Habitat Complexity as a Determinant of Juvenile Blue Crab Survival

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HABITAT COMPLEXITY AS A DETERMINANT OF JUVENILE BLUE CRAB SURVIVAL

A Thesis
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

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

by
Jessica L. Schulman
1996
APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

Master of Arts

Jessica L. Schulman

Approved, December 1996

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Habitat structure influences community dynamics, from abundance and diversity of organisms to predator-prey relationships. In Chesapeake Bay, juvenile blue crabs (*Callinectes sapidus*) are abundant in vegetated habitats such as seagrass beds. In this investigation, I experimentally examined juvenile blue crab survival and abundance through tethering three crab stages in patches of artificial eelgrass (*Zostera marina*) situated within a natural eelgrass bed. Survival and abundance were quantified for three juvenile stages of blue crab as a function of artificial eelgrass shoot density (0, 50, 100, 200, 400, 800, 1600, 2000 shoots/m²). The survival response was classified through several empirical models. Whereas the response of both larger stages was positively related to eelgrass density, threshold for larger juvenile crabs in early summer and hyperbolic for 7th to 9th instars in late summer, the small juveniles displayed an inverse survival response. The response of the smallest crabs may reflect an interaction with a different predator suite. These results indicate the existence of survival functions which vary through the ontogeny of juvenile blue crabs.

In conjunction with the survival response experiments, colonization of artificial eelgrass plots by juvenile crabs was also quantified. Both large and medium juvenile crabs utilized artificial eelgrass habitats as predicted by their survival functions, but small juvenile abundance differed significantly across eelgrass densities. In general, medium and large juveniles were most abundant and survived at higher rates in dense eelgrass, whereas smaller juveniles had poorer survival in dense eelgrass, and their abundance was not significantly related to eelgrass density. These differences may result from cannibalism of small crabs by larger juveniles in dense eelgrass or from size-specific differences in food availability and the predator suite as a function of eelgrass density.
HABITAT COMPLEXITY AS A DETERMINANT OF JUVENILE BLUE CRAB SURVIVAL
INTRODUCTION

The role of habitat structure in controlling community composition has been the focus of numerous ecological studies in terrestrial, marine, and freshwater environments (Bell et al., 1991). Specifically, habitat complexity, such as the quality or quantity of vegetation, can strongly influence the abundance (Cooper and Crowder, 1979; Heck and Thoman, 1984; Orth et al., 1984; Marx and Herrnkind, 1985; Bell and Westoby, 1986a; Gotceitas, 1990a; Worthington et al., 1992) and diversity (MacArthur and MacArthur, 1961; Heck and Wetstone, 1977; Stoner, 1980) of animal species in a community. This influence may result from interactions between habitat features and competition, recruitment, and predator-prey interactions (Huffaker, 1958; Coull and Wells, 1983; Orth et al., 1984; Gotceitas and Colgan, 1989). For example, predator success, prey vulnerability, and prey mortality are often negatively related to increasing habitat complexity.

Organisms respond to the availability of resources, such as refuge, living space, and food availability, which are a function of the structural complexity of the habitat. How an organism responds is based on its shape, size, and interactions with prey, predators, and competitors (Leber, 1985; Ryer, 1988; Wilson et al., 1990). Within marsh, reed, and Zostera marina (eelgrass) habitats, differential predation and habitat selection are the most significant of several potential mechanisms driving the positive relationship between abundance or survival and vegetation density (Bell and Westoby, 1986b; Gotceitas and Colgan, 1989; Nelson and Bonsdorff, 1990; Hayse and Wissing, 1996).

The relationship between prey survival and habitat complexity (i.e., the survival response function) is similar to that of a functional response, which depicts the feeding rate of an animal the density of its prey varies (Real, 1977, 1979; Lipcius and Hines, 1986; Main, 1987). As with the
Figure 1. Potential survival response functions to habitat complexity. Shown are positive and inverse forms of a, b) linear, c, d) hyperbolic, and e, f) sigmoid responses.
Figure 1

Habitat Complexity

Survival
functional response, there is much debate over the shape of the survival response curve. The function may be linear -- suggesting a direct impact of habitat structure on survival (Nelson and Bonsdorff, 1990), hyperbolic -- implying a level of maximum benefit (Lipcius et al., unpublished), or sigmoid -- indicating a habitat threshold for survival (Gotceitas and Colgan, 1989) (Figure 1).

A linear survival response indicates that the refuge provided by habitat structure is proportional to the amount of structure present. The response can exist in positive or inverse form (Figure 1a, b), and is the simplest relationship that can exist. In a positive, linear relationship, predation success decreases proportionally with the amount or complexity of structure, probably due to a structural barrier between the predator and prey.

One second order, or curvilinear, response is that of a hyperbolic change with habitat complexity (Figure 1c, d). The increase in survival associated with a given increase in habitat complexity is greater at low levels of complexity and decreases progressively toward the upper asymptote (Figure 1c). The inverse relationship shows an equal and opposite decreasing trend in survival associated with increasing habitat complexity (Figure 1d), which can occur when predators are most abundant in increasingly complex habitats. In such conditions, the highest risk of predation exists in areas of moderate to high habitat structure.

The final response model is a sigmoid function (Figure 1e, f), which is characterized by a threshold level of habitat complexity for survival. In contrast to the hyperbolic function, a positive sigmoid response is characterized by a rising proportional benefit in survival associated with a fixed increase in habitat complexity from low levels of complexity to the inflection point (Figure 1e). Thereafter, the pattern is equivalent to that of the hyperbolic function. The inverse response is equivalent, but corresponds to some sharply increasing detriment associated with increased habitat complexity (Figure 1f), toward a lower asymptote of minimal survival. The primary difference between the sigmoid and hyperbolic functions is that, in a sigmoid response, the rate of change of survival first increases, then decreases within the range of habitat complexity, whereas, within hyperbolic functions, survival changes at a decreasing rate for the entire range of habitat
complexity.

All response models, linear, hyperbolic, or sigmoid, can behave in one of three ways as they approach the upper end of the habitat complexity range (Figure 2). The first potential shape is that of no limit to the response (Figure 2a): survival increases monotonically throughout the entire range of habitat complexity. A second potential relationship reaches an asymptote (Figure 2b): the slope of the survival function approaches zero monotonically within the specified range of habitat complexity (Figure 2b). This function indicates the presence of an absolute maximum or minimum in survival. If the asymptote is neither zero nor 100 percent survival, it is likely that habitat complexity is not the only factor influencing survival. The final response is not monotonic and changes direction, from a positive to negative slope or vice versa, at low or high levels of complexity (Figure 2c). This shape indicates that a number of factors may be interacting to determine survival. These factors may be directly or indirectly related to habitat complexity. A convex, or dome-shaped, survival curve may exemplify a predator-prey interaction in which the predator avoidance behavior of the prey is impeded in highly structured habitats (e.g., the prey becomes entangled in dense seagrass), allowing the predator to increase its capture efficiency. Similar features characterize survival response curves that are negatively correlated with habitat complexity.

While many studies have addressed the relationship between habitat complexity and prey survival, most do so without evaluating the survival response function (Nelson and Bonsdorff, 1990). Given insufficient sampling of the complexity range or qualitative, rather than quantitative, habitat complexity treatments, it is impossible to evaluate the form of the survival response (Figure 3). In addition to the problems associated with having few treatments, treatment allocation can contribute to inadequate representation of the survival function. Due to the potential curvilinear forms, survival responses can best be evaluated using logarithmically spaced treatments as opposed to equally spaced intervals. Small intervals at low levels of habitat complexity allow for detection of any departure from linearity within the survival function.
Figure 2. The upper limit of a survival response function can have one of three shapes: a) continuous increases over the entire range of habitat complexity, b) asymptotic approaches a maximum survival limit, and c) reverse changes direction at high values of the abscissa.
Figure 2

(a) Survival vs. Habitat Complexity

(b) Survival vs. Habitat Complexity

(c) Survival vs. Habitat Complexity
Figure 3. Influence of treatment allocation on analysis of a survival response. Too few data points (e.g., three, shown here) result in inability to describe the response function. Data are fit to a) linear, b) hyperbolic, and c) sigmoid responses.
Figure 3

a) 

b) 

Survival

Habitat Complexity
However, by continually increasing the distance between complexity treatments, it is impossible to
determine the shape of the tail of the survival function.

Quantitative experiments designed to evaluate the relationship between survival and
habitat complexity have generally focused on the response of a particular species to its
environment. Some studies, however, have also considered the possibility of different response
functions in different environments (Murdoch and Oaten, 1975; Hassell, 1978). Changes in
functional response with environmental conditions have been observed in insects (Hildrew and
Townsend, 1977; Kaiser, 1983; Folsom and Collins, 1984) and blue crabs (Lipcius and Hines, 1986;
Eggleston et al., 1994). Furthermore, Connell and Jones (1991) indicated a shift in the shape of a
predator's functional response with age. Thus, if habitat features or predator behavior impact
functional response, prey survival may vary with habitat or prey physiology.

This study addresses the survival response functions for different juvenile stages of the
blue crab (Callinectes sapidus) in its nursery habitat, seagrass beds. The blue crab is a
commercially and ecologically important species throughout the Chesapeake Bay, Western
Atlantic, and Gulf of Mexico, where it utilizes seagrass beds differentially throughout its life
history. Postlarvae settle in vegetated areas dominated by Zostera marina (eelgrass) and Ruppia
maritima (widgeon grass) within the lower Chesapeake Bay (Orth and van Montfrans, 1987;
Lipcius et al., 1990; Olmi et al., 1990). Juvenile crabs, particularly those smaller than sixth
juvenile instar, are significantly more abundant in seagrass beds than adjacent unvegetated or
marsh habitats (Heck and Orth, 1980; Penry, 1982; Heck and Thoman, 1984; Orth and van
Montfrans, 1987).

Blue crabs larger than 11 mm mean cw (carapace width) occur increasingly in unvegetated
habitats (Orth and van Montfrans, 1987). For example, large juveniles inhabit up-river habitats
where their growth is enhanced in low salinity habitats (Hines et al., 1987). While these crabs
reach a relative size refuge where they are not entirely dependent on the structural complexity of
grass beds for safety (Orth et al., 1996; Pile et al., 1996), large juvenile and adult blue crabs remain
abundant in seagrass beds.

The variable nature of utilization of seagrass beds by small juvenile crabs as a refuge from predation and as a foraging ground for large juveniles and adults emphasizes the complex dynamics of blue crab ecology and the potential for intra-specific cannibalism. Blue crabs are generalist predators that readily consume small conspecifics (Darnell, 1959; Tagatz, 1968; Laughlin, 1982; Martin et al., 1989; Peery, 1989; Hines et al., 1990; Mansour, 1992; Moody, 1994). Because the size or age composition of a population within a particular habitat is commonly regulated by predation or competition in that habitat (Kneib, 1987; Connell and Jones, 1991; Pile et al., 1996; Moksnes et al., unpublished), the varied use of vegetation by blue crabs implies an influence of intra-specific dynamics on population structure.

The ontogenetic shifts in vegetated habitat use by C. sapidus, though documented (Orth and van Montfrans, 1987; Pile et al., 1996), are not fully understood, mechanistically. Because predation is likely to be important in regulating juvenile blue crab density, quantitative analysis of the relationship between habitat structure and blue crab survival will allow for determination of the changing importance of habitat features. The dependence of the blue crab population on habitat is a matter of timely importance in that the areal coverage of seagrasses in Chesapeake Bay has varied significantly in recent decades (Orth and Moore, 1983). Thus, the application of research into the relationship between the blue crab and its primary habitat is important for restoration ecology.

Thus, the objective of this study was to quantify the relationship between survival of three stages of juvenile Callinectes sapidus as a function of habitat complexity (Zostera marina density) through manipulative and observational field studies. I tested three juvenile stages of blue crab: 1) small instars that primarily inhabit vegetated areas; 2) mid-sized instars that undergo migration out of grass beds; and 3) large juveniles that reach a relative size refuge from predation outside highly structured habitats. In conjunction with the evaluation of size-specific survival response functions, I quantified size-specific abundance of these juvenile blue crab stages in eelgrass.
METHODS

Study Site

Field experiments and observations were conducted in a large, monospecific eelgrass (*Zostera marina*) bed adjacent to Allens Island in the York River, a tributary of Chesapeake Bay in Virginia, USA (Figure 4). *Zostera* is the dominant seagrass species in the lower Bay and often co-occurs with widgeon grass (*Ruppia maritima*) (Orth and Moore, 1986). The study site was located in approximately 1 m of water (MLW). Shoot densities in this area range up to 2000 shoots/m\(^2\) (pers. obs.), which is within the general range of densities found in the lower Chesapeake Bay (Orth and Moore, 1986). Eelgrass in Chesapeake Bay exhibits bi-modal seasonal growth with peak standing crop in June, a rapid defoliation in summer, and a second, lower peak in standing crop in late fall (Orth and Moore, 1986). The eelgrass bed at Allens Island, and many others throughout the lower Chesapeake, have small zones of bare sand, sometimes attributed to cownose ray activity (Orth, 1975). These bare areas are bounded by varying densities of *Z. marina*.

Experimental Design and Field Methodology

The field experiment was designed to evaluate the survival and patterns in habitat use of three stages of juvenile blue crabs. Habitat complexity experiments were conducted with artificial seagrass made from extruded polypropylene ribbon, to remove the confounding effects of various characteristics such as food availability and chemical cues associated with natural seagrass. Experimental eelgrass plots were 26 cm in diameter and consisted of artificial leaves rooted in a base of Vexar mesh (a woven plastic material) attached to a circular, steel frame and underlain by 1 mm mesh fabric. Polypropylene ribbon was folded in two and tied to the Vexar such that a...
Figure 4. Map of field site; Allens Island eelgrass bed lies to the south of Allens Island, York River, Virginia.
The shoot consisted of two leaves. The total number of shoots differed among the density treatments. The 1-mm mesh fabric covered the underside of the Vexar with artificial eelgrass and both were sewn to the steel frame. A brass swivel was affixed to the center of each plot such that one crab could be tethered to each plot per trial.

Eight density treatments were logarithmically spaced between 0 and 1600 shoots/m², with an additional maximum density of 2000 shoots/m². The eight density treatments were 0, 50, 100, 200, 400, 800, 1600, and 2000 shoots/m². By using the highest natural density of eelgrass found in the lower Chesapeake Bay, the risk of inaccurately describing a response by not considering the entire range of habitat density was eliminated.

Three size classes of juvenile blue crabs were used in the experiments with artificial eelgrass: small (second and third instars: 3.1 - 5.9 mm cw), medium (seventh through ninth instars: 10.7 - 16.1 mm cw), and large (the average 0+ age class crab in the early summer: 11.7 - 34.8 mm cw). Table 1 shows the size classes used for these instars, which is taken from Pile et al. (1996). Small crabs are post-settlement juveniles and are generally present in large numbers in eelgrass beds from late summer through fall. Medium crabs are also abundant in eelgrass beds in generally the same time period, but at lower densities, and are found in increasing abundance in unvegetated areas because they reach a relative size refuge from predation (Orth and van Montfrans, 1987; Pile et al., 1996). The large crabs in this experiment represent those that have over-wintered in the Bay, and whose size range was determined by suction sampling (Orth and van Montfrans, 1987) the study site in June 1995. Crabs equal in size to the large juveniles studied herein may be found in Chesapeake Bay at any time throughout the year, thus the classification of large implies crabs of a given size range present only in the late spring and early summer. Medium and large juvenile crabs are not distinct with regard to their size classes, but rather the season in which their survival was analyzed.

Experiments evaluating survival of the juvenile crabs were conducted at different times of the year. The large crabs, present in the early summer, were studied in June and July, when
1. Size range of juvenile blue crab instars as a function of spine to spine carapace width, adapted from Pile et al. (1996).

<table>
<thead>
<tr>
<th>Instar</th>
<th>Minimum CW (mm)</th>
<th>Maximum CW (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>First</td>
<td>2.2</td>
<td>3.0</td>
</tr>
<tr>
<td>Second</td>
<td>3.1</td>
<td>4.2</td>
</tr>
<tr>
<td>Third</td>
<td>4.3</td>
<td>5.9</td>
</tr>
<tr>
<td>Fourth</td>
<td>6.0</td>
<td>7.4</td>
</tr>
<tr>
<td>Fifth</td>
<td>7.5</td>
<td>9.1</td>
</tr>
<tr>
<td>Sixth</td>
<td>9.2</td>
<td>10.6</td>
</tr>
<tr>
<td>Seventh</td>
<td>10.7</td>
<td>12.6</td>
</tr>
<tr>
<td>Eighth</td>
<td>12.7</td>
<td>14.1</td>
</tr>
<tr>
<td>Ninth</td>
<td>14.2</td>
<td>16.1</td>
</tr>
</tbody>
</table>
Figure 5. Schematic diagram representing the factors addressed in the experimental design of this study.
Figure 5

Temporal Variation

Juvenile Blue Crabs

Eelgrass Complexity

Early Summer: June - July

Late Summer: Aug - Oct

Crab Stages
Large - 0+ Average Size
Medium - 7-9 Instars
Small - 2-3 Instars

Shoot Length
Early Summer - 30-50 cm
Late Summer - 20-40 cm

Density Treatments
0, 50, 100, 200, 400, 800, 1600, 2000 shoots/m²
eelgrass shoot length was at its maximum. At this time, the length of the artificial eelgrass leaves was between 30 and 50 cm. In the late summer, when the small and medium juvenile crabs became available, the grass leaf lengths were shortened to 20 to 40 cm, corresponding to the natural eelgrass at that time. Thus, medium and small crabs were analyzed at the same time, in late summer, whereas large crabs were only tested in early summer. A schematic of this design is given in Figure 5.

Survival of juvenile crabs was examined using a tethering technique which has been used successfully in a number of other experiments utilizing blue crabs (Heck and Thoman, 1981; Wilson et al., 1987, 1990; Pile et al., 1996). The technique involves attaching a piece of monofilament line to the carapace of the blue crab using cyanoacrylate glue. This allows the crab limited mobility within the habitat in which it is tethered. This technique measures relative predation rates, rather than absolute rates, and can be a useful tool in comparing survival across a number of treatments. As addressed in Peterson and Black (1994), tethering can also be problematic when treatment-specific bias is not evaluated. Tethering, as conducted in these experiments, has been considered for its relative impact on juvenile blue crabs in varying grass densities. Pile et al. (1996) evaluated the utility of tethering on several stages of juvenile crabs in densely and sparsely vegetated artificial seagrass in the laboratory with similar artificial seagrass plots. No treatment-specific bias was detected in Pile et al. (1996). Hence, it was assumed that tethering did not produce treatment-specific bias in these experiments, which were conducted with equivalent sizes of blue crabs and artificial eelgrass habitats.

Twenty field plot locations were randomly chosen within the study site. Density treatments were randomly allocated to the 20 experimental plot locations, with each trial incorporating two replicates of all density treatment levels and four additional, randomly chosen treatments. Artificial plots were set in field sites 24 h in advance of tethering trials. The same day, prey crabs were tethered and allowed to acclimate to tethers in laboratory aquaria for one day. Tethered crabs were then attached to the plots for 24 h. After the 48 h trial (i.e., 24 h
acclimation and 24 h tethering), tethered crabs were retrieved and the entire artificial eelgrass plot was collected. Plots were collected using a cylindrical sampling device which was lowered over the artificial grass plots and inserted into the sediment. The open end of the tube was covered with a 1-mm mesh bag. After this device was fit snugly over the entire artificial eelgrass plot, the entire apparatus (the sampling tube, mesh collection bag, and eelgrass plot) was inverted and the experimental plot and its contents were washed into the collection bag. By sampling the mobile macrobenthic fauna within each artificial grass plot, abundance of juvenile blue crabs could be quantified.

**Statistical Analyses**

Survival can be viewed as a Bernoulli trial, a series of binary, mutually exclusive events which form a binomial distribution. Survival results were tested for independence between eelgrass density treatments using a Mantel-Haenszel Chi-square statistic, which tests for directional relationships within ordered, categorical data (Agresti, 1990). If a significant relationship between eelgrass density and survival was detected, three quantitative models (i.e., linear, hyperbolic, and sigmoid) were tested for fit to the data. First, a linear regression was conducted. Next, linearly-transformed functions representing hyperbolic or sigmoid curves were fitted. If the data were best fit by the sigmoid curve, a logistic regression was conducted. In all cases, the residuals were analyzed visually and with a residual fit parameter, defined by Agresti (1990) as the sum of standardized error terms, or z-score:

\[
e_i = \frac{y_i - n_i \pi_{1|i}}{\sqrt{n_i \pi_{1|i} \cdot (1 - \pi_{1|i})}} \]

\[
z\text{-score} = \sum e_i^2
\]

- \(e_i\) - standardized error
- \(y_i\) - observed value
- \(n_i\) - number of trials
- \(\pi_{1|i}\) - probability of outcome
The residuals were determined to be a good fit if the z-score was not significant ($t_{0.05} = 1.96$). The simplest model that (1) significantly fit the data, (2) had randomly distributed residuals (as determined visually), and (3) a non-significant z-score was selected.

Abundance distributions of juvenile crabs as a function of eelgrass density were analyzed using categorical analyses (SAS, 1985). First the data were tested for independence with a Chi-square statistic. If a significant relationship was found between abundance of the juvenile stages and artificial eelgrass density, a cumulative logit model using proportional odds was fitted (Agresti, 1990). This model analyzes the individual response of each stage of juvenile crab to changes in eelgrass density while evaluating the total portion of the variation in the data explained by the relationship between abundance and eelgrass density.

**Size-specific Relationships Between Survival and Abundance**

Two issues regarding the relationship between survival and abundance of juvenile blue crabs were addressed. If predation is the key factor governing abundance, then the mean density per plot of crabs of each size class should be correlated significantly with the proportional survival of that size class. The results of the correlation between abundance and survival from each size class were analyzed using simple linear regression on untransformed data if relationships were linear, or on data linearized through transformation.

The other relationship that was considered stems from the cannibalistic nature of the blue crab. Given that the major predators of small juvenile blue crabs are larger conspecifics (Mansour, 1993), survival of small crabs can be hypothesized to be a function of medium or large crab abundance. This was tested with simple linear regression; the independent variable was abundance of large and medium crabs and the dependent variable was survival of small crabs.
RESULTS

Survival

Survival of small juveniles was highly variable, particularly in low to moderate eelgrass densities (Figure 6a). In spite of the scatter in survival at densities below 800 shoots/m² (relative survival had a minimum value of nearly 20% and a maximum of almost 90%), there was a significant, inverse relationship between eelgrass density and survival. The function which best described the data was an inverse logistic regression (Table 2), but, over the range of eelgrass densities in Chesapeake Bay (0 - 2000 shoots/m²) the function is slightly concave. Thus, the model more resembles an inverse hyperbolic form than that of a threshold function (Figure 6a).

Lowest survival rates for medium crabs were in sparse eelgrass, below 100 shoots/m² (Figure 6b). Survival increased very rapidly with increasing eelgrass density, and above 200 shoots/m² there was no significant difference in survival. At the five highest levels of eelgrass density, relative survival ranged from 70% to 90%. The model which best described medium survival was a positive, hyperbolic function (Table 2) which reached an asymptote of 80% relative survival (Figure 6b).

Of the large juveniles, maximum relative survival was 73% at 2000 shoots/m² (Figure 6c). In comparison, all tethered crabs were eaten in four of the five lowest levels of eelgrass density. The model which best described the data was a positive sigmoid, or threshold, function (Table 2). At low eelgrass densities (i.e., shoot densities below 800 shoots/m²) the model predicts that crabs experience less than 20% relative survival. The survival model increases dramatically above a threshold of approximately 1000 shoots/m², and approaches an asymptote of approximately 80% relative survival at maximum levels of eelgrass density (Figure 6c).
Figure 6. Survival, defined as the proportion of total number of individuals tethered that survived (excluding molted and dead-on-tether), and best fit survival response function are shown for a) small crabs, b) medium juveniles, and c) large juvenile crabs.
2. Models of small, medium, and large juvenile blue crab survival as a function of eelgrass shoot density.

<table>
<thead>
<tr>
<th></th>
<th>Small</th>
<th>Medium</th>
<th>Large</th>
</tr>
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<tbody>
<tr>
<td>Best Fit Model</td>
<td>Logistic Regression:</td>
<td>Positive Hyperbolic</td>
<td>Positive Logistic</td>
</tr>
<tr>
<td></td>
<td>Inverse Hyperbolic within density range</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Function</td>
<td>$\frac{e^{0.2553 + (0.00082 \times \text{Density})}}{1 + e^{0.2553 + (0.00082 \times \text{Density})}}$</td>
<td>$0.845 - (27.3/\text{Density})$</td>
<td>$\frac{e^{-3.4144 + (0.00248 \times \text{Density})}}{1 + e^{-3.4144 + (0.00248 \times \text{Density})}}$</td>
</tr>
<tr>
<td>p-value</td>
<td>0.0182</td>
<td>0.003</td>
<td>0.0001</td>
</tr>
<tr>
<td>z-score</td>
<td>0.461</td>
<td>0.0464</td>
<td>0.4579</td>
</tr>
</tbody>
</table>
Field Abundance

Total abundance of juvenile blue crabs, of all sizes, in the artificial eelgrass plots was positively related to shoot density (Mantel-Haenszel Chi-square = 29.431, df = 1, p < 0.001). Over 10 weeks, 140 field abundance samples were taken. Of the 177 blue crabs collected, 99 juvenile crabs were within the size ranges used in the tethering experiments. The cumulative logit model depicted a significant, positive relationship between abundance of medium and large crabs and eelgrass density (Table 3).

In the first set of experiments, those which evaluated the survival of large crabs, juvenile crabs did not colonize the sampling gear. This likely reflects either the low relative abundance or activity of juvenile crabs in the seagrass bed at Allens Island in early summer. Hence, abundance was only evaluated in the second set of experiments during late summer and fall. At this time, crabs larger than the size class used as medium were substituted for true large crabs, which are present in spring and early summer.

There was no significant response of abundance of small crabs to eelgrass density (Figure 7a). There were, however, few second and third instar crabs collected (mean crab density = 0.12 crabs per plot, compared to 0.18 and 0.22 crabs per plot for medium and large crabs respectively). Nonetheless, the relationship between abundance and eelgrass density appeared to differ between the smallest instars and all other crabs as depicted by the results of the cumulative logit model (Table 3).

Medium crabs increased in abundance with increasing eelgrass density. Medium crabs were infrequently sampled in eelgrass densities between 100 and 400 shoots/m² (Figure 7b). Above 800 shoots/m², as with large crabs, the number of crabs increased dramatically.

Large crabs had a similar response to that of medium crabs, increasing in abundance with eelgrass density. No large crabs were found in experimental densities less than 200 shoots/m² (Figure 7c). In experimental densities of 200 and 400 shoots/m² a total of 1 and 2 large crabs
3. Cumulative logit model of abundance of three stages of juvenile blue crabs vs. eelgrass shoot density.

<table>
<thead>
<tr>
<th>Variable</th>
<th>df</th>
<th>Parameter Estimate</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept for the odds of large vs. medium and small</td>
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<td>-2.3103</td>
<td>0.0001</td>
</tr>
<tr>
<td>Intercept for the odds of large and medium vs. small</td>
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<td>-0.8266</td>
<td>0.008</td>
</tr>
<tr>
<td>Eelgrass density</td>
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<td>0.00146</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

Criteria for Assessing Model Fit

<table>
<thead>
<tr>
<th>Variable</th>
<th>df</th>
<th>Chi-Square</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
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<td>Proportional Odds Assumption</td>
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<td>1.0190</td>
<td>0.3128</td>
</tr>
<tr>
<td>Covariates (-2 log likelihood)</td>
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<td>32.877</td>
<td>0.0001</td>
</tr>
</tbody>
</table>
Figure 7. Abundance distributions of a) small, b) medium, and c) large crabs sampled throughout the late summer portion of the experiment.
Figure 7

(a) Density of Crabs (Individuals/plot)

(b) Density of Crabs (Individuals/plot)

(c) Density of Crabs (Individuals/plot)

Grass Density (shoots/m²)
were collected, respectively, throughout the experiment. In comparison, the three highest eelgrass density levels had between 10 and 16 total crabs per density treatment, equivalent to 0.46 to 0.70 crabs per plot.

Size-specific Relationships Between Survival and Abundance

Survival in the experiments adequately predicted the sampled abundance of medium and large crabs, but not that of small crabs (Table 4). A linear regression of the relationship between the density and survival of small crabs at different grass densities indicated no deviation from random ($p = 0.94, R^2 = 0.1$). The mean density of medium crabs per plot was zero at low eelgrass densities and reached a maximum value of 0.545 crabs per plot (i.e., 9.82 crabs per m$^2$). After the data were transformed to linear, a significant regression ($p = 0.011, R^2 = 0.686$) was found. The mean density of large crabs was significantly predicted by their survival ($p = 0.002, R^2 = 0.809$).
4. Survival - abundance correlations for small, medium, and large juvenile blue crabs.

<table>
<thead>
<tr>
<th>Regression</th>
<th>Small</th>
<th>Medium</th>
<th>Large</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Not Significant</td>
<td>Linearized Data survival - hyperbolic transform abundance - sigmoid transform</td>
<td>True Data</td>
</tr>
<tr>
<td>p-value</td>
<td>0.94</td>
<td>0.011</td>
<td>0.002</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.1</td>
<td>0.686</td>
<td>0.809</td>
</tr>
</tbody>
</table>
DISCUSSION

Three distinct survival responses were found for the three stages of juvenile blue crab evaluated. Of these crab stages, two showed significant differences in abundance with eelgrass density that supported the patterns of habitat use predicted by their survival responses. The findings indicate that survival responses can be curvilinear and vary ontogenetically.

Juvenile Blue Crabs and Eelgrass

Survival of small juvenile crabs was inversely related to eelgrass density, with the highest survival at low to moderate densities. Moreover, survival at low grass densities was highly variable, which indicated that other factors likely influence the relationship between survival and eelgrass density. The possibility of an inverse survival response is unique, and has not been addressed in prior studies. The probable explanation for this novel relationship is that larger predators associated with dense eelgrass (e.g., large juvenile crabs) may pose more of a threat to the small crabs than the mobile piscine predators that feed on larger conspecifics. Predation success varies with predator and prey size (Stoner, 1982; Ryer, 1987, 1988). Small predatory pinfish (*Lagodon rhomboides*) foraged more effectively within dense seagrass than larger conspecifics (Stoner, 1982). Similarly, vulnerability of amphipod prey within vegetation varied with prey size and vegetation abundance for large pipefish predators (*Syngnathus fuscus*) but not small ones (Ryer, 1987, 1988).

The lack of a significant relationship between small juvenile abundance and eelgrass density implied that survival is not the sole determinant of abundance for these crabs, probably because there are other influential processes affecting the distribution of small blue crabs. For
instance, food distribution or even currents, as very small juveniles are dependent on currents for much of their mobility, shape habitat use by small blue crabs. In addition to the high degree of variability found in survival and abundance of small juvenile crabs at low seagrass densities, few small crabs were collected using the abundance sampling techniques. Thus, conclusions regarding the relationship between abundance of small juvenile crabs and eelgrass density are preliminary.

The hyperbolic survival response of medium crabs with increased eelgrass density indicated that these crabs survived well in moderate to high eelgrass densities with low survival only observed at sparse densities less than 200 shoots/m². Thus, medium-size juveniles survived better than large juveniles at low to moderate eelgrass densities. Similar to the large juveniles, however, medium-size juveniles survived poorly in sparse eelgrass. A similar hyperbolic survival function characterizes survival of medium size juveniles of the spiny lobster (*Panulirus argus*) as a function of algal biomass (Lipcius *et al.*, unpublished). The importance of these findings is two-fold: 1) very small increases in habitat complexity at low eelgrass densities can enhance survival significantly, and 2) habitat complexity may not increase survival without bounds, such that the upper asymptote may be well below 100% survival. For instance, some predators may be either more abundant or capable of foraging in complex habitats.

Habitat use and survival of medium-size crabs were inconsistent at moderate eelgrass densities. The abundance results showed that medium crabs utilized all eelgrass densities above 100 shoots/m², which corresponded to the lowest eelgrass density at which survival was substantially increased. While survival results predicted that medium crabs could safely utilize moderate levels of eelgrass density, they were not found in large numbers below 800 shoots/m². Gotceitas and Colgan (1989) found a similar pattern of prey choice of habitat at complexity levels above that needed to provide sufficient refuge. The discrepancy between abundance and survival patterns of medium crabs may be due to prey availability, which may be low in moderately dense eelgrass.

Large juvenile crabs had a threshold (i.e., sigmoid) survival response as a function of
eelgrass density, with an inflection point at approximately 1000 shoots/m². The survival model was near zero at 0 - 400 shoots/m², and was still increasing at 2000 shoots/m² towards an upper asymptote. Such a threshold function of survival as determined by habitat complexity is common in aquatic organisms (Heck and Thoman, 1981; Coull and Wells, 1983; Orth et al., 1984; Gotceitas and Colgan, 1989). Nelson and Bonsdorff (1990) argued against the existence of a threshold survival function, claiming that sigmoid results stemmed from experiments with too few treatments or too little replication per treatment. Here, however, Nelson and Bonsdorff's concerns about experimental design have been addressed, and the survival response is clearly sigmoid in form for large juveniles.

A threshold pattern of refuge benefit implies that large juvenile crabs should differentially utilize eelgrass habitats, with increasing affinity for dense eelgrass. The abundance data for the pre-winter large juvenile crabs in artificial eelgrass plots supported this prediction. Few crabs were found in habitats with low eelgrass density, and significantly more occurred in high density habitats at or above their survival threshold of approximately 1000 shoots/m². The linear correlation between survival and habitat use implies that large juveniles primarily inhabit dense patches of eelgrass due to high predation rates in sparse patches. Natural blue crab densities for the 0+ age class are on the order of 10 crabs/m² (Orth and van Montfrans, 1987; Pile et al., 1996), which correlates with the maximum densities found in this experiment.

These results allow formulation of a conceptual model detailing size-specific habitat utilization by juvenile blue crabs. The medium and large juvenile crabs survived better in dense than in sparse eelgrass. The abundance patterns of these two stages of crabs were similar, with both found in low to moderate densities of eelgrass (between 200 and 400 shoots/m²), but with highest abundance in dense eelgrass. Juvenile blue crabs larger than the fifth instar shift from primarily vegetated habitats to a broad range of habitats (Hines et al., 1987; Orth and van Montfrans, 1987). While the density of juvenile crabs in grass habitats decreases with increasing crab size (Pile et al., 1996), there are significantly more crabs of all sizes found in vegetated than
unvegetated habitats (Penry, 1982; Orth and van Montfrans, 1987; Montane et al., 1995).

The similarity in abundance of medium and large juvenile crabs may have been associated with their similarity in size and the fact that both were collected during the same time period. The larger two stages in the survival experiment were not distinguished by their carapace width, but on the time of year they are found in the lower Chesapeake Bay. The difference in their survival patterns may have been due to a shift in the predator suite or predation intensity in response to the abundance of alternative prey items associated with temporal variation.

In contrast to their similarity in abundance distributions, the survival responses of medium and large juvenile crabs varied in shape. While the large juveniles had a threshold survival response, the medium juveniles had a hyperbolic response. The threshold response of the large juveniles could result from the presence of large predators which forage effectively in sparse eelgrass, but not dense eelgrass. In addition, a large predator may not feed in a habitat that is associated with a low prey capture rate, such as dense eelgrass. The difference between the large survival response and the hyperbolic shape of medium survival may be due to some undefined variable. One possibility is the presence of some size-specific influence at moderate levels of eelgrass density. Another potential explanation is seasonal variations in the predator suite between early summer, and late summer/fall. Since experiments with large crabs were conducted in early summer, and those with medium crabs in late summer and fall, one cannot distinguish between crab size and other factors changing over time.

The dynamics of habitat use and the factors determining the survival of small juvenile crabs were unique from those related to large and medium crabs. The structural refuge provided by dense eelgrass for larger juvenile blue crabs may have been a detriment to the smallest instars. One explanation for this is that small crabs have a large suite of potential predators. In areas of low structure within eelgrass beds, small juvenile crabs share the predator suite of larger juveniles. Any organism capable of foraging in an area of low structural refuge is a potential predator, including highly mobile animals over a wide range of sizes, such as juvenile and adult fish and
crabs. Gotceitas and Colgan (1987) demonstrated such behavior, foraging in an unvegetated area near refuge habitats and seeking refuge only in the presence of a predator, in small fish.

Unlike the survival responses for medium and large juvenile crabs, although there is a risk of predation in sparse vegetation, the survival function reaches its minimum in dense eelgrass. This result may stem from an additional suite of predators that are capable of feeding in densely structured habitats. One of the primary predators for small blue crabs is larger conspecifics (Darnell, 1959; Tagatz, 1968; Laughlin, 1982; Martin et al., 1989; Peery, 1989; Hines et al., 1990; Mansour, 1992; Moody, 1994). Given that large conspecifics are abundant in dense eelgrass, cannibalism on smaller conspecifics may be high in this habitat. The survival response of the small crabs may not be indicative of a refuge in unvegetated areas, but of an unsafe, predator-rich habitat in dense vegetation. Thus, small crabs may experience a relative refuge in sparse vegetation with respect to the high risk of predation associated with dense eelgrass.

Survival and Habitat Structure

While habitat structure can be estimated by eelgrass density, grass density is related to a variety of factors which influence survival, including successful predator avoidance and predator foraging behavior. In this study, three stages of juvenile blue crab were introduced to the same levels of habitat structure and exhibited three different survival responses. Crabs of different sizes can take advantage of structure in different ways. Small crabs are not larger than the width of a blade of Z. marina, thus, they can be hidden behind a single shoot of eelgrass. Larger crabs probably rely on the tangle of eelgrass leaves to obscure their presence or inhibit predators who may not have the capability to forage within complex structure.

Another factor affecting survival differently despite the same levels of habitat complexity is the predator suite. The primary predators of large juvenile blue crabs are large fish, rays, and adult blue crabs (Darnell, 1959; Tagatz, 1968; Moody, 1994). Apparently, these organisms are not effective foragers in highly structured habitats. While medium size juveniles share the same
predator suite, they may have the additional advantage of their small size being less detectable in moderate levels of eelgrass density. Small instars are preyed on by larger juvenile conspecifics (Darnell, 1959; Tagatz, 1968; Laughlin, 1982; Martin et al., 1989; Peery, 1989; Hines et al., 1990; Mansour, 1992; Moody, 1994), which results in an inverse relationship between survival and eelgrass density.

Habitat structure is an important factor determining survival. The results from this study indicate that survival responses to habitat complexity can be curvilinear, as those associated with juvenile *Callinectes sapidus* in *Zostera marina* habitats. A response can vary in shape (i.e., hyperbolic and sigmoid) as well as direction (i.e., positive and inverse responses) for one species in response to the same habitat feature. The findings support the existence of variable response functions in relation to the size of an organism, which reflect the change in importance of a variety of factors regulating population structure throughout the ontogeny of the organism. Such information is necessary to define those characteristics most important to the survival and abundance of species utilizing seagrass beds, and therefore, necessary for the successful protection, enhancement, and restoration of seagrass habitats.
LITERATURE CITED


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VITA

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Ms. Schulman was born in Livingston, New Jersey, 11 January 1974, and graduated from Columbia High School in Maplewood, New Jersey in 1990. In 1994, she earned a Bachelor of Science with a major in Earth Systems from Stanford University in California. Entering the Master of Arts program at the College of William and Mary, School of Marine Science, Virginia, Ms. Schulman completed her research in spring of 1996. She is currently working as an Ecological Consultant with ICF Kaiser International, Inc.