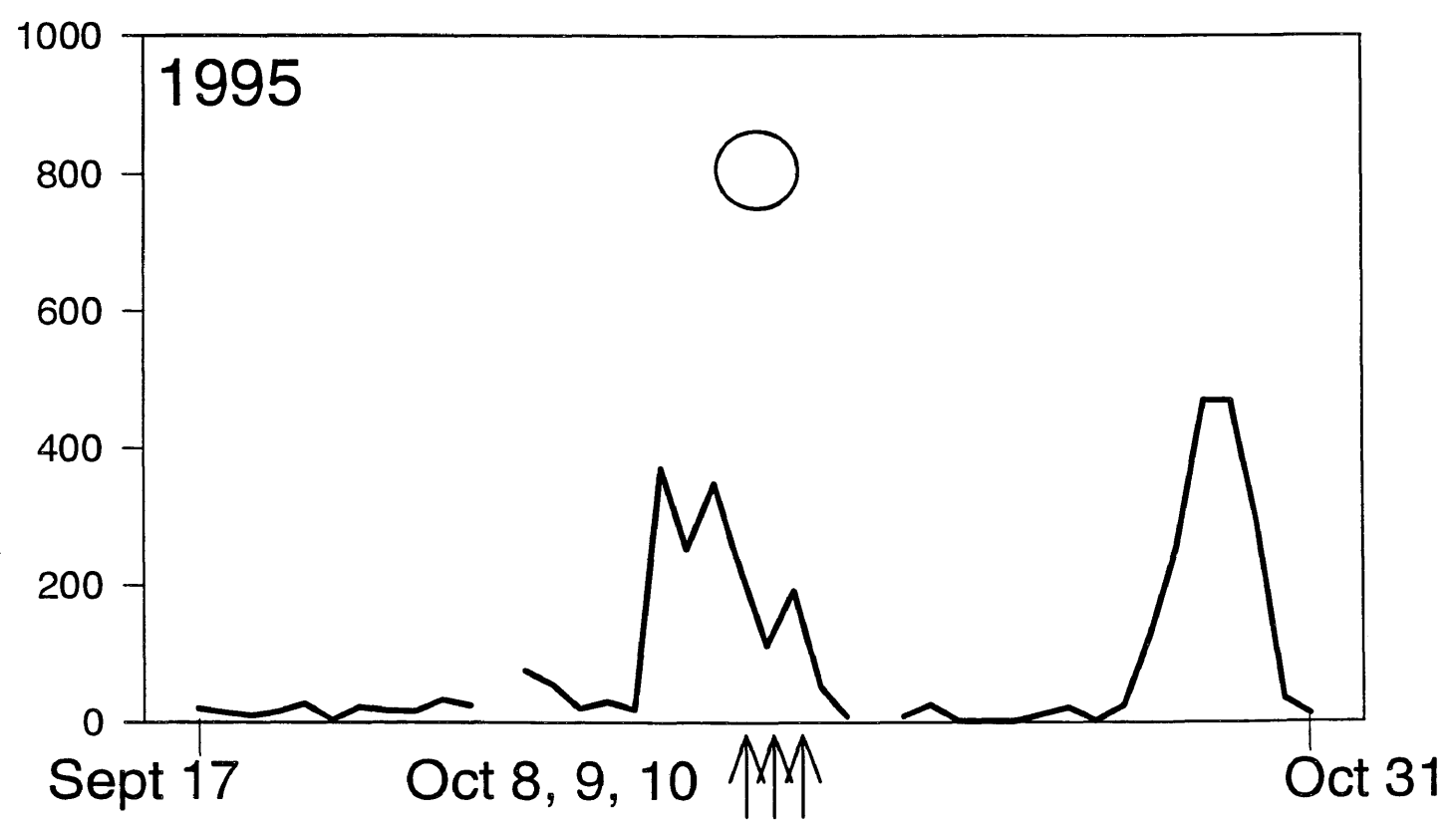
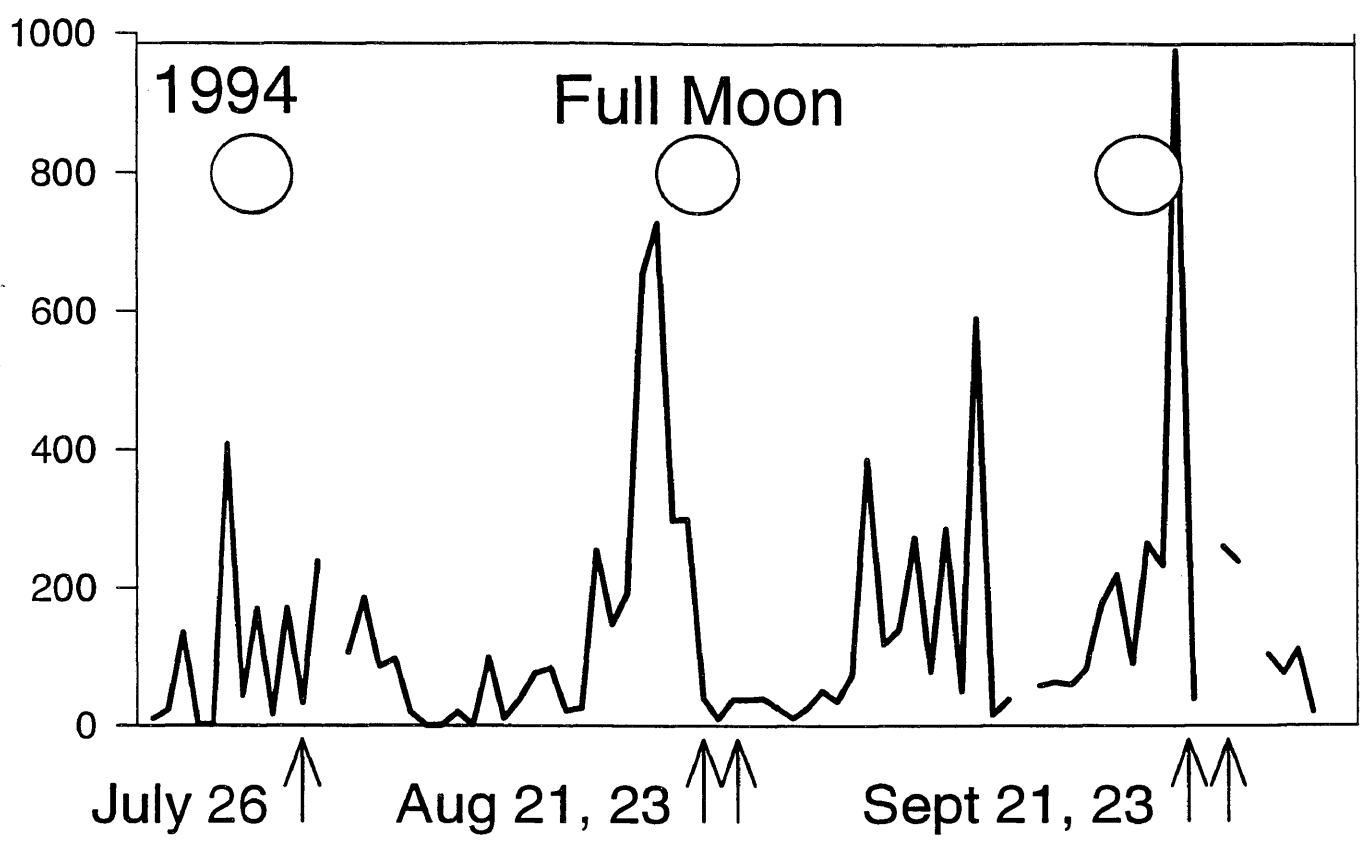
Blue crabs were grouped into 3 size classes for analyses: megalopae and first instars (< 3.1 mm), 2nd - 5th instars (3.1-9.1 mm), and remaining crabs (> 9.1 mm) (Pile *et al.* 1996). Each size class was analyzed with logistic regression, a nonparametric test which uses maximum likelihood estimates in order to relate dependent and independent variables. A binary or Bernoulli response is required in the simplest model (Agresti 1990). In my analyses, each crab was considered independent, and binary responses were between *R. maritima* and *Z. marina*, or between north and south shores. The assumption of independence is justified as follows: 1) Settlement is related to individual detection of environmental cues (lunar cycle, van Montfrans *et al.* 1990, 1995; chemical cues, Forward *et al.* 1994; DeVries *et al.* 1994), and developmental stage (Metcalf and Lipcius 1992).

2) Postlarvae and early instars observed in aquaria and flume studies did not appear to react to each other (Robert Orth, pers. comm.). 3) Each treatment (shore/seagrass species for each crab size class) was tested against a Poisson distribution using a Chi² test (Elliott 1971). Generally, the X² value was between the 5% significance levels, and the test failed to reject the hypothesis of randomness (p>0.05). A contagious distribution was found in only 3 out of 25 tests: in August, for 2nd to 5th instars on the south shore (*R. maritima*: X² = 51.47, p<0.05; *Z. marina*: X² = 40.84, p<0.05), and in September, for postlarvae to 1st instars, on the north shore, in *R. maritima* beds (X² = 32.88, p<0.05).

The logistic function, $\pi = \exp(a + \beta x) / 1 + \exp(a + \beta x)$, was fit to data using maximum likelihood estimates (π = the probability of a crab found in *R. maritima*, or on the north shore; $1 - \pi$ = the probability of a crab found in *Z. marina*, or on the south shore; a and β = the y-intercept and the slope, respectively, of the linearized equation; x = explanatory variable, time: July, August, September, or site: north, south). On the north or the south shore, the density of each crab size class was compared between *R. maritima* and *Z. marina* through time. Similarly, in *R. maritima* or *Z. marina*, the density of each crab size class was compared between the north and south shores through time. Crab densities in *R. maritima* and *Z. marina* (or on the north and south shores) 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). Interactions between site, time and grass species were analyzed with loglinear models (Agresti 1990).

Fig. 2. Abundance of blue crab postlarvae, collected nightly from plankton during maximum flood tide at Gloucester Point during summers of 1994 and 1995. Labelled arrows represent sampling dates.

Number of Planktonic Postlarvae in 20 Minutes



Because results from 1994 indicated that seagrass species, depth or site could influence early stage blue crab distributions, the study was continued during the summer of 1995 with some modifications, to differentiate between these effects. The study was conducted on the north shore of the York River to minimize site effects. Two bed types were classified in the York River: 1) R-Z beds had monospecific *R. maritima* in shallow water which graded into monospecific *Z. marina* in deep water. 2) Z-Z beds were composed entirely of monospecific *Z. marina*, in shallow and deep water. Because *R. maritima* rarely grows in water greater than 70 cm MLW in the Chesapeake Bay, there were no R-R or Z-R beds. Thus, bed type, rather than seagrass species, was used as a main effect in the 1995 analyses. Deep (70-100cm MLW) and shallow (25-50cm MLW) sites were randomly selected in R-Z beds and Z-Z beds, resulting in four treatments: shallow R-Z, deep R-Z, shallow Z-Z, and deep Z-Z (Figure 1). Randomly selected sites were marked with stakes prior to sampling. Sampling was initiated when a peak in postlarval settlement had been detected with plankton samples and settlement substrates. Four suction samples (Orth and van Montfrans 1987) were randomly taken in each treatment on each of three consecutive days: October 8- October 10, 1995 (Figure 2), using a 1.67 m² sampling ring. The ring was deployed next to the field marker, and the enclosed contents were suctioned for 6 minutes, followed by 3 minutes of dipnetting. This method has been shown to be statistically powerful with a 88 % efficiency in crab capture in seagrass beds (Orth and van Montfrans 1987). Before sampling crabs, plant biomass cores (0.02 m²) were taken inside each sampling ring to determine aboveground dry

weight, shoot density and canopy height of vegetative *R. maritima* and vegetative *Z. marina*. Sediment samples were also taken with each sample. All samples were frozen for later analysis as in 1994. Temperature, salinity, depth, time and GPS coordinates were recorded for each sample.

According to qualitative results, and to aid statistical analyses, blue crabs were grouped into 6 size classes: megalopae and 1st instars (<3.1 mm spine to spine carapace width), 2nd - 3rd instars (3.1-5.9 mm), 4th to 7th instars (6.0-12.6 mm), 8th to 9th instars (12.7-16.0 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; covariates: grass dry weight, shoot density, canopy height, distance upriver). Data were tested for homogeneity of variances and log-transformed when necessary (Zar 1984). Linear regressions were conducted when covariates were significant. Plant dry weight and shoot density were similarly tested as dependent variables by bed type and depth. Salinity, temperature, and sediment type were evaluated qualitatively.

Results

1994 Results

Effects of Seagrass Species within Site: On the south shore, all crab stages were evenly distributed between *Z. marina* and *R. maritima*, with one exception. In August, crabs greater than the 5th instar were significantly more abundant in *R. maritima* than in *Z. marina* ($p < 0.05$). Also, the percentage of crabs greater than

the 5th instar significantly decreased in *R. maritima* from July to September ($p < 0.05$). Postlarvae through 5th instars were evenly distributed between *Z. marina* and *R. maritima*, and did not significantly change through time (Figure 3).

On the north shore, all crab stages were significantly greater in *R. maritima* than in *Z. marina* ($p < 0.05$), with one exception. In August, postlarvae and 1st instars were evenly distributed between *R. maritima* and *Z. marina*. The percentage of postlarvae and 1st instars significantly increased in *R. maritima* from August to September ($p < 0.05$). The distribution of crabs greater than the 2nd instar did not significantly change through time, however (Figure 3).

Effects of Site within Seagrass Species: Samples on the north shore were generally taken in deeper water than those on the south shore (Figure 4). In *Z. marina* beds, all crab stages were significantly more abundant on the shallower, south shore ($p < 0.05$), and there were no significant changes through time (Figure 5). In contrast, comparisons of crab abundances between north and south *R. maritima* beds were inconsistent. In August, postlarvae through 5th instars were evenly distributed between the north and south shores; crabs greater than the 5th instar were significantly more abundant in the shallower, south *R. maritima* beds. In September, crabs were significantly more abundant in the deeper, north *R. maritima* beds ($p < 0.05$), with the exception of 2nd to 5th instars, which were evenly distributed between shores (Figure 5).

Loglinear modelling indicated a model of conditional independence for postlarvae through 1st instars, and greater than 5th instars: within site, interactions

did not occur between time and grass species. For 2nd to 5th instars, within seagrass species, interactions did not occur between time and site.

Seagrass: Sampling grids were established in monospecific stands of the respective seagrass beds. Some samples, however, contained small amounts of the other grass species (Figure 6). Also, some grass samples were covered in red algae, including *Ceramium*, which was very difficult to remove, especially from *R. maritima*, which has very fine shoots. Red algae made up a large proportion of many *R. maritima* samples. Red algae also grew on *Z. marina*, but was easy to remove. With these caveats in mind, only qualitative comparisons were made, and comparisons between the standing crop of *R. maritima* and *Z. marina* were precluded. Grass standing crop did not appear to vary between the north and south shores through time. *Ruppia maritima* biomass decreased through time, and *Z. marina* did not appear to change (Figure 6).

Fig. 3. Comparison of observed crab densities between *R. maritima* and *Z. marina* on the north or south shore of the York River in 1994. Crabs are evenly distributed between *R. maritima* and *Z. marina* if standard error bar overlaps line drawn at 50%. If percentages exceed 50%, crab densities are higher in *R. maritima*. If percentages are below 50%, crab densities are higher in *Z. marina*. Asterisks indicate significant differences between crab densities in *R. maritima* and *Z. marina* ($p < 0.05$). When there is no significant change through time, crab percentages are collapsed across time and represented by a single bar.

Percentage of crabs in *Ruppia maritima* Relative to *Zostera marina*

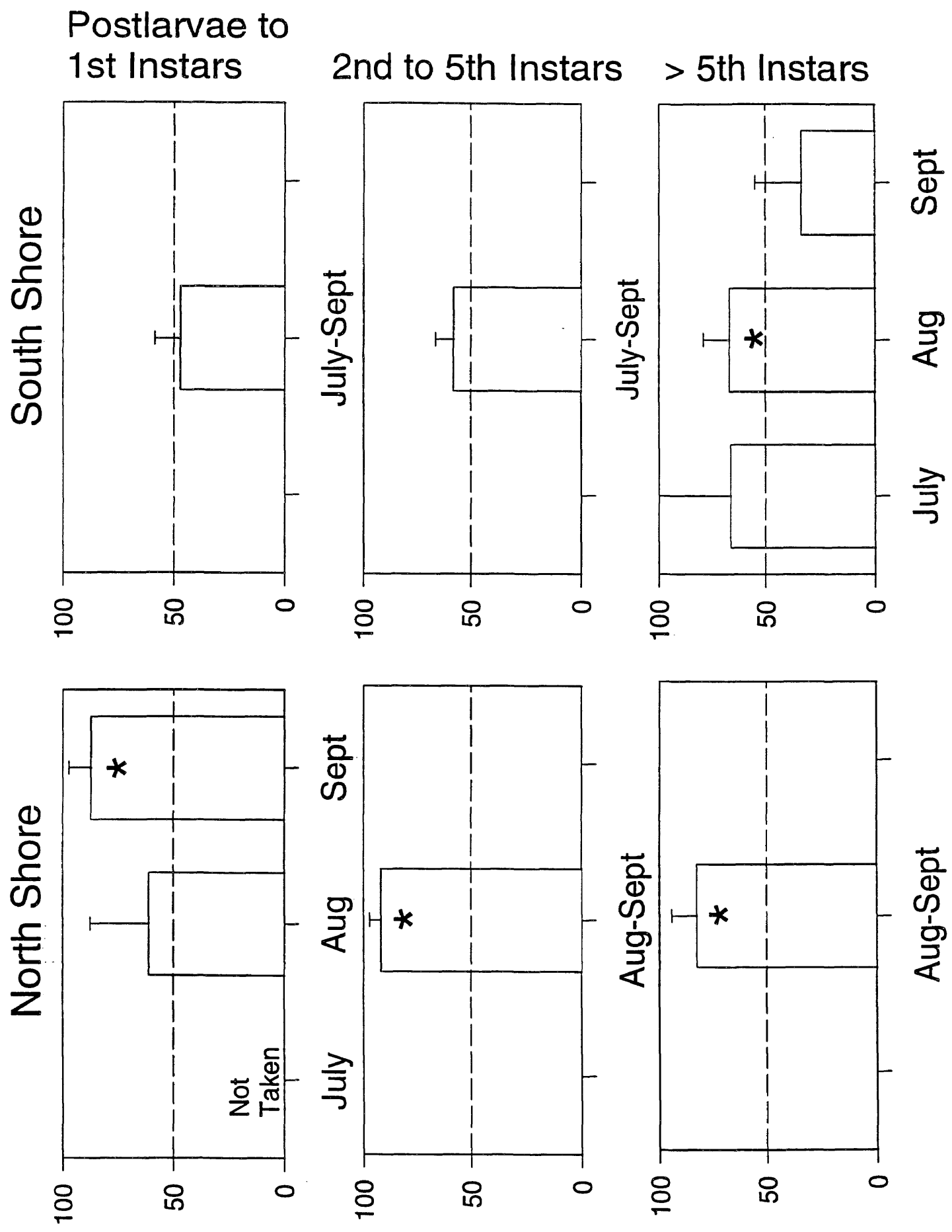


Fig. 4. Mean water depth (standardized to MLW) for samples collected in *Z. marina* and *R. maritima* beds along the north and south shores of the York River, VA, in 1994.

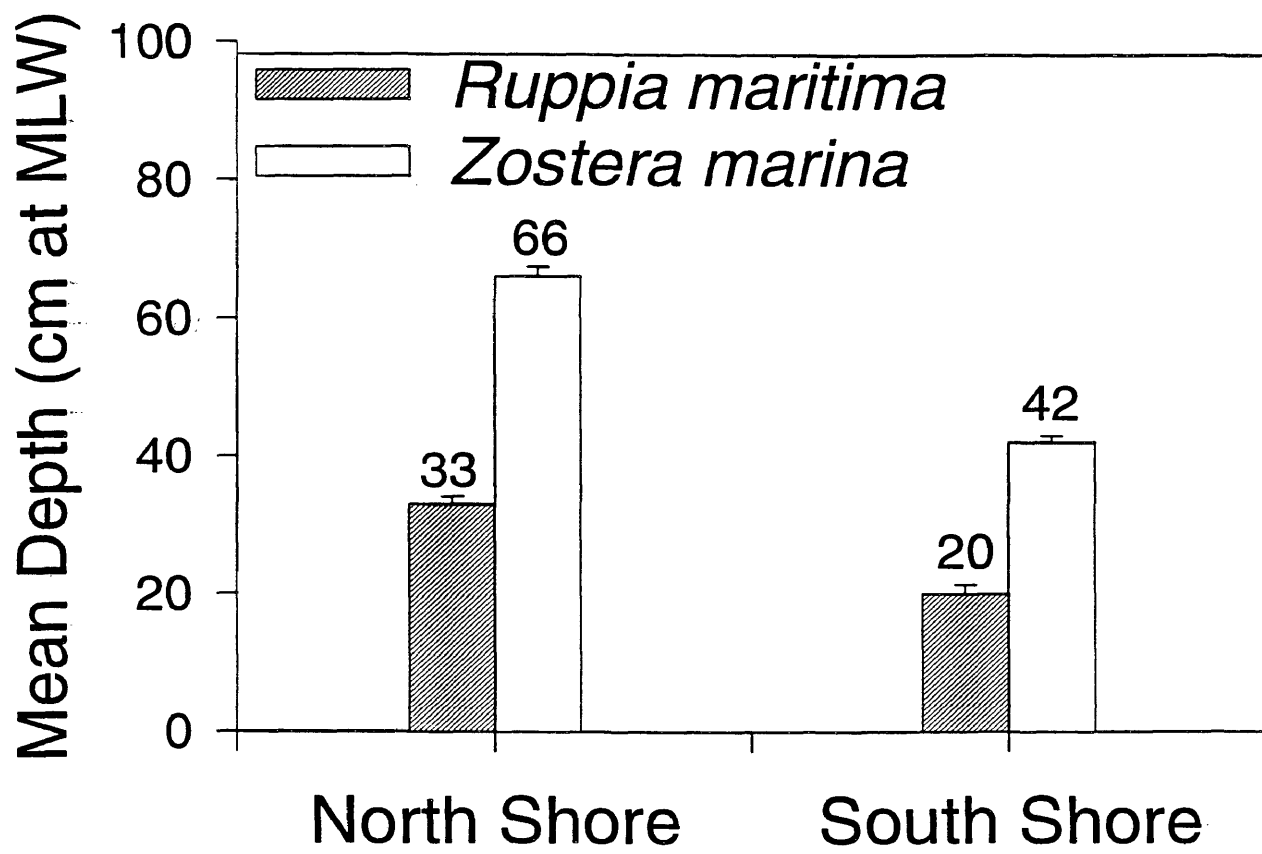


Fig. 5. Comparison of observed crab density between the north and south shore of the York River in *R. maritima* or *Z. marina*, in 1994. Crabs are evenly distributed between the north and south shores if standard error bar overlaps line drawn at 50%. If percentages exceed 50%, crab densities are higher on the north shore. If percentages are below 50%, crab densities are higher on the south shore. Asterisks indicate significant differences between crab densities on the north and south shores ($p < 0.05$). When there is no significant change through time, crab percentages are collapsed across time and represented by a single bar.

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Percentage of crabs on North Shore
Relative to South Shore

Zostera marina

Ruppia maritima

Postlarvae to
1st Instars

2nd to 5th Instars

> 5th Instars

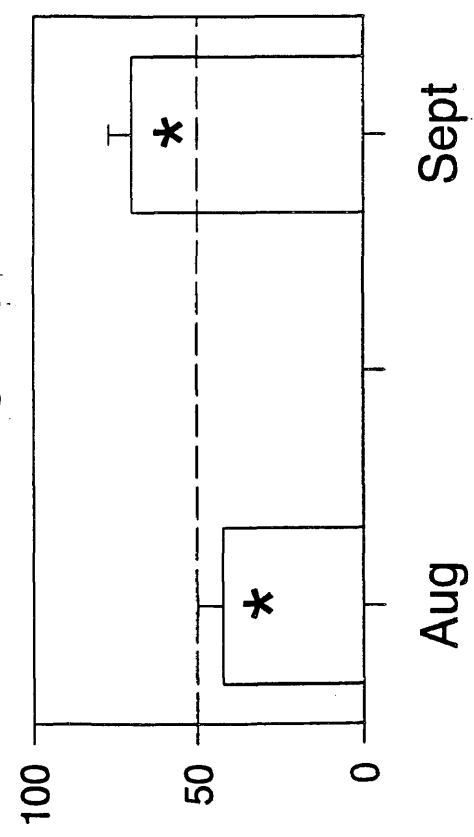
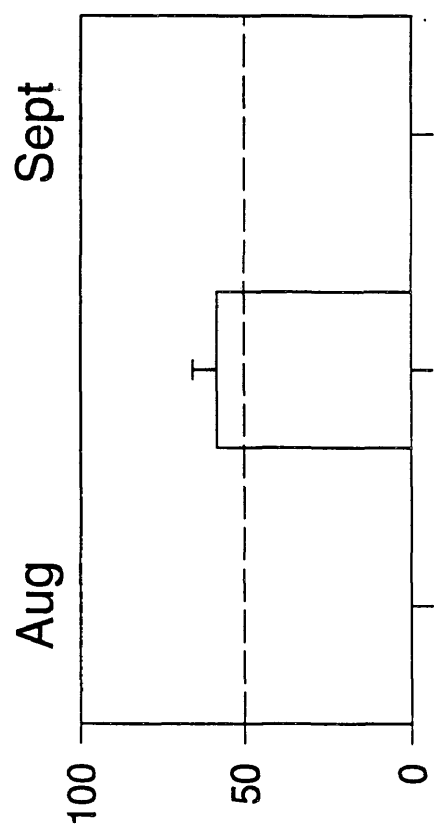
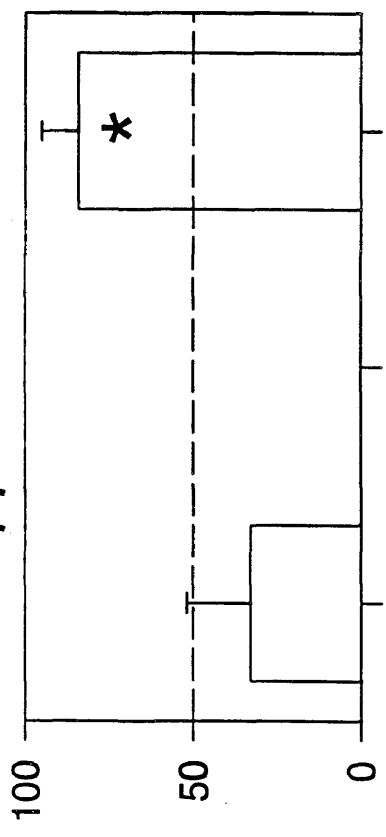
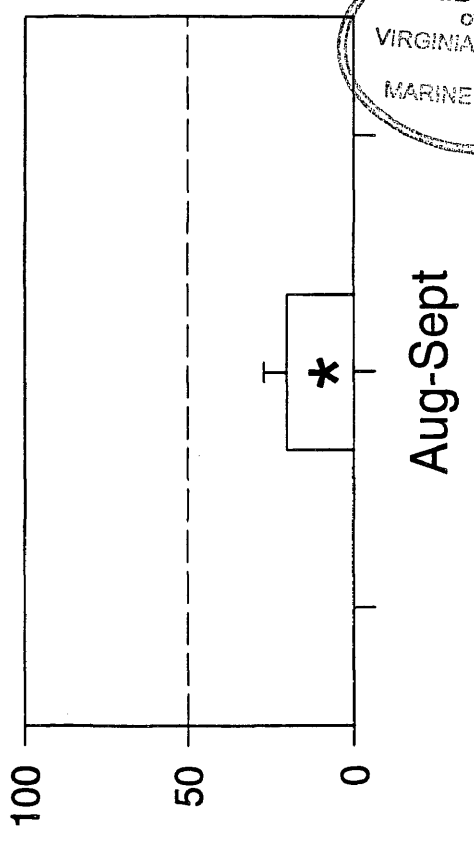
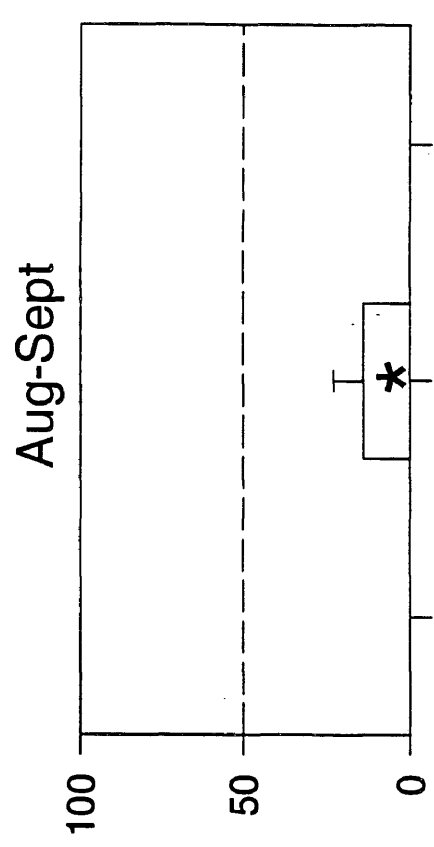
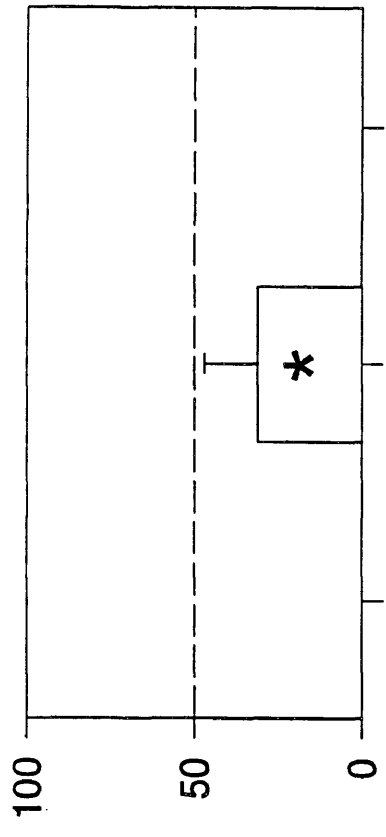
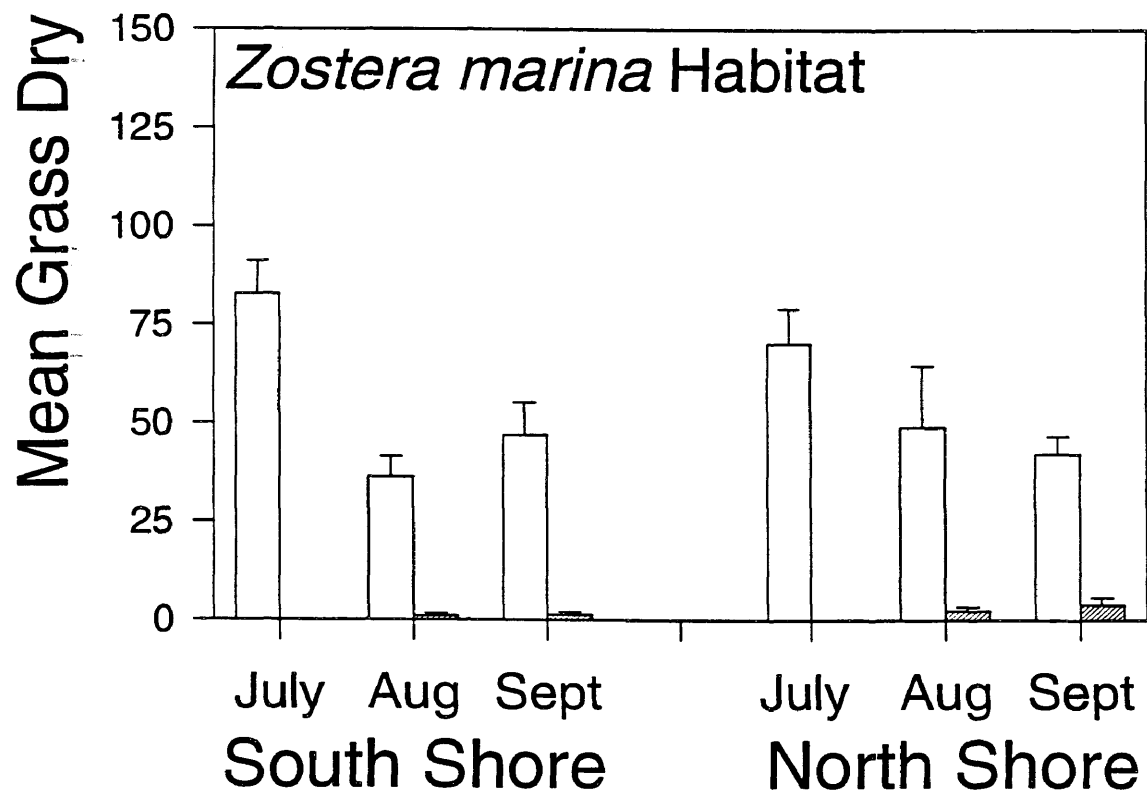
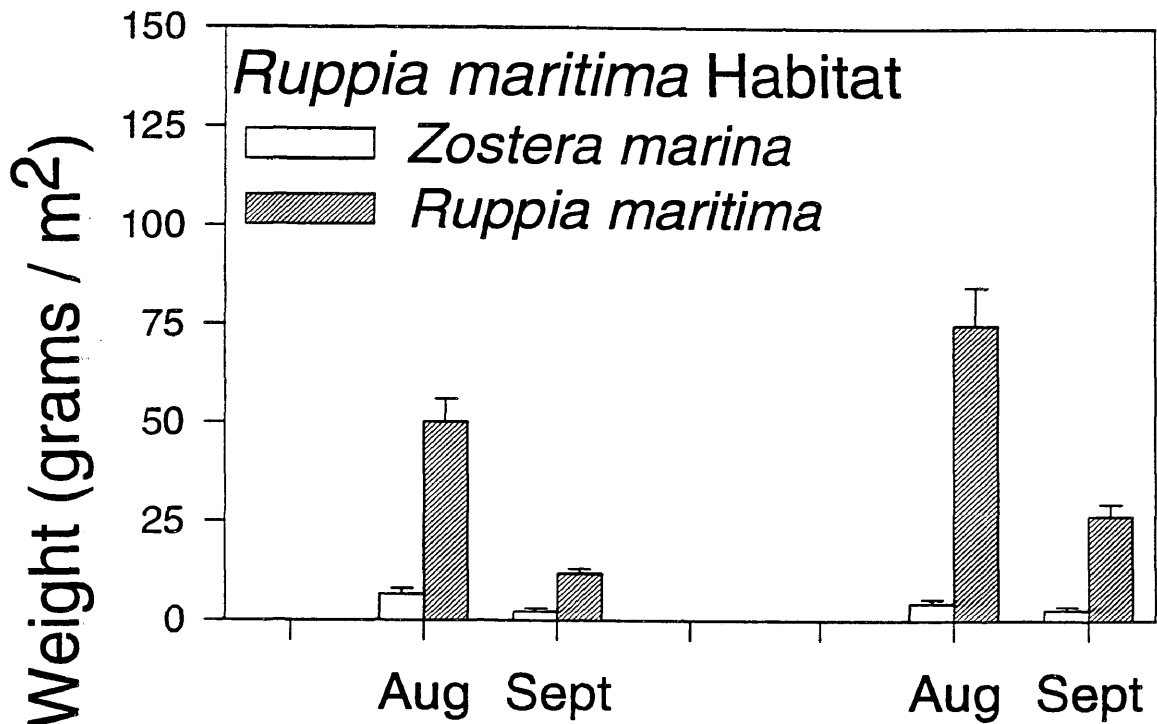


Fig. 6. Mean grass dry weights in *R. maritima* and *Z. marina* habitats on the north and south shores of the York River in 1994. Standard error bars are shown.



1995 Results

Samples were taken in sandy areas (80-90% sand, 10-20% fine sediment).

Temperatures ranged between 20 and 25°C. Salinity ranged between 20 and 25‰.

Early instars: Postlarvae, 1st instars, and 2nd to 3rd instars showed similar results by bed type, depth, and distance upriver (Table 1, Figure 7). Crab densities averaged 1.97/m² (postlarvae), 6.76/m² (1st instars), and 3.36/m² (2nd to 3rd instars). There were no significant differences by bed type or depth for postlarvae, 1st instars and 2nd to 3rd instars (ANCOVA, $p > 0.05$). First instars were significantly related to date (ANCOVA, $F=4.18$, $p=0.025$) (Table 1).

The covariates, grass dry weight and shoot density, were nonsignificant for all early crab instars (ANCOVA, $p > 0.05$). The covariate, canopy height, was nearly significant for postlarvae (ANCOVA, $F= 4.09$, $p=0.053$). Postlarvae were negatively correlated with *R. maritima* canopy height (Regression, $R^2=34.5$, $p=0.013$) (Figure 8). Although postlarval density increased with *Z. marina* canopy height, there was no significant correlation. The covariate, distance upriver, was significant for postlarvae (ANCOVA, $F= 6.14$, $p = 0.02$), 1st instars (ANCOVA, $F = 8.26$, $p = 0.008$), and 2nd to 3rd instars (ANCOVA, $F = 6.26$, $p = 0.018$). Linearly transformed regressions indicated that postlarvae (Regression, $R^2 = 17.3$, $p = 0.004$), 1st instars (Regression, $R^2 = 30.8$, $p = 0.000$) and 2nd to 3rd instars (Regression, $R^2 = 23.1$, $p = 0.003$) increased significantly with distance upriver. Hyperbolic functions provided the best fit between postlarvae through 3rd instars and distance upriver (Figure 9).

Late instars: Bed type and depth were more important for crabs greater than the 3rd

instar (Table 1, Figure 7). There was a significant interaction between depth and bed type for 4th through 7th instars (ANOVA, $F = 16.9$, $p < 0.001$). A Tukey's test indicated that 4th to 7th instars were significantly greater in shallow R-Z beds than in deep R-Z beds or shallow Z-Z beds (Table 2). 8th to 9th instars were significantly greater in shallow than in deep water (ANOVA, $F = 8.07$, $p = 0.008$), and the interaction between bed type and depth was nearly significant (ANOVA, $F = 3.12$, $p = 0.087$) (Table 1, Figure 7). A Tukey's test revealed that 8th to 9th instars were significantly more abundant in shallow R-Z beds than in deep R-Z beds (Table 2). Greater than 9th instars were significantly greater in R-Z than in Z-Z beds regardless of depth (ANOVA, $F = 6.11$, $p = 0.019$). The covariates, grass dry weight, shoot density, and distance upriver, were nonsignificant for crabs greater than the 3rd instar (Table 1).

Although the covariate, shoot density, was nonsignificant, late stage crab densities reflect this distinguishing seagrass characteristic (see below). After exclusion of *Z. marina* samples, *R. maritima* shoot densities, which ranged between 700 and 4800 shoots/m², were almost significantly correlated with the number of 4th to 7th instars (Regression, $R^2 = 30.3\%$, $p = 0.064$) (Figure 10). Shoot density in *Z. marina* beds, which ranged from 50 to 550 shoots/m², was not significantly related to crab abundance.

Seagrass: Seagrass dry weight and shoot density varied by bed type and depth (Table 3, Figure 11). Dry weight averaged 20.06g/m² in *R. maritima* beds (shallow R-Z), and 7.83g/m² in *Z. marina* beds (deep R-Z, shallow Z-Z and deep Z-Z). Shoot density

averaged 3062 shoots/m² in *R. maritima* beds and 220 shoots/m² in *Z. marina* beds. The interaction between bed type and depth was nearly significant for grass dry weight (ANOVA, $F = 3.68$, $p = 0.065$). A Tukey's test indicated that grass dry weight was significantly greater in shallow R-Z beds than in deep R-Z beds or shallow Z-Z beds. Grass dry weight also was significantly greater in deep Z-Z beds than in shallow Z-Z beds (Table 4). There was a significant interaction between bed type and depth for shoot density ($p < 0.001$) (Table 3). A Tukey's test indicated that there were significantly more shoots in shallow R-Z beds than in deep R-Z beds or shallow Z-Z beds (Table 4). Overall, grass dry weight and shoot density were greater in shallow *R. maritima* beds than in deep R-Z beds (*Z. marina*) or *Z. marina* beds.

Table 1. ANCOVA performed on each blue crab instar, from 1995 sampling, with Bed type and Depth as main effects. Dependent variable, number of crabs, is log transformed when necessary. Date is a blocked factor. Distance Upriver and Canopy Height are covariates. Only significant covariates are included in analyses and table. Significance at $P < 0.05$.

| | Factor | DF | F | P-value | Power |
|----------------------|------------------|----|-------|---------|-------|
| Postlarvae | Bed type | 1 | 1.09 | 0.305 | 0.15 |
| | Depth | 1 | 0.93 | 0.344 | 0.00 |
| | B*D | 1 | 0.99 | 0.330 | 0.00 |
| | Date | 2 | 0.15 | 0.863 | 0.00 |
| | Distance Upriver | 1 | 6.14 | 0.020 | |
| | Canopy Height | 1 | 4.09 | 0.053 | 0.74 |
| 1st Instars | Bed type | 1 | 0.03 | 0.860 | 0.45 |
| | Depth | 1 | 2.29 | 0.141 | 0.00 |
| | B*D | 1 | 0.00 | 0.991 | 0.00 |
| | Date | 2 | 4.18 | 0.025 | |
| | Distance Upriver | 1 | 8.26 | 0.008 | |
| Log(2nd-3rd Instars) | Bed type | 1 | 0.75 | 0.393 | 0.00 |
| | Depth | 1 | 0.78 | 0.383 | 0.00 |
| | B*D | 1 | 1.31 | 0.261 | 0.00 |
| | Date | 2 | 1.14 | 0.335 | 0.00 |
| | Distance Upriver | 1 | 6.26 | 0.018 | |
| Log(4th-7th Instars) | Bed type | 1 | 11.92 | 0.002 | |
| | Depth | 1 | 11.50 | 0.002 | |
| | B*D | 1 | 16.90 | 0.000 | |
| | Date | 2 | 0.91 | 0.412 | 0.00 |
| Log(8th-9th Instars) | Bed type | 1 | 0.49 | 0.488 | 0.00 |
| | Depth | 1 | 8.07 | 0.008 | |
| | B*D | 1 | 3.12 | 0.087 | 0.55 |
| | Date | 2 | 0.40 | 0.672 | 0.00 |
| Log(> 9th Instars) | Bed type | 1 | 6.11 | 0.019 | |
| | Depth | 1 | 2.23 | 0.146 | 0.30 |
| | B*D | 1 | 1.53 | 0.226 | 0.15 |
| | Date | 2 | 1.58 | 0.224 | 0.15 |

Table 2. Tukey's test performed on instars, from 1995 sampling, when there was a significant interaction between depth and bed type in ANCOVA. Comparisons are between log transformed mean number of crabs in different treatments. Parentheses enclose these means. The test statistic used in Tukey's test is q.

| Category | Factor | Levels | Tukey's Diff. ^a | P | |
|-----------------------------|------------------|----------|---------------------------------------|-------|----|
| Log (4th-7th Instars) | Bed type R-Z | Depth | Deep (0.33) Shallow (1.12) | 0.790 | ** |
| | | Depth | Deep (0.40) Shallow (0.409) | 0.009 | ns |
| | Depth Shallow | Bed type | Z-Z (0.409) R-Z (1.12) | 0.711 | ** |
| | | Bed type | R-Z (0.33) Z-Z (0.40) | 0.070 | ns |
| Log (8th-9th Instars) | Bed type R-Z | Depth | Deep (0.238) Shallow (0.759) | 0.521 | ** |
| | | Depth | Deep (0.351) Shallow (0.492) | 0.141 | ns |
| | Depth Shallow | Bed type | Z-Z (0.492) R-Z (0.759) | 0.267 | ns |
| | | Bed type | R-Z (0.238) Z-Z (0.351) | 0.113 | ns |

^aTested against $D_{0.05}$ or $D_{0.01}$, calculated as $D_x = (\text{Error Mean Square} / (1/n_a + 1/n_b))^{1/2} * (q)$, 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, *P < 0.05, ns P > 0.05.

Table 3. ANOVA performed on seagrass characteristics, from 1995 sampling, with Bed type and Depth as main effects. Dependent variable was total dry weight or shoot density. Shoot density was log transformed. Date is a blocked factor. Significance at P= 0.05.

| | Factor | DF | F | P-value | Power |
|------------------------|----------|----|-------|---------|-------|
| Total Dry Weight | Bed type | 1 | 4.43 | 0.044 | |
| | Depth | 1 | 0.00 | 0.973 | 0.00 |
| | B*D | 1 | 3.68 | 0.065 | 0.70 |
| | Date | 2 | 0.97 | 0.392 | 0.00 |
| Log (Shoot Density) | Bed type | 1 | 31.35 | 0.000 | |
| | Depth | 1 | 28.03 | 0.000 | |
| | B*D | 1 | 37.23 | 0.000 | |
| | Date | 2 | 0.92 | 0.412 | 0.00 |

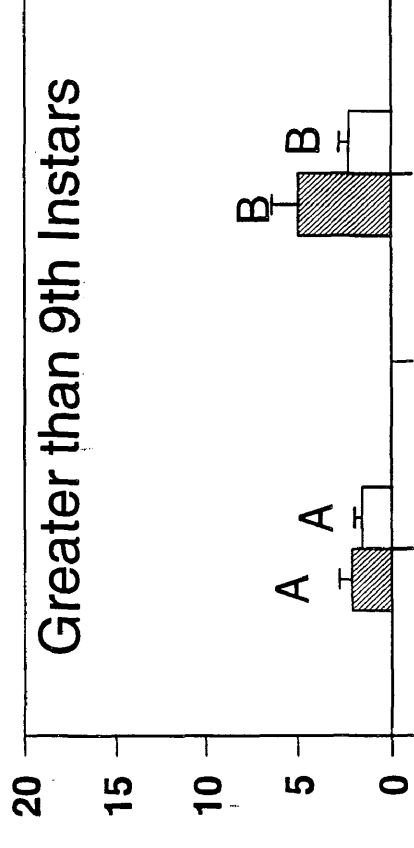
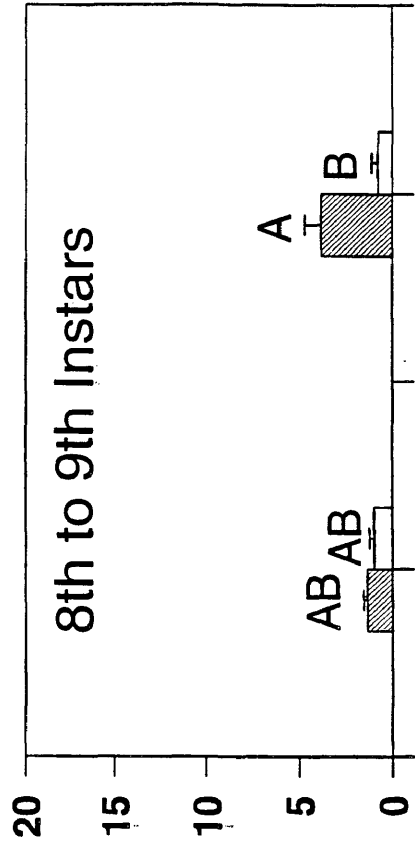
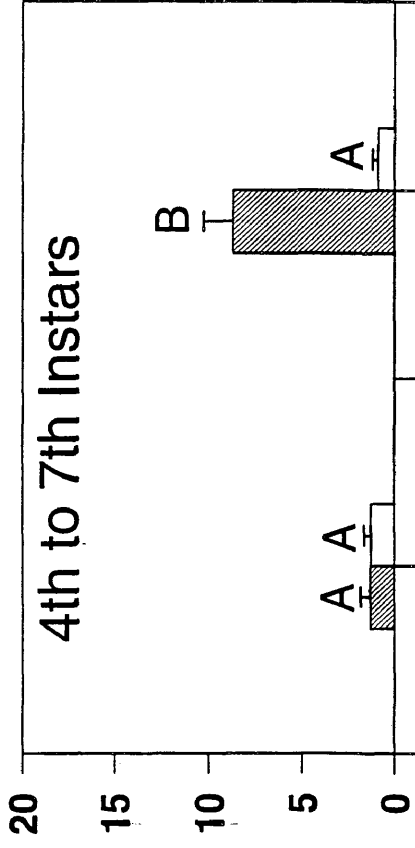
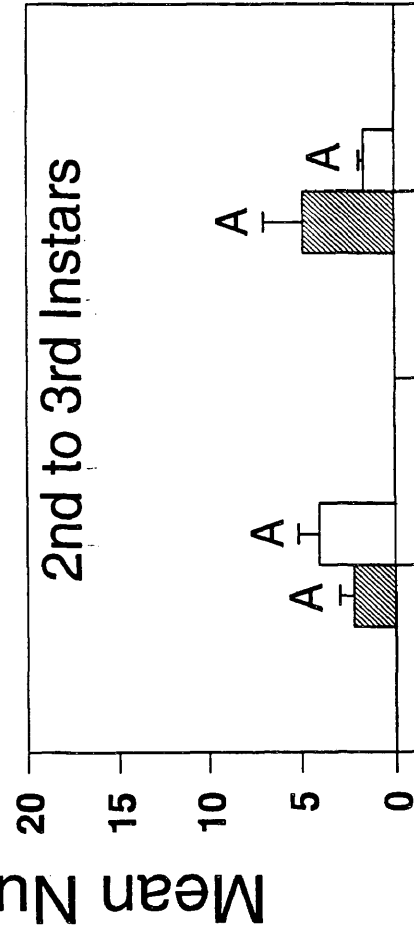
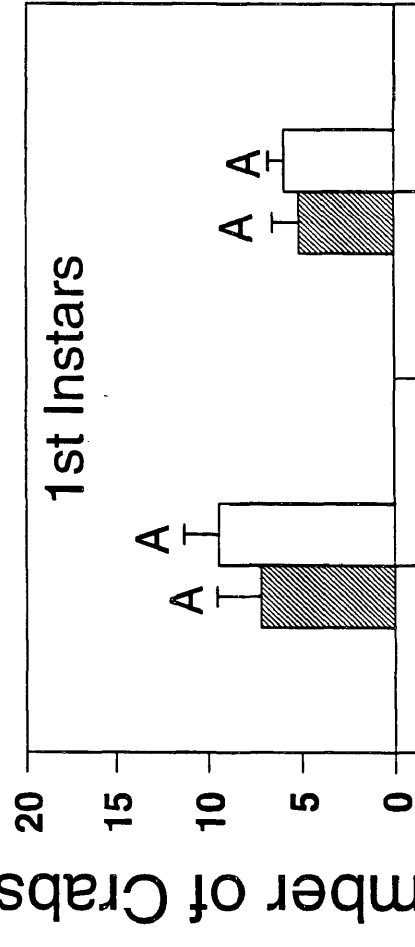
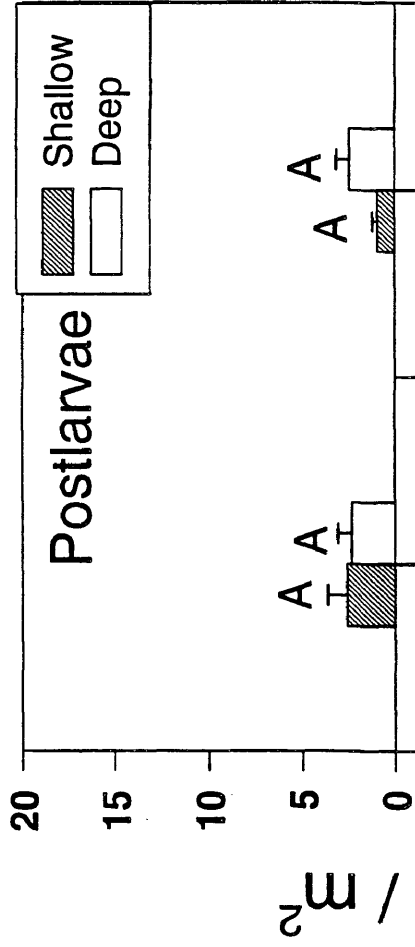
Table 4. Tukey's test performed on seagrass characteristics, from 1995 sampling, when there was a significant interaction between depth and bed type in ANOVA. Comparisons are between grass dry weight or log transformed shoot density in different treatments. Parentheses enclose these means. The test statistic used in Tukey's test is q.

| Category | | Factor | Levels | | Tukey's Diff. ^a | P |
|---------------------------|------------------|----------|-----------------|--------------------|----------------------------|----|
| Dry Weight | Bed type R-Z | Depth | Deep (0.183) | Shallow (0.401) | 0.218 | ** |
| | Z-Z | Depth | Deep (0.173) | Shallow (0.114) | 0.059 | ** |
| | Depth Shallow | Bed type | Z-Z (0.114) | R-Z (0.401) | 0.287 | ** |
| | Deep | Bed type | R-Z (0.183) | Z-Z (0.173) | 0.010 | ns |
| Log (Shoot Density) | Bed type R-Z | Depth | Deep (1.626) | Shallow (2.787) | 1.161 | ** |
| | Z-Z | Depth | Deep (1.663) | Shallow (1.626) | 0.037 | ns |
| | Depth Shallow | Bed type | Z-Z (1.626) | R-Z (2.787) | 1.161 | ** |
| | Deep | Bed type | R-Z (1.643) | Z-Z (1.663) | 0.020 | ns |

^aTested against $D_{0.05}$ or $D_{0.01}$, calculated as $D_x = (\text{Error Mean Square} / (1/n_a + 1/n_b))^{1/2} * (q)$, 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, *P < 0.05, ns P > 0.05.

Fig. 7. Mean number of crabs by depth and bed type in 1995. 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.



R-Z

Z-Z

Bed Types

R-Z

Z-Z

Mean Number of Crabs / m²

Fig. 8. Correlation between number of postlarvae and *R. maritima* canopy height in 1995. Triangles represent individual samples. Linearly transformed regression equation: $\text{Ln}(\text{Postlarvae}) = 2.63 - 0.307 (\text{Canopy height})$, (Regression, $R^2 = 34.5$, $p = 0.013$).

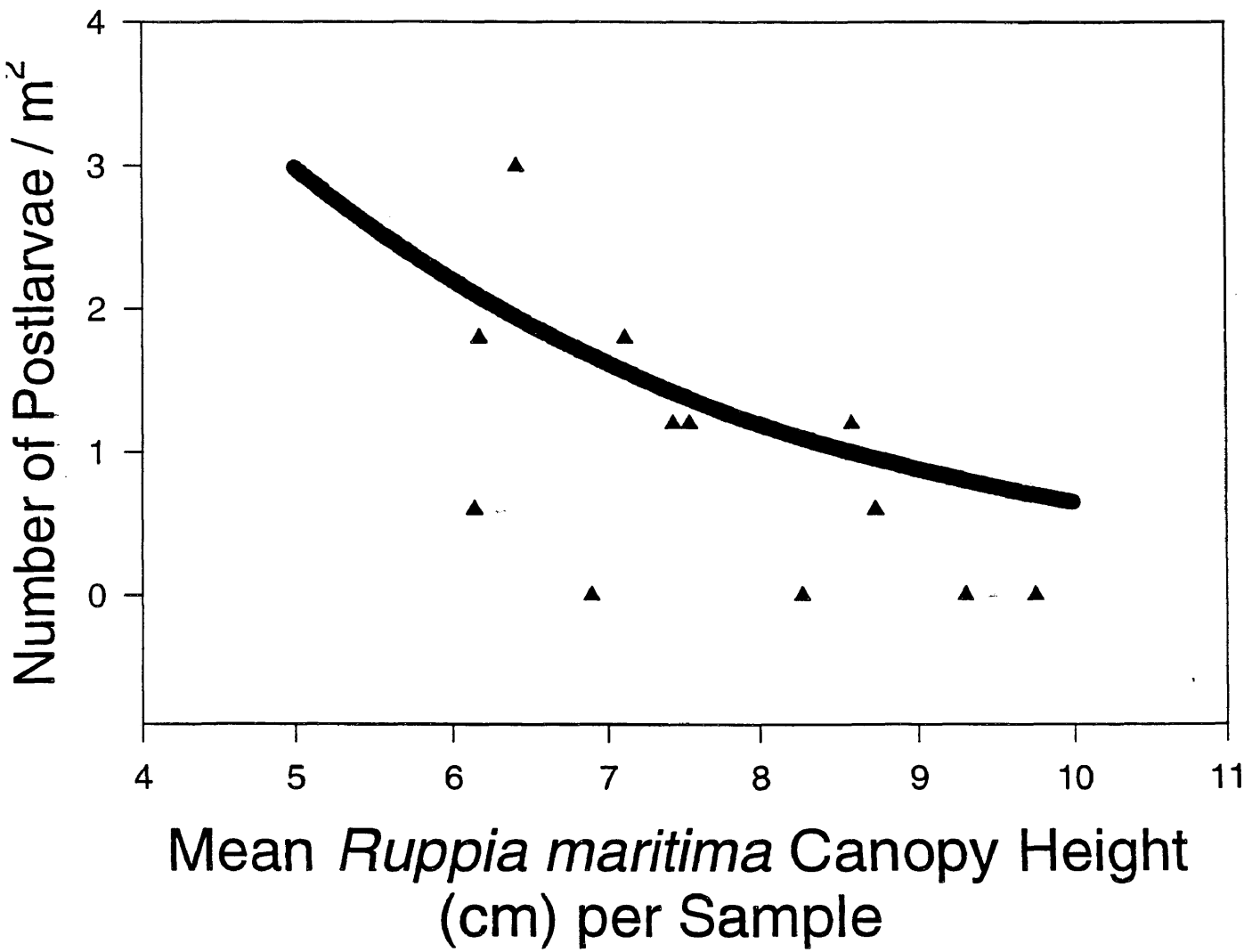


Fig. 9. Correlation between distance along the York River and number of postlarvae, first instars, and second to third instars in 1995. Symbols represent individual samples. Linearly transformed regression equations: 1) Postlarvae = $14.73 - 3.47 \text{ Log}(\text{Distance upriver})$, (Regression, $R^2 = 17.3$, $p = 0.004$). 2) 1st instars = $47.78 - 11.14 \text{ Log}(\text{Distance upriver})$, (Regression, $R^2 = 30.8$, $p < 0.001$). 3) $\text{Ln}(\text{2nd-3rd Instars}) = 1.78 - 0.000144 (\text{Distance upriver})$, (Regression, $R^2 = 23.1$, $p = 0.003$).

Number of Crabs vs. Distance Along York River

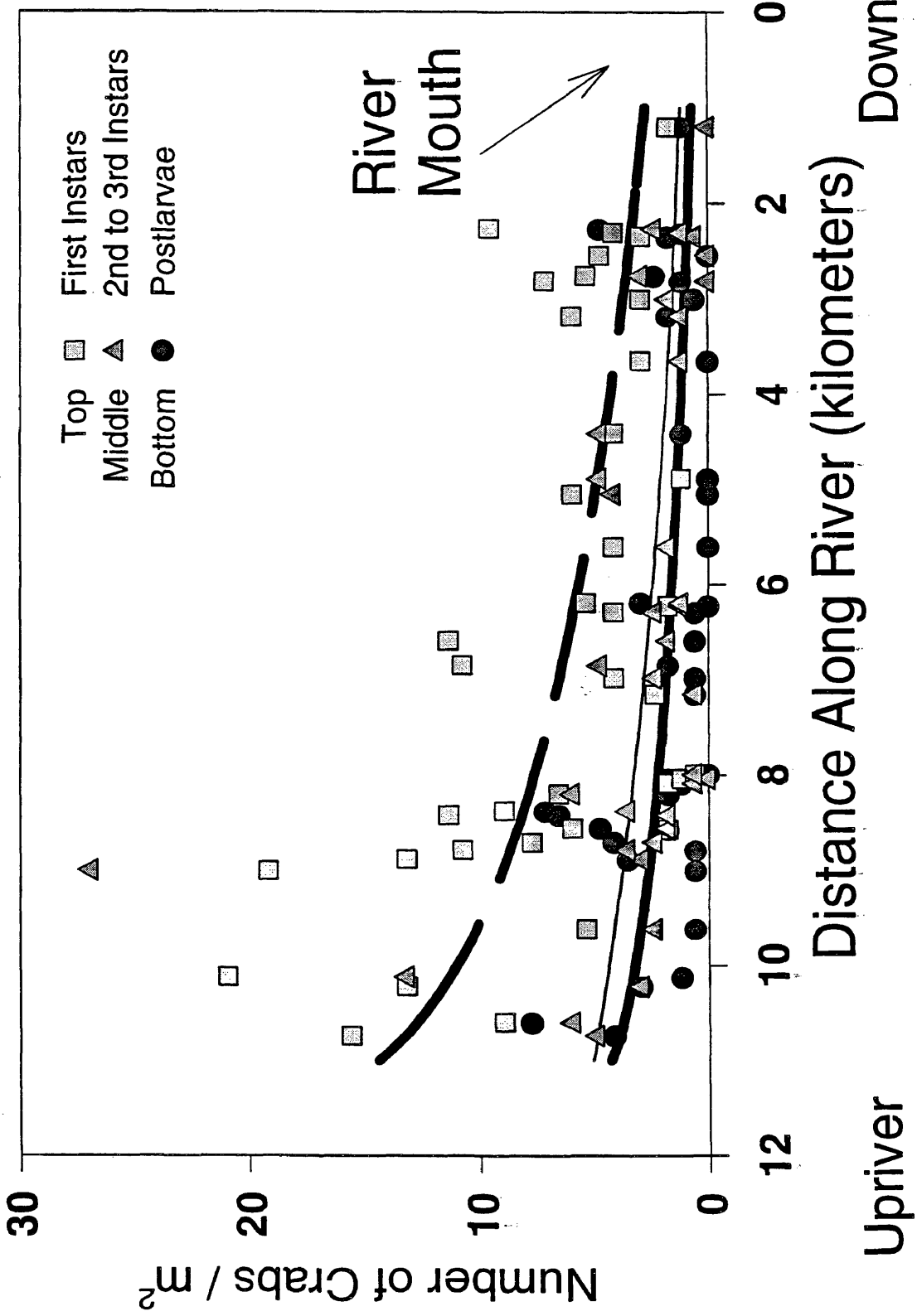


Fig. 10. Correlation between number of 4th to 7th instars and the number of *R. maritima* shoots in 1995. Triangles represent individual samples. Linearly transformed regression equation: $\text{Log}(4\text{th to } 7\text{th instars}) = -0.233 + 0.652 \text{ Log}(\text{Shoot number})$, (Regression, $R^2 = 30.3\%$, $p = 0.064$).

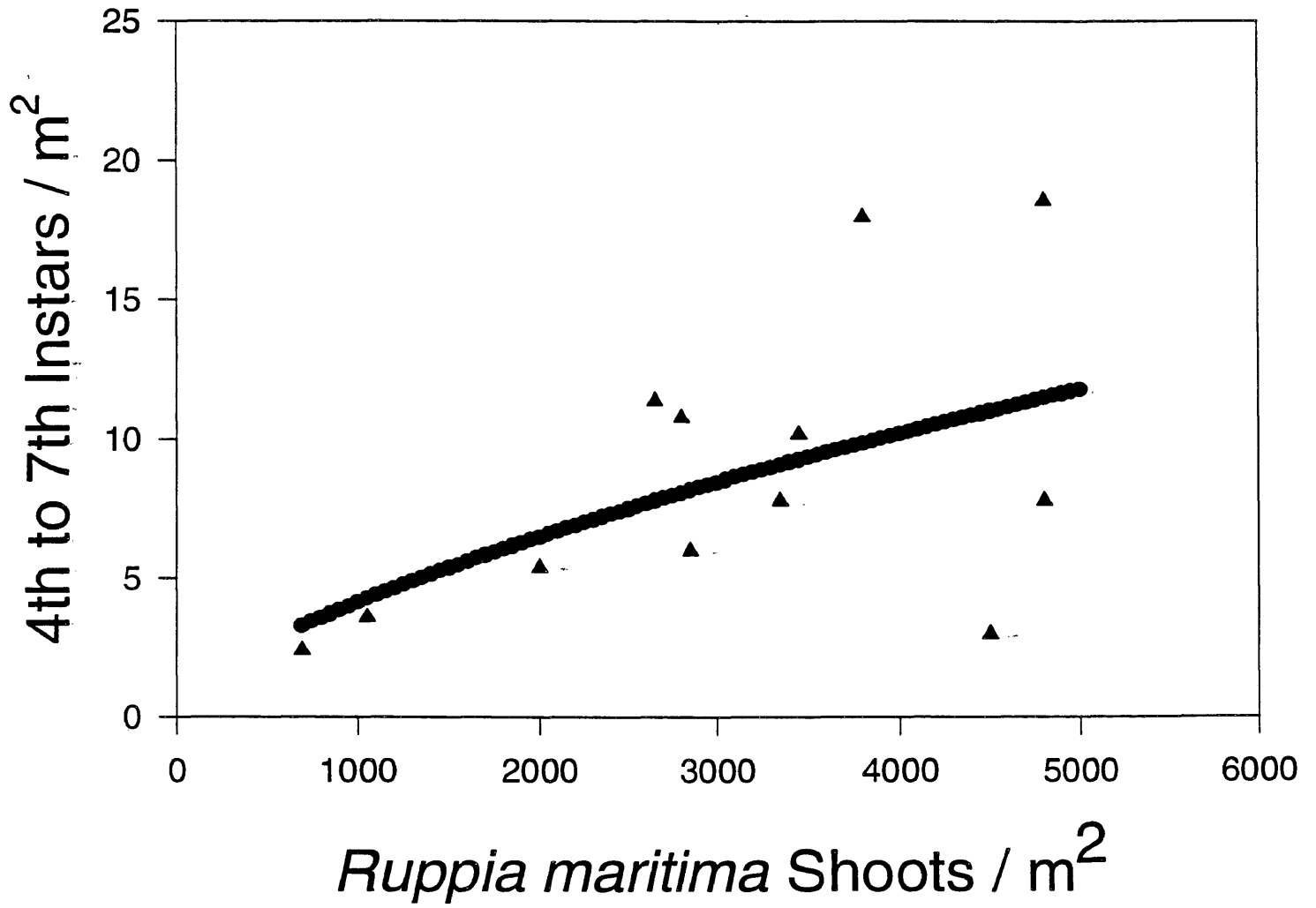
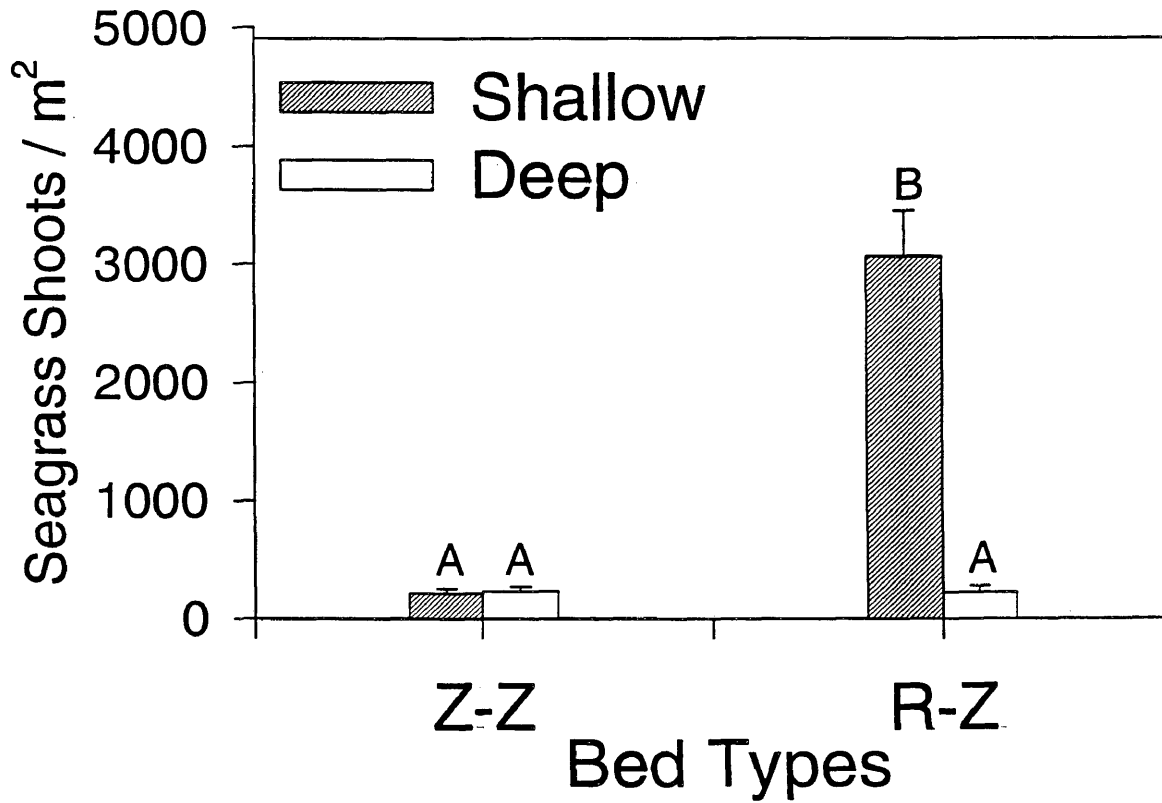
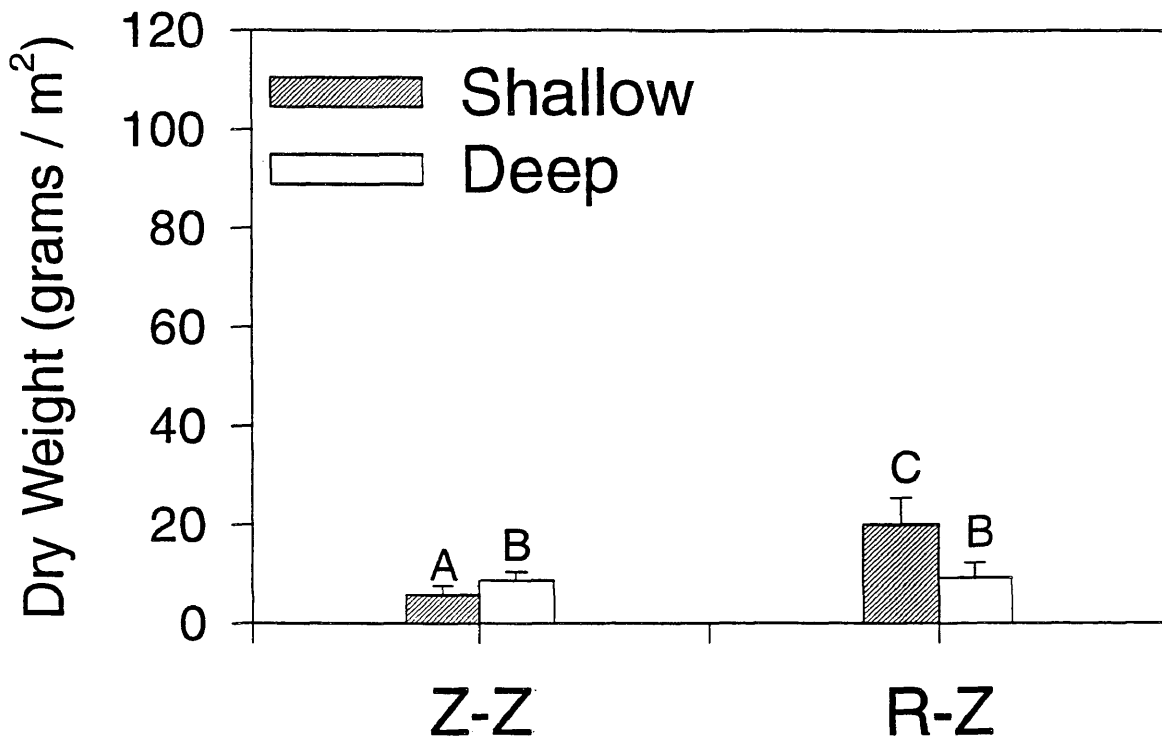


Fig. 11. Seagrass dry weight and shoot density at different depths and bed types in 1995. Letters depict significant differences calculated from Tukey's test ($p < 0.05$): Bars sharing the same letters indicate nonsignificance.



Discussion

In multispecies seagrass beds, habitat use changes ontogenetically for early stage blue crabs, which suggests that during growth, blue crabs are subject to varying physical and biological forces. Studies from 1994 provide evidence that site, depth or seagrass species influence early stage blue crab distributions. Studies were continued in 1995 to differentiate between these effects. Crabs smaller than the fifth instar are rarely found outside of seagrass beds, possibly because of intense predation (Orth and van Montfrans 1987). Therefore, early instars were expected to be strongly influenced by seagrass species and depth, factors which are known to provide varying shelter and nutrition to some species (Hacker and Steneck 1990; Ruiz *et al.* 1993; Ryer 1987; Schneider and Mann 1991a, 1991b). In 1995, however, early instars (megalopae through 3rd instars) were not significantly influenced by seagrass species or depth, but were related to site, increasing density with distance upriver. This evidence suggests that larval supply and physical forces, such as current or wind patterns, affect early instar distributions. Conversely, later instars (>3rd instars), which may gain some refuge in size after the fifth instar (Pile *et al.* 1996), were more abundant in *R. maritima* beds, probably because of high shoot densities. These distributions indicate that habitat selection and differential mortality are more important for > 3rd instars. This study provides evidence that site, seagrass species and water depth influence early stage blue crab distributions.

Effect of Site

In both 1994 and 1995, early instar distributions were significantly related to site. In 1994, on the north shore, crabs were generally more abundant in *R. maritima* than in *Z. marina*, while on the south shore, crabs were evenly distributed between grass species. Current and wind patterns, and larval supply may have differed between shores. In 1995, postlarvae through 3rd instars significantly increased with distance up the York River. Postlarvae use onshore winds and current patterns to reinvade estuaries (Olmi 1994; Goodrich *et al.* 1989). Therefore, physical forces could strongly affect early blue crab distributions. It should be noted, however, that the effect of distance upriver only explained between 17 and 30 percent of the variation in abundances of postlarvae through 3rd instars. In a concurrent study, postlarval density was also related to site, decreasing with distance from the mouth of the Chesapeake Bay and producing a "shadow effect" (Karen Metcalf, unpublished data). The same pattern was found for postlarval settlement in Mobile Bay, Alabama and attributed to postlarval salinity tolerances (Morgan *et al.* 1996). The "shadow effect" may also be a function of the distance from the source of postlarvae, the baymouth, and operate on a much larger scale than in my study, tens of kilometers versus kilometers (Karen Metcalf, pers. comm.). In the York River, postlarvae through 3rd instars increased with distance upriver. In this study, different physical mechanisms such as current patterns or wind events may have influenced crab distributions. Also, crab density patterns may simply reflect a postlarval pulse moving up the river - sampling was initiated when high numbers

of postlarvae were collected in nighttime plankton samples upriver (Figure 1), where the highest densities of postlarvae through 3rd instars were also caught in suction samples. In 1995, later instars (> 3rd instar) were not significantly related to site. With size, blue crabs become highly mobile (juvenile crabs > 20mm vs. adult crabs, Hines *et al.* 1995; Pile *et al.* 1996). This movement could obscure any physical site effect on later stage distributions.

Effect of Seagrass Species

Physical processes are obviously important in structuring species distributions. Results from 1995 suggest that habitat selection and differential mortality, by seagrass species or depth, did not occur for postlarvae through 3rd instars. Power in all nonsignificant tests was low, however, so the effects of bed type and depth cannot be dismissed (Table 1). In 1994, although evenly distributed on the south shore, early stages were significantly more abundant in *R. maritima* than in *Z. marina* beds on the north shore. Postlarvae are capable of detecting chemical cues, molting more quickly in the presence of *Z. marina* and estuarine water (Forward *et al.* 1994). Settlement of pre-molt postlarvae is also significantly higher on substrates containing *Z. marina* than on substrates containing potential predators or controls (J. Welch, pers. comm.). Bell and Westoby (1986) hypothesize that over a large-scale, distributions are random because of the risk in moving between disjoint habitats (i.e. between grassbeds), but over the small-scale, organisms may actively select habitats (i.e. within a grassbed). Because postlarvae

are capable of swimming up to 12.6 cm/sec, they could actively select habitats at low to moderate current speeds (Luckenbach and Orth 1992). Also, early stage blue crabs are extremely vulnerable to predation (Olmi and Lipcius 1991; Pile *et al.* 1996). Not surprisingly, in 1995, smaller crabs were not significantly abundant, at an alpha level of 0.05, in dense *R. maritima* beds, which supported a significantly greater number of larger, cannibalistic crabs (Figure 7) (Lipcius and Van Engel 1990; Peery 1989). Similarly, in oyster shell habitats, early cohorts of the Dungeness crab, *Cancer magister*, reduced the density of subsequent cohorts, through cannibalism, competition or avoidance (Fernandez *et al.* 1993). Also, rapid growth may obscure biological influences on the earliest instars. In lab experiments, blue crab postlarvae molted to 4th instars in an average of 12 days, at 28^o C. At 18^o C, postlarvae molted to 4th instars in an average of 40 days (Anderson 1993). During the 1995 study, water temperatures ranged between 20 and 25^oC. Molting would also be quicker in the presence of chemical cues (Forward *et al.* 1994). The influence of biological factors, such as differential predation or habitat selection, were not detectable for postlarvae through 3rd instars, possibly because of the rapid growth and the frequent flux of postlarvae into the York River (Figure 2).

Crabs greater than the 3rd instar were significantly influenced by seagrass species and by bed type, in 1994 and 1995, respectively. In 1994, crabs on the north shore were generally more abundant in *R. maritima* beds, a distribution which held for crabs greater than the 3rd instar in 1995. As discussed previously, blue crabs are capable of selecting habitats. Predation also structures blue crab populations, an

effect which varies with grass density and crab size (Pile *et al.* 1996; J. Schulman, unpublished data). In 1995, *R. maritima* habitats had a significantly higher shoot density than *Z. marina* habitats (Figure 11). Fourth to seventh instar abundances were clearly related to shoot density (Figure 10). Based on predation studies, Pile *et al.* (1996) found that 5th instars gain a refuge from predation with size, and are able to exist outside of seagrass beds. Even crabs greater than the 9th instar, however, are more abundant in vegetated than in unvegetated areas (Orth and Van Montfrans 1987). In my study, even crabs greater than the 9th instar were more abundant in dense *R. maritima* than in *Z. marina*. These crab distributions may have resulted from habitat selection, differential predation or differential nutrition.

The summer of 1995 was unusually hot, with temperatures above 32°C for over 20 consecutive days prior to sampling. *Zostera marina* defoliated considerably during this heat wave. *Zostera marina* reaches peak biomass during the late spring, and defoliation of older shoots occurs when temperatures exceed 25°C. Further defoliation of *Zostera marina* occurs during prolonged heat spells (Orth and Moore 1986). *Ruppia maritima* reaches peak growth during the late summer, when temperatures exceed 25°C. Reproductive *R. maritima*, which has a very complex structure, appears from June to September (Orth and Moore 1988). Changes in seagrass density may lead to changes in habitat use by blue crabs: juvenile blue crabs may be more abundant in *Z. marina* beds prior to yearly summer defoliation. In a recent study, blue crab postlarvae settled in higher abundances on *Spartina alterniflora* than on *Ruppia maritima* or *Juncus roemarianus* in August; in

September, more postlarvae settled on *R. maritima* (Morgan *et al.* 1996). *R. maritima* may be a more important habitat during the late summer after *Z. marina* defoliates. In another study, vegetation die-back caused an increase in prawn abundance but a decrease in fish abundance (Halliday 1995). Further studies should examine temporal changes in early stage blue crab habitat use, which may be correlated with changes in grass density.

Effect of Water Depth

In 1995, the effect of seagrass species may have overshadowed the effect of depth as a refuge. In a similar study, benthic invertebrates, including the polychaetes, *Ceratonereis acquisetis* and *Capitella capitata*, and the gastropod, *Hydrococcus brazieri*, were significantly more abundant in shallow water (<1.0 m) than in deep water (2.0-2.5 m). *Ruppia megacarpa* was also significantly more dense in shallow water and may have influenced species distributions by providing refuge and nutrition (Platell and Potter 1996). In 1995, although 8th to 9th instars were significantly more abundant in shallow water, Tukey's test indicated that this was due to the effect of *R. maritima* beds. Power in all nonsignificant tests was very low, because of the difficulty of finding shallow, monospecific *Z. marina* beds in 1995, and the effect of depth cannot be dismissed.

Although it is not possible to separate the effects of depth and site, data from 1994 suggest that water depth influences blue crab distributions, especially in *Z. marina* beds. The north shore was generally deeper than the south shore. In *Z.*

marina beds, juvenile blue crabs were significantly more abundant on the shallower, south shore. In unvegetated areas, predation is less intense in shallow water (Ruiz *et al.* 1993), which may have provided additional refuge for crabs in *Z. marina* beds. In *R. maritima* beds, blue crabs were sometimes evenly distributed between shores, and sometimes more abundant in the south or in the north. The high complexity of *R. maritima* beds could buffer the effect of predation in deep water, overshadowing any depth refuge effect. Reproductive *R. maritima*, present during the 1994 study, is highly branched, with thinly divided leaves, and is more complex than the linear, broad leafed structure of *Z. marina*. Also, predation intensity may not vary over the shallow depth range (< 50 cm MLW) where *R. maritima* was sampled.

In *R. maritima* beds, postlarvae through 1st instars, and greater than 5th instars were significantly more abundant on the deeper, north shore in September. Aboveground standing crop of *R. maritima* was lower in September, after defoliation of reproductive shoots. Over shallow depth gradients, environmental stresses such as temperature and oxygen fluctuations may be less extreme in deeper water during periods of defoliation and decomposition. In a seagrass bed at the Goodwin Islands, dissolved oxygen fluctuations were qualitatively greater at 40 cm MLW than at 60 cm MLW, during June and August (Moore *et al.* 1995). In a recent study, shallow, dense *R. maritima* habitats contained fewer macroinvertebrates than *Z. marina*, sand and mud habitats, possibly because of low nighttime dissolved oxygen levels, which resulted from decomposition of *R. maritima* detritus. These

beds were located in inlets, where water circulation was limited (Heck *et al.* 1995). In my 1994 study, *R. maritima* beds were located at the mouth of the York River, where water circulation is considerable. Also, dissolved oxygen fluctuations are more extreme during warmer months (Moore *et al.* 1995). In *R. maritima* beds, crabs were more abundant on the deeper, north shore during September, the coolest month that was sampled.

In both 1994 and 1995, distributions of early stage blue crabs were related to site and seagrass species. In 1994, there was evidence that depth influenced crab distributions in *Z. marina* beds: crabs were always significantly more abundant on the shallow, south shore. This effect, however, could not be separated from the site effect. In 1995, depth effects were nonsignificant. I propose the following model: the abundance of early stage blue crabs (megalopae through 3rd instars) in a particular habitat is strongly influenced by larval supply and physical forces such as currents and winds, resulting in significant site effects. Rapid growth at these early stages and the frequent settlement of postlarvae, which is subject to changing physical conditions, i.e., shifting winds, overshadows biological influences such as habitat selection and differential predation. Depending on estuarine circulation at times of settlement, some sites may provide more important settlement and nursery habitats for early stage blue crabs. Seagrass restoration would be more effective at sites where high settlement is known to occur. Crabs greater than the 3rd instar are strongly influenced by seagrass species, through grass density. Changes in seagrass density, which occur each summer, resulting in the domination of different seagrass species

at different times of the year, may influence early stage blue crab distributions.

Efforts to restore and protect seagrass beds should consider both *R. maritima* and *Z. marina* habitats.

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