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The effect of seagrass habitat fragmentation on juvenile blue crab survival

Kevin Hovel
College of William and Mary - Virginia Institute of Marine Science

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THE EFFECT OF SEAGRASS HABITAT FRAGMENTATION ON JUVENILE BLUE CRAB SURVIVAL

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

In Partial Fulfillment
Of the Requirements of the Degree of
Doctor of Philosophy

by
Kevin A. Hovel
1999
APPROVAL SHEET

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

Doctor of Philosophy

Kevin A. Hovel

Approved September 1999

Romuald N. Lipcius, Ph.D.
Committee Chairman/Advisor

Emmett Duffy, Ph.D.

Robert J. Ortl, Ph.D.

Mark R. Patterson, Ph.D.

David B. Eggleston, Ph.D.
North Carolina State University
Raleigh, North Carolina

Elizabeth A. Irlandi, Ph.D.
Florida Institute of Technology
Melbourne, Florida

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Chapters 1, 2 and 3 of this dissertation are written as separate manuscripts for publication in peer-reviewed journals (at the time of this writing, chapters 1 and 2 have been submitted for publication). Due to the common underlying theme of this study, readers of this dissertation will note some unavoidable redundancy in these chapters.

The reader will also note the similarity of the first chapter (“Effects of seagrass habitat fragmentation on juvenile blue crab survival and abundance”) and the second chapter (“Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival”). Chapter 1 measures the effect of seagrass fragmentation on juvenile blue crabs under natural conditions, and compares the influences of several environmental variables on juvenile blue crab survival. Chapter 2 measures the effect of seagrass fragmentation on juvenile blue crab survival in the absence of a covarying environmental variable (seagrass shoot density) found to be an important influence on survival in Chapter 1. Chapter 3 incorporates the results presented in the first and second chapters into a model for juvenile blue crab survival in fragmented seagrass landscapes. Finally, Chapter 4 summarizes the major results of the study, and discusses the relationship between the various components of the study. I refer the reader to this concluding chapter, and to the discussion sections of each chapter for information on the relationships between the chapters of this dissertation.
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Habitat fragmentation is increasingly common on land and in the sea, leading to small, isolated habitat patches in which ecological processes may differ substantially from those in larger, continuous habitats. Seagrass is a structurally complex but fragmented subtidal habitat that provides food and serves as a refuge from predation for juveniles of the blue crab, *Callinectes sapidus* Rathbun. The influence of seagrass habitat fragmentation (e.g. patch size) on crab survival is unknown, and is difficult to quantify because seagrass complexity (e.g. shoot density) and patch size are often confounded and vary temporally. In this study, I compared the effects of eelgrass (*Zostera marina* L.) patch size and shoot density on juvenile blue crab survival and abundance both before (June) and after (September) shoot defoliation and cownose ray disturbance changed eelgrass habitat, and used artificial seagrass to determine the influence of eelgrass patch size on juvenile blue crab survival in the absence of covarying shoot density. I then used the results of these experiments to model the effect of eelgrass fragmentation and loss on juvenile blue crab survival.

Crab survival was inversely correlated with eelgrass patch size in the absence of covarying shoot density, in contrast to patterns typically observed in fragmented terrestrial landscapes; this was likely due to low predator abundance in small patches. Under natural conditions, eelgrass patch size and shoot density both influenced juvenile blue crab survival, but crab survival patterns varied temporally. In June, the effect of fragmentation was non-linear: crab survival, crab density and seagrass shoot density all were lowest in large (3000 m²), spatially-isolated patches and in unvegetated sediment, and were higher in smaller patches (0.25 and 8 m²) and in the largest patch (i.e. continuous seagrass: 30000 m²). In September, crab survival was low and did not differ among patch sizes. Crab density increased with seagrass shoot density at both times and was greater in September than in June. Crab survival declined from June to September, probably due to density-dependent cannibalism, decreased eelgrass shoot density due to defoliation, or increased habitat fragmentation caused by cownose ray bioturbation. Density-dependent cannibalism likely caused crab survival to decrease with shoot density in September.

The inverse relationship between crab survival and eelgrass patch size suggests that juvenile blue crab survival may be maximized at an intermediate level of seagrass fragmentation, where the negative effects of large patch size and low proportional seagrass cover both are reduced. I tested this hypothesis by modeling the joint effects of patch size and proportional cover on juvenile blue crab survival. When I assumed predation on crabs to be independent of crab density, maximal crab survival (ca. 34 %) occurred at intermediate values of seagrass percent cover. However, under the more realistic scenario of density-dependent survival, about 18 % of crabs survived irrespective of the proportion of the landscape covered by seagrass.

My findings indicate that (i) effects of habitat fragmentation on survival may differ between seagrass and terrestrial landscapes, (ii) seagrass habitat fragmentation has a significant but not overriding influence on faunal survival, and (iii) seagrass patch size, seagrass complexity, and blue crab density all influence juvenile blue crab survival, but their effects vary temporally. Habitat fragmentation studies should incorporate multiple scales of space and time, as well as potentially confounding environmental variables.
THE EFFECT OF SEAGRASS HABITAT FRAGMENTATION ON JUVENILE BLUE CRAB SURVIVAL
Chapter 1

The effect of seagrass habitat fragmentation on juvenile blue crab survival and abundance
ABSTRACT

Seagrasses form temporally dynamic, fragmented subtidal landscapes in which both large- and small-scale habitat structure may influence faunal survival and abundance. I compared the relative influences of eelgrass (*Zostera marina* L.) habitat fragmentation (patch size and dispersion), complexity (shoot density) and month (June vs. September) on survival and density of 0 + year class juvenile blue crab (*Callinectes sapidus* Rathbun) in a Chesapeake Bay seagrass meadow. I also determined if juvenile blue crab density and seagrass shoot density varied between the edge and the interior of patches. The effect of eelgrass patch size (0, 0.25, 8, 3000, and 30000 m²) on juvenile blue crab survival and density was non-linear and varied temporally. In June, crab survival, crab density and seagrass shoot density all were lowest in large (3000 m²) spatially-isolated patches, and were higher in smaller patches (0.25 and 8 m²) and in the largest patch (i.e. continuous seagrass, 30000 m²). Survival in the large isolated patches was comparable to the low survival in unvegetated sediment (0 m²). In September, crab survival was low throughout the landscape and did not differ among patch sizes. Crab survival was not correlated with shoot density in early summer, but was inversely correlated with shoot density in late summer. This inverse correlation was likely due to density-dependent predation by larger juvenile conspecifics; juvenile blue crab density increased with seagrass shoot density and was greater in late than in early summer. Though shoot density did not differ between the edge and the interior of patches, crabs were more abundant in the interior of patches than at the edge. These results indicate that seagrass fragmentation does not have an overriding influence on juvenile blue crab survival and density; instead, complex dynamics involving habitat fragmentation, habitat
complexity, time, proximity to patch edge, and cannibalism influence juvenile blue crab survival and density in fragmented seagrass landscapes. Though some levels of seagrass fragmentation may provide poor refuge for juvenile blue crabs (i.e. large, isolated patches), simple relationships between seagrass habitat fragmentation and juvenile blue crab survival are unlikely.

INTRODUCTION

Habitat structure strongly influences processes that govern the abundance and distribution of organisms in space and time (Gause 1934, Huffaker 1958, Real and Levin 1991). Landscape ecology is a recently-emerged discipline that focuses on biotic responses to large-scale patterns of habitat structure in spatially-heterogeneous habitat mosaics (Forman and Godron 1986, Robbins and Bell 1994, McGarigal and McComb 1995). Recent attention given to landscape-scale (e.g. 10s – 100s of kilometers in terrestrial ecosystems) processes may largely be due to widespread anthropogenic habitat fragmentation, which reduces continuous, extensive habitat to small, spatially isolated remnant patches surrounded by an unstructured matrix (Meffe and Carroll 1997). Habitat fragmentation may have a profound influence on organismal behavior and movement (van Appeldoorn et al. 1992), gene flow among populations (Andrén 1994, Hanski and Gilpin 1997), and biotic interactions that structure communities (Kareiva 1987, Paton 1994). For instance, the unstructured matrix surrounding remnant patches facilitates movement of large, mobile predators among patches but limits the movement of prey organisms that rely on structured habitat for refuge (Forman and Godron 1986, Small and

Though many marine habitats such as seagrasses (Robbins and Bell 1994), kelp forests (Dayton and Tegner 1984), intertidal mussel beds (Paine and Levin 1981) and oyster reefs (Eggleston et al. 1998) form fragmented subtidal or intertidal landscapes, few large-scale studies of habitat structure have been conducted in these systems (Bell and Hicks 1991, Irlandi 1994, 1997, Robbins and Bell 1994, Irlandi et al. 1995). Instead, marine ecologists have generally focussed on the influence of small-scale habitat structure (i.e. habitat complexity) on organismal survival and abundance. Complexity (commonly measured as the density, surface area, or biomass of habitat structural components such as macrophyte shoots or bivalve shells) interferes with the detection and capture of prey by predators (Heck and Crowder 1990). Prey survival therefore is generally high in complex habitats such as seagrass (Heck and Orth 1980, Heck and Thoman 1981, Orth and van Montfrans 1982, Bell and Westoby 1986, Heck and Wilson 1987, Wilson et al. 1987, see reviews by Heck and Crowder 1990, Orth et al. 1984, Orth 1992), kelp forests (Carr 1989, 1991, 1994, Bologna and Steneck 1993), algal beds (Herrnkind and Butler 1986, Haywood et al. 1995, Lipcius et al. 1998), shell and rock
substrata (Sponaugle and Lawton 1990, Connell and Jones 1991, Tupper and Boutilier 1997) and even on irregular surfaces of sessile organisms (e.g., the solitary ascidian *Styela plicata* provides habitat for the bryozoan *Bugula neritina*; Walters 1992). Prey abundance also is high in complex marine habitats where survival, living space or food are enhanced (Heck and Orth 1980, Orth 1992, Perkins-Visser et al. 1996) or where buffering of currents increases the passive deposition of larvae or postlarvae (Eckman 1983, Orth 1992). Additionally, some complex habitats are actively selected, producing high densities therein (Bell and Westoby 1986, Orth 1992, Worthington et al. 1992, Eggleston and Armstrong 1995).

Seagrasses harbor dense and diverse faunal assemblages in coastal shallows worldwide (Petersen 1918, Orth 1992). Seagrass meadows may be extensive and continuous, or they may be fragmented by forces such as waves and currents, animal foraging and dredging into mosaics of discrete patches surrounded by a matrix of unvegetated sediment (Fonseca et al. 1982, Robbins and Bell 1994, Fonseca and Bell 1998, Townsend and Fonseca 1998, personal observation). Seagrass structural characteristics such as shoot density, shoot biomass, and canopy surface area (Heck and Crowder 1990, Irlandi 1995) and seagrass root and rhizome biomass (Blundon and Kennedy 1982, Peterson et al. 1984, Irlandi, 1994, 1997) inhibit predator search and capture of prey. In Chesapeake Bay, eelgrass, *Zostera marina* L., meadows are fragmented into discrete patches ranging from < 1 m$^2$ to > 30,000 m$^2$ at shoot densities of 300 - 3000 shoots m$^2$ (Orth and Moore 1986). Both eelgrass fragmentation and complexity vary temporally. Eelgrass shoot density, shoot length, and above- and below-ground biomass peak in early summer (May - June), but are two- to three-fold lower in
late summer (August - September) following a rapid temperature-induced defoliation (Orth and Moore 1986). Eelgrass edge habitat increases in mid summer because cownose rays invade Chesapeake Bay and excavate seagrass in search of infaunal bivalves (Orth 1975, personal observation). Thus, eelgrass meadows in Chesapeake Bay are fragmented, dynamic landscapes that exhibit heterogeneity at multiple spatial and temporal scales.

The blue crab (*Callinectes sapidus* Rathbun) is a ubiquitous, commercially-important decapod crustacean of the Eastern and Gulf coasts of North America (Williams 1984). In Chesapeake Bay, adult females release larvae at the bay mouth from June to September (Van Engel 1958, McConaugha et al. 1988), and postlarvae (megalopae) re-invade Chesapeake Bay in late summer and fall after developing through 7 - 8 planktonic zoeal stages (van Montfrans et al. 1990). Seagrass is the primary settlement habitat for blue crab megalopae in Chesapeake Bay, and crabs remain in seagrass after metamorphosing to the juvenile form (van Montfrans et al. 1995, Pile et al. 1996). Predation by finfish and larger conspecifics, the chief predators of juvenile blue crabs (Hines et al. 1990, Mansour 1992, Moody 1994, Moksnes et al. 1997) is dramatically lower in seagrass than in unvegetated sediment (Heck and Orth 1980, Heck and Thoman 1981, Orth and van Montfrans 1987, Pile et al. 1996), making seagrass a critical refuge habitat for *C. sapidus* juveniles.

The singular effects of seagrass complexity and fragmentation (patch size, shape, and dispersion) on survival of prey such as juvenile blue crabs have been difficult to distinguish because of their covariation; for instance, small, isolated patches often are less complex than are larger patches (e.g. Irlandi 1994, 1997). Thus, in this study I compared
the relative effects of eelgrass habitat fragmentation (= patch size) and habitat complexity
(= shoot density) on juvenile blue crab survival and abundance both before (June) and
after (September) seasonal changes in eelgrass habitat structure. I made these
comparisons by measuring seagrass complexity and C. sapidus (0 + year class) survival
and density in seagrass patches spanning five orders of magnitude in size, and then
determining if differences in crab survival and density among patches were correlated
with Z. marina complexity. I also measured juvenile blue crab density in the edge and
the interior of patches, and determined if edge vs. interior differences in density were
correlated with seagrass complexity.

MATERIALS AND METHODS

Study site

This research was performed in seagrass beds adjacent to the Goodwin Islands
(76° 24' W x 37° 13' N), a group of small islands forming a Chesapeake Bay National
Estuarine Research Reserve in the lower York River, Virginia, USA (Figure 1). The
islands are separated from the shoreline by a narrow channel (approx. 0.5 km wide).
Depths at low tide within beds are ca. 0.5 m. Mean water temperature and salinity in the
lower York river vary annually from 4 - 28 °C and 16 - 22 psu, respectively. Seagrass at
the Goodwin Islands is primarily Z. marina, though some widgeongrass, Ruppia
maritima L., is present in the shallows.
Seagrass mapping

In May of 1998 I mapped the Goodwin Islands seagrass beds using aerial photography and a geographic information system (GIS). Eight color 20 cm x 20 cm overhead photographs (two overlapping transects of four photos each) were taken from a small plane flying at an altitude of 400 m. Each photo covered an area of 240,000 m², and the two transects encompassed the entire seagrass meadow. Before photographs were taken, I affixed one 1 m x 1 m white Styrofoam board to each of 25 permanent PVC stakes dispersed uniformly throughout the meadow, and obtained the position of each board (accuracy ± 1 m) with a Trimble Geoexplorer handheld differential GPS (Trimble Navigation Limited, The Woodlands, TX). These boards were visible in the photographs and served as georeferenced points for rectification.

I scanned each photograph at a resolution of 300 dpi with a Hewlett Packard 6100 C color scanner. Digital images then were rectified and combined into a single mosaic showing the entire seagrass meadow using ARC/INFO® (Environmental Systems Research Institute, Redlands, CA). Digital images consisted of grid cells (pixels), each of which was classified as “seagrass” or “unvegetated sediment.” The 300 dpi resolution allowed me to measure seagrass patches as small as 0.05 m². I used the digital mosaic to delineate separate areas of seafloor (“fragmentation types”) containing seagrass patches of different sizes for use in blue crab survival and abundance experiments (Figure 2, Table 1). The “small patch” fragmentation type was characterized by very small patches (ca. 0.25 m² in size) that were usually isolated from other patches by approximately 20 m of unvegetated sediment. The “medium patch” fragmentation type was composed of intermediately-sized patches, ca. 8 m² in size, that generally were separated by < 5 m of
unvegetated sediment. The "large patch" fragmentation type was characterized by large, elongated patches approximately 3000 m² in size that were isolated by ca. 20 m of unvegetated sediment. The "continuous" fragmentation type was one extremely large patch (ca. 30,000 m² in size) interspersed with occasional small patches of unvegetated sediment. Finally, the "unvegetated" fragmentation type consisted of areas devoid of seagrass.

Habitat complexity measurements

To test for differences in Z. marina complexity among fragmentation types and between early and late summer, I haphazardly took four seagrass cores (15 cm diameter x 20 cm deep) in each of four randomly located sites within the continuous, large, medium and small patch fragmentation types in early summer (9-11 June 1998; n = 4 cores/site • 4 sites/fragmentation type • 4 fragmentation types = 64 cores), and one core in each of four randomly located sites in each fragmentation type in late summer (8-9 August 1998; n = 1 core/site • 4 sites/fragmentation type • 4 fragmentation types = 16 cores). I counted the number of Z. marina shoots in each core and measured the length of the longest blade per shoot to determine mean shoot density and blade length. Above- and below-ground biomass were measured by separating shoots from roots and rhizomes and weighing each after drying at 60 °C for 48 h. Although shoot density, shoot length, and above- and below-ground biomass measure different aspects of seagrass complexity, they were collinear (all Pearson-product-moment correlation coefficients > 0.75 with P values ≤ 0.05; see Hovel and Lipcius 1999a). I therefore used seagrass shoot density as a single, representative measure of complexity. I used a two-way, fixed-factor analysis of
variance (ANOVA) to test if mean shoot density differed among patch sizes and between early and late summer. I tested for homogeneity of variance with Cochran's C test, and based post-hoc multiple comparisons on Student-Newman-Keuls tests in this and all subsequent analyses (Underwood, 1997).

Seagrass coring also was used to test for differences in shoot density between the edge and interior of large patches in late summer 1997. From 31 July to 10 August 1997 I haphazardly took four seagrass cores in the edge and four cores in the interior of 12 randomly chosen large patches. Only large patches were used for edge vs. interior comparisons because edge and interior samples from medium and small patches likely would be non-independent. I defined the edge of patches as < 1 m from the nearest seagrass–unvegetated sediment border, and the interior of patches as > 4 m from the nearest border. I tested for differences in mean shoot density between the edge and interior of patches with a paired t-test.

Blue crab survival

Blue crab survival in the four patch sizes and in unvegetated sediment was tested by tethering, which is widely used to measure relative survival among treatments (e.g., Heck and Thoman 1981, Heck and Wilson 1987, Wilson et al. 1987, Eggleston et al. 1990, Pile et al. 1996, Shulman 1996, Ryer et al. 1997, Lipcius et al. 1998). Juvenile blue crabs (0 + year class, 1.0 – 3.0 cm spine-to-spine carapace width (CW)) were collected by trawling seagrass beds in the lower York River and held in running seawater in an outdoor flume. No crab was held more than 48 h. Crabs were tethered by affixing them to 5 cm segments of monofilament line with cyanoacrylate glue (Pile et al. 1996).
Crabs were acclimated to tethers for 24 h in running seawater before placement in the field. In the field, tethered crabs were tied to small (10 cm) metal stakes that were completely inserted into the sediment. Small stakes were tied to larger (30 cm) metal stakes with 1 m of monofilament line. Large stakes also were inserted into the sediment but were marked with a small buoy to permit relocating the tethered crabs. Placing the tethered crab 1 m away from the marker buoy decreased the likelihood of the tethering apparatus attracting predators to the crab.

I conducted 24 h tethering trials beginning on 6 June 1998 (early summer) by tethering 5 randomly selected crabs in each of the 4 randomly-located sites in each fragmentation type. A distance of at least 3 m separated crabs tethered within the same site. Upon retrieval crabs were categorized as (1) live, (2) eaten (fragments of the carapace remaining on the tether), (3) molted (entire carapace remaining on the tether), or (4) missing (no parts of the carapace remaining on the tether). Crabs that molted or died on tethers were excluded from the analysis, and if three or more crabs molted or died within 24 h in the same site then data from the entire site was discarded. The 24 h trials were repeated until two successful tethering trials were conducted in each site (n = 2 trials/site • 4 sites/fragmentation type = 8 trials/fragmentation type total; N = 200 crabs). The experiment was terminated on 13 June 1998. The experiment was repeated from 6 – 16 September 1998 (late summer) except that three tethering trials were conducted at each haphazardly located site (n = 3 trials/site • 4 sites/fragmentation type = 12 trials/fragmentation type total; N = 300 crabs). Sites were moved to new randomly-chosen locations in each fragmentation type before the late summer experiment was conducted.
Missing crabs may have escaped from tethers, or may have been pulled off by predators. Adult blue crabs often carry off prey before consuming them (*personal observation*) and predatory fishes such as puffers also may remove crabs entirely from tethers. To assess the likelihood that missing crabs were either (1) pulled off tethers by predators, or (2) escaped from tethers, one crab was tethered within a galvanized steel cage (1.0 cm mesh) in each fragmentation type on five dates between 6 – 13 June 1998. After 24 h, all caged crabs remained attached to tethers. Additionally, no crabs escaped from tethers when held in flumes for 24 h before experiments. I therefore assumed that missing crabs had been taken off tethers by predators, and calculated the proportional survival of crabs in each site as the number of crabs alive on tethers after 24 h ÷ number of crabs originally tethered.

I tested for differences in mean proportional survival among the five fragmentation types and between June and September with a two-way, fixed-factor ANOVA. To quantify the relation between proportional crab survival and seagrass shoot density in early summer, I regressed mean proportional crab survival at each site on mean seagrass shoot density at each site (n = 4 sites/fragmentation type · 4 fragmentation types = 16 points). The unvegetated fragmentation type (= 0 shoots m⁻²) was excluded from the early summer regression because shoot densities in the vegetated fragmentation types all were much greater (≥ ca. 1600 shoots m⁻²). To quantify the relation between proportional crab survival and seagrass shoot density in late summer, we regressed mean proportional crab survival at each site on mean seagrass shoot density at each site in each of the five fragmentation types (n = 4 sites/fragmentation type · 5 fragmentation types =
20 points). Statistical assumptions for regressions were checked through visual examination of residuals (Chatterjee and Price 1991).

Though tethering is prone to treatment-specific bias when seagrass shoot densities differ among treatments due to tangling of the tether among shoots, no bias was detected for juvenile blue crabs tethered in three different artificial shoot densities in the lab (Hovel and Lipcius 1999b). Similarly, Pile et al. (1996) detected no treatment-specific bias for blue crabs tethered in either vegetated or unvegetated sediment. I therefore assumed that tethering experiments were not affected by treatment-specific bias (Peterson and Black 1994).

**Blue crab density**

To find how juvenile blue crab density varied with seagrass fragmentation, I sampled for blue crabs within the five fragmentation types with a suction dredge equipped with a 500 μm mesh collecting bag (Orth and van Montfrans 1987, Pile et al. 1996). From 18-20 June (early summer) and 24-25 September (late summer) 1998 I haphazardly deployed four 0.24 m² (0.55 m diameter) cylindrical suction rings at each of the four randomly-chosen sites within each of the five fragmentation types. Suction rings consisted of a 1-m-high 500-μm mesh cylinder affixed to the top of a 20-cm-high weighted metal cylinder. I deployed rings by drifting to each site in a small boat and then tossing them overboard where they quickly sank to the bottom. Six small buoys kept the mesh cylinder vertically oriented; this prevented mobile epifauna from swimming out of the suction ring. Rings were suctioned for 2 minutes. Efficiency studies (R. Lipcius and M. Montane, unpublished data) showed that > 80 % of crabs within rings of this size are
captured after 1.5 minutes of suctioning. Blue crabs in each sample were enumerated and measured (CW) to the nearest 0.1 mm with vernier calipers.

I used the mean density and size of blue crab juveniles at each site as dependent variables in two-way, fixed-factor ANOVA models with fragmentation type and time (June and September) as factors. I used a multiple linear regression, with time (June vs. September, coded as a dummy variable) and mean seagrass shoot density as independent variables, and mean crab density as the dependent variable to test for a relation between crab density and seagrass complexity. I also tested for relationships between blue crab survival and blue crab density by regressing mean blue crab survival at each site on mean blue crab density at each site (June), and mean blue crab survival in each fragmentation type on mean blue crab density in each fragmentation type (September). The late summer regression was limited to means for each fragmentation type because sites where crab density data were collected did not exactly correspond to sites for tethering experiments.

Suction sampling also was used to test for a difference in juvenile blue crab density between the edge and the interior of large seagrass patches. Two randomly chosen patches were sampled on 11 August and on 17 September 1997, and three patches were sampled on 31 October 1997. Within each patch three suction rings were haphazardly deployed within the patch edge and three rings within the patch interior. Rings were suctioned for two minutes, and blue crabs were enumerated and measured from each sample. Blue crab density did not differ significantly among the three sampling dates (ANOVA: df = 2, 11, F = 0.2, P = 0.8); therefore, I pooled data from the
three dates and used a paired t-test to test for differences in mean blue crab density between the edge and interior of patches.

RESULTS

Seagrass complexity

Zostera marina shoot density was highest in small patches, lowest in large patches and was significantly higher in June than in September (Figure 3, Table 2). There was no difference in Z. marina shoot density between the edge and the interior of large patches in late summer 1997 (edge: $1122.7 \pm 83.1$ shoots m$^{-2}$ SE; interior: $1193.3 \pm 128.4$ shoots m$^{-2}$ SE; $t = -0.5$ with 11 df; $P = 0.6$).

Blue crab survival

Seagrass fragmentation. There was a significant interaction effect of fragmentation type and month (June vs. September) on crab survival (Figure 4, Table 3). Crab survival was lowest in large patches and in unvegetated sediment in early summer, but was equally low in all fragmentation types in late summer. Survival decreased significantly from early to late summer in continuous seagrass, medium patches, and small patches, but not in large patches or in unvegetated sediment.

Seagrass complexity. Crab survival was not correlated with seagrass shoot density in June 1998 (regression: $df = 1, 14, F = 1.7, P = 0.21, r^2 = 0.11$) but was inversely correlated with shoot density in late summer 1998 (regression: $df = 1, 18, F = 11.3, P < 0.01, r^2 = 0.39$; Figure 5).

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Blue crab density

Seagrass fragmentation. A total of 175 juvenile blue crabs was captured in early and late summer 1998. All crabs were captured in seagrass; I found no crabs in unvegetated sediment. The mean density of juvenile blue crabs was higher in late than in early summer, and significantly higher in small patches and continuous seagrass than in large patches (Figure 6, Table 4). Crabs were significantly smaller in late summer (mean CW = 12.2 ± 0.2 mm) than in early summer (mean CW = 28.1 ± 0.16 mm SE), but crab size did not differ among the five fragmentation types (Table 5).

Seagrass complexity. Crab density was highly correlated with seagrass shoot density, and significantly higher in late than in early summer (Figure 7, Table 6). Blue crab density increased by ca. 1 crab m⁻² for every 100 shoots m⁻² increase in Zostera marina density in both early and late summer.

Patch edge vs. patch interior. A total of 187 crabs was captured in the edges and interiors of large patches in 1997. Crab density was significantly higher in the interior of large patches than at the edge (paired t-test: t = -2.67 with 6 df, P = 0.03; Figure 8). Though crabs captured in the interior of patches were somewhat larger than those captured in the edge (22.1 ± 4.6 mm SE vs. 18.7 ± 0.9 mm SE, respectively), there was no significant difference in crab size between patch edges and patch interiors (paired t-test: t = 0.72 with 6 df, P = 0.5).

Survival vs. crab density. Crab survival and crab density were not correlated in early summer (linear regression, df = 1, 14, F = 0.15, P = 0.71, r² = 0.01; Figure 9). Crab survival was highest at intermediate (ca. 4-6 crabs m⁻²) densities, and was reduced at low (0-1 crabs m⁻²) and high (7-9 crabs m⁻²) densities, suggesting a parabolic relationship.
between crab survival and density. I therefore used the Ricker function to fit a parabolic curve to the data, and found a marginally-significant curvilinear relationship between blue crab survival and density (df = 1, 14, F = 4.2, P = 0.06, $r^2 = 0.23$). In late summer there was a significant inverse correlation between juvenile blue crab density and survival (linear regression, df = 1, 3, F = 10.8, $P < 0.05$, $r^2 = 0.78$; Figure 9).

DISCUSSION

In this comparison of the effects of large- and small-scale seagrass habitat structure on blue crab survival and density, the findings indicate that (1) the effect of seagrass habitat fragmentation (= patch size) on crab survival and density is non-linear, (2) the effect of habitat fragmentation on survival varies temporally, (3) juvenile blue crab density varies temporally and is positively correlated with seagrass complexity, (4) inverse correlations between blue crab survival and seagrass complexity likely are due to density-dependent predation by juvenile conspecifics, and (5) juvenile blue crab density is greater in the interior of patches than at the edge. Thus, complex dynamics involving habitat fragmentation, habitat complexity, time, proximity to patch edge, and interactions with juvenile conspecifics influence blue crab survival and density in fragmented seagrass landscapes.

*Habitat fragmentation and blue crab survival*

In fragmented forests, songbird egg survival decreases and songbird nest parasitism increases as patch size is reduced (Brittingham and Temple 1983, Wilcove 1985, Small and Hunter 1988, Johnson and Temple 1990, Andrén 1992, Robinson et al.)
In contrast, juvenile blue crab survival and density were low in large patches, and were higher in medium and small patches and in continuous seagrass. This non-linear effect of seagrass patch size on blue crab survival and density may in part be due to seagrass complexity; low shoot densities in large patches may have allowed predators such as large blue crabs and fishes to more easily find and capture tethered crabs (Heck and Crowder 1990, Orth 1992). Seagrass complexity may influence spatial variation in faunal survival, and modify relationships between faunal survival and seagrass habitat fragmentation. For example, hard clam survival was significantly higher, and seagrass shoot density and below-ground biomass were 50% higher in large than in small seagrass patches in Back Sound, North Carolina, but there was no difference in clam survival between large and small patches when artificial seagrass was used to standardize complexity between patch sizes (Irlandi 1997). High seagrass complexity in continuous seagrass also may have been responsible for reduced clam mortality and reduced sub-lethal predation (i.e. siphon nipping) on hard clams in continuous vs. patchy seagrass (Irlandi 1994).

Variation in juvenile blue crab survival among patches was not solely due to seagrass complexity; crab survival was not correlated with shoot density in early summer, and survival was significantly higher in medium than in large patches despite small differences (ca. 56 shoots m$^{-2}$) in complexity. Patch dispersion in the landscape also may have influenced juvenile blue crab survival. In fragmented forests, roads and agricultural fields that isolate patches may be used as corridors by predators, raising predation rates along patch edges and in small patches with high edge-to-interior ratios (Small and Hunter 1988). Similarly, the great amounts of unvegetated sediment surrounding large
seagrass patches may have acted as a corridor for predators to move among patches, thereby lowering crab survival. Though small patches also were well-isolated, their high shoot densities may have increased crab survival rates. Unvegetated sediment may have facilitated predator (e.g. blue crabs, whelks) movement among seagrass patches in Back Sound, North Carolina, causing bay scallop (*Argopecten irradians* Say) survival to be lower in patchy than in continuous seagrass (Irlandi et al. 1995). Similarly, lower scallop survival along seagrass patch edges than in patch interiors in St. Joseph Bay, Florida likely was due to predators moving from unvegetated sediment to patch edges to forage (Bologna and Heck 1999). Predator movement from unvegetated sediment to patch edges also may have caused juvenile blue crab density to be lower in patch edges than in patch interiors in our study.

Low crab survival in large patches, and moderate survival in small patches (June) may have been due to greater predator abundance in those regions of the landscape. However, large blue crabs, the main predator of juvenile conspecifics (Mansour 1992, Moody 1994, Moksnes et al. 1997), were significantly less abundant in large and small seagrass patches than in continuous seagrass in August 1998 (Chapter 2), but I did not measure predator abundance in June.

Crab survival was extremely low in unvegetated sediment in June; only one out of forty crabs tethered was alive after 24 h. Late-instar juvenile blue crabs like those used here (e.g. 10 – 30 mm carapace width) may utilize unvegetated sediment more than early-instar crabs, because larger juveniles have a relative size refuge from some predators (Orth and van Montfrans 1987, Pile et al. 1996, Schulman 1996). However, seagrass
apparently is an important refuge even for late-instar juveniles in early summer (Orth and van Montfrans 1982, Heck and Wilson 1987, Schulman 1996).

**Crab survival vs. crab density**

The cannibalistic nature of blue crabs (Peery 1989, Perkins-Visser et al. 1996, Moksnes et al. 1997) may cause unexpected trends in survival with seagrass habitat structure. Blue crab survival was inversely correlated with seagrass shoot density in September; this may have been due to density-dependent predation by juvenile conspecifics, wherein proportional survival decreases as crab density increases (Perkins-Visser et al. 1996, Pile et al. 1996). Survival of juvenile blue crabs placed in experimental enclosures at high densities (50 crabs m\(^{-2}\)) was ca. 30% lower than for crabs at low densities (10 crabs m\(^{-2}\)) in seagrass meadows of the lower York river, Virginia (Perkins-Visser et al. 1996). In the present study, blue crabs were densest in patches with high shoot densities in both June and September, and there was an inverse correlation between juvenile blue crab survival and crab density in September. In June, the relationship between crab survival and crab density appeared parabolic, suggesting that crab survival was inversely density-dependent at low-to-intermediate crab densities, and density-dependent at intermediate-to-high crab densities (Lipcius and Van Engel 1990, Pile et al. 1996). Juvenile blue crab survival therefore may have increased with seagrass shoot density until high crab densities begin to reduce survival.

Density-dependent predation by juvenile conspecifics also may have caused juvenile blue crab survival to generally be lower in September than in June; blue crabs were more than twice as abundant in September than in June in seagrass. Alternatively,
reduced survival in late summer may have resulted from changes in the seagrass landscape that occurred during mid-summer. Higher amounts of habitat edge caused by cownose ray bioturbation (Townsend and Fonseca 1998) or lower shoot densities caused by seagrass defoliation may have increased predator access to tethered crabs. To evaluate the likelihood that decreased shoot density caused survival to be lower in late summer, we regressed the change in mean survival from early to late summer on change in mean shoot densities in the five fragmentation types. There was no relationship between change in mean survival and change in mean seagrass shoot density (linear regression, df = 1, 3, F = 0.4, P = 0.5, r^2 = 0.14). Additionally, decreases in survival were highest in continuous seagrass and medium patches which were least fragmented by rays (personal observation), and lowest in large patches which were heavily fragmented by rays. These results suggest that density-dependent mortality, not changes in eelgrass habitat, resulted in decreased survival with time, though changes in eelgrass habitat may have been partially responsible as well.

Blue crab density

Blue crab density was positively correlated with shoot density in both early and late summer, and was significantly higher in patch interiors than in patch edges. These results may be explained by (1) active selection of high shoot densities and patch interiors by crabs, (2) reduced predation on crabs in high shoot densities and in patch interiors, or (3) both of these processes. Juvenile blue crabs and other seagrass fauna actively select habitats of greater complexity to avoid predators (Bell and Westoby 1986, Williams et al. 1990). Late-instar juvenile blue crabs selected high density seagrass over low density.
seagrass and unvegetated sediment in laboratory experiments (Williams et al. 1990). Similarly, spiny lobster (*Panulirus argus*) postlarvae and juveniles selected highly complex red algae (*Laurencia* spp.) over less complex shoalgrass *Thalassia testudinum* in the absence of predators (Herrnkind and Butler 1986). In Australia, seagrass macrofauna (crabs, finfish, and shrimp) all preferred dense to sparse seagrass even when predators were experimentally removed from plots (Bell and Westoby 1986). In our study, crab density was not linearly related to patch size, but was strongly correlated with seagrass shoot density in a linear fashion even though variation in shoot density among patch sizes was limited (range of means = 585 and 835 shoots m\(^{-2}\) in June and August, respectively) and patch size varied by five orders of magnitude. This trend was evident in both early and late summer despite different trends in crab survival with shoot density. Juvenile blue crabs become increasingly mobile with size (Orth and van Montfrans 1987, Pile et al. 1996) and large juveniles traverse unvegetated sediment to move from patch to patch (Sogard 1989). Thus, juvenile blue crabs may seek out patches with high shoot densities, even if patches are small and well-isolated.

Though shoot densities did not differ between the edge and the interior of patches, crabs were more abundant in patch interiors. Crabs may inhabit the interior of patches to avoid predators foraging at the patch edge, or crab survival may be reduced at patch edges. Survival of prey such as juvenile blue crabs likely would be reduced at patch edges if unvegetated sediment between large patches serves as a corridor for predators such as large blue crabs and finfish to move among patches (Irlandi 1994). Additionally, predators of newly-settled blue crabs such as grass shrimp (*Palaemonetes* spp.) inhabit patch edges because they periodically move to adjacent bottom and salt marshes to forage.
(Eggleston et al. 1998). Grass shrimp were nearly twice as abundant at the edges of large patches than in the interiors at my study site (Hovel, unpublished data). Though grass shrimp likely do not prey on late-instar blue crabs such as those found here, they are important predators of blue crab megalopae (Olmi and Lipcius 1991); high post-settlement predation at patch edges on early instar crabs therefore may have contributed to differences in crab density between patch interiors and patch edges.

Conclusions

In this study of the effects of large- and small-scale habitat structure in a marine ecosystem, seagrass fragmentation, seagrass complexity, time, and interactions with juvenile conspecifics jointly influenced the survival and density of juvenile blue crabs. Faunal survival and abundance in fragmented seagrass landscapes therefore may depend on a mix of deterministic processes that vary both spatially and temporally. Future studies on faunal survival and abundance in seagrass therefore should be conducted over a range of spatial scales, and must incorporate covarying factors such as predator distribution and time to generate a more complete understanding of the effects of seagrass habitat structure on population and community-level processes.
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Chapter 2

Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival
ABSTRACT

Habitat fragmentation is increasingly common on land and in the sea, leading to small, isolated habitat patches in which ecological processes may differ substantially from those in larger, continuous habitats. Seagrass is a productive but fragmented subtidal habitat that serves as a refuge from predation for many animals because its structural complexity limits the detection and capture of resident prey. The singular influence of seagrass habitat fragmentation (e.g., patch size) on faunal survival is largely unknown, and has been difficult to quantify because seagrass habitat complexity (e.g., shoot density) and patch size are often confounded and vary seasonally. In July 1998 I quantified the effect of seagrass habitat fragmentation on juvenile blue crab (*Callinectes sapidus*) survival in the absence of covarying complexity by exposing tethered crabs to predators in density-controlled, artificial eelgrass (*Zostera marina*) plots embedded within natural seagrass patches of four broad size classes (<1m$^2$ to >30,000 m$^2$). I repeated this experiment in September 1998 with three different shoot densities, after predictable environmental events (defoliation and bioturbation) had increased seagrass habitat fragmentation and decreased shoot density. In July, crab survival was inversely correlated with seagrass patch area. Fragmentation increased survival of juvenile blue crabs, in contrast to patterns typically observed in terrestrial and marine systems. This pattern appears to have been due to low abundance of adult blue crabs, the chief predator of juvenile conspecifics, in fragmented seagrass. In September, blue crab survival was greater than in early summer, and survival increased with artificial seagrass shoot density but did not vary with patch size. The breakdown of the relationship between crab survival and patch size in late summer may have resulted from influx of cownose rays,
which fragmented large, continuous patches of seagrass into smaller patches in mid summer, potentially equalizing fragmentation across the seagrass meadow. These results show that (1) fragmented seagrass landscapes hold significant refuge value for juvenile blue crabs, (2) fragmentation and crab survival vary temporally, and (3) crab survival increases with habitat complexity (shoot density) regardless of fragmentation. The findings indicate that habitat fragmentation and complexity jointly drive organismal survival, and that their influence differs temporally in this dynamic landscape. Thus, ecological processes are sensitive to landscape structure, and studies of habitat structure should incorporate multiple scales of space and time, as well as potentially confounding structural variables.

INTRODUCTION

As humans sequester more of the Earth's natural habitat for their own use, ecologists have become increasingly concerned with the effects of habitat fragmentation on flora and fauna (Forman and Godron 1981, 1986, Saunders et al. 1991). Fragmentation of habitats often produces a landscape of small, isolated remnant patches embedded within an inhospitable matrix (Saunders et al. 1991, van Apeldoorn et al. 1992, Andrén 1994). Species requiring cover to avoid predators, forage, and reproduce may be restricted to remnants, but larger and more mobile predators may be able to move safely among patches (Yahner 1988). Predator-prey encounter rates therefore may be highest near the perimeter of patches, and in small patches that contain proportionally more "edge" than larger patches (Gates and Gysel 1978). Increased edge habitat in fragmented landscapes raises predation rates on birds (Brittingham and Temple 1983, Wilcove 1985,

Though landscape studies largely have been restricted to terrestrial habitats such as forests, many marine habitats, including seagrasses (Orth et al. 1984, Orth 1992, Robbins and Bell 1994), kelp forests (Dayton and Tegner 1984, Dayton et al. 1984, Bologna and Steneck 1993), as well as coral and oyster reefs (Eggleston et al. 1998) are often severely fragmented as well. Seagrass is a highly productive subtidal vegetation that serves as nursery area for many species and supports a high density and diversity of fishes and invertebrates in coastal marine habitats (Peterson 1918, Heck and Orth 1980, Orth 1992). Seagrass is fragmented by waves and currents, animal burrowing and bottom feeding, and boaters and fishers into patches ranging in size from less than 1 m² to 1000s of m² (Orth 1977, 1992, Fonseca et al. 1982, Townsend and Fonseca 1998). Seagrass patches and surrounding unvegetated sediments therefore may represent an aquatic analog to fragmented terrestrial landscapes, and processes governing floral and faunal responses to habitat fragmentation on land may act there as well (Robbins and Bell 1994).

Seagrass serves as a refuge for many species because the structural complexity of emergent shoots (measured as shoot density, canopy biomass, or canopy surface area) inhibits the detection and capture of prey by predators (Orth 1992). Thus, the refuge value of seagrass generally increases with complexity (Stoner 1979, Heck and Orth 1980, Heck and Thoman 1981, Bell and Westoby 1986, Heck and Wilson 1987, Wilson et al. 1987, Heck and Crowder 1990, Lipcius et al. 1998; also see reviews by Orth et al. 1984

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and Orth 1992, and additional references therein). The functional relationship between seagrass complexity and faunal survival (i.e. the habitat-survival function, Lipcius et al. 1998) typically is non-linear (Orth 1992); common forms of the function are sigmoid, in which survival does not increase below a threshold level of complexity (e.g. Nelson 1979, Heck and Thoman 1981, Gotceitas and Colgan 1987, Schulman 1996), or hyperbolic, in which small increases in complexity enhance survival below an upper asymptote (Crowder and Cooper 1979, Schulman 1996, Lipcius et al. 1998).

In Chesapeake Bay, the seagrass _Zostera marina_ L. ("eelgrass") forms extensive meadows composed of discrete patches ranging from 1 m² to > 10,000 m² at shoot densities of 300 - 3000 shoots/m² (Orth and Moore 1986). Eelgrass fragmentation and complexity vary seasonally. Shoot density and biomass peak in early summer (June - July) when growth is robust, but are lower and more variable among patches in late summer (August - September) after a rapid temperature-induced defoliation (Orth and Moore 1986, Schulman 1996). Cownose rays (_Rhinoptera bonasus_) invade seagrass beds in mid-summer in the Chesapeake Bay and increase seagrass fragmentation by excavating seagrass to feed on infaunal bivalves such as hard clams (_Mercenaria mercenaria_) and soft-shell clams (_Mya arenaria_) (Orth 1975, Townsend and Fonseca 1998, personal observation).

The effects of fragmentation and complexity on prey survival are difficult to distinguish because they often co-vary, with larger seagrass patches having higher shoot densities or biomass (Irlandi 1994, 1997). Thus, prey survival may be reduced in small seagrass patches due to either low complexity or high proportional edge. Moreover,
reduced complexity due to defoliation, coupled with increased fragmentation due to bioturbation, may alter this relation temporally.

I mapped *Z. marina* fragmentation patterns in a small Chesapeake Bay seagrass landscape using aerial photography and a geographic information system (GIS). I then quantified the effect of seagrass fragmentation on juvenile blue crab survival in the absence of covarying complexity by exposing crabs to naturally occurring predators in density-controlled, artificial eelgrass plots embedded within *Z. marina* patches. This methodology allowed me to examine survival over the entire range of naturally occurring eelgrass patch sizes, which spanned several orders of magnitude, and further allowed me to quantify the interactive effect of complexity (= shoot density) and habitat fragmentation on survival. I also determined how seasonal changes in complexity and fragmentation influenced crab survival. In addition, I quantified the relationship between fragmentation and complexity in both early and late summer, and determined how fragmentation influenced the habitat-survival function for juvenile crabs. I hypothesized that (1) survival would increase with patch size, (2) survival would increase with complexity in large patches, but not in small patches due to their high proportional edge, and (3) survival would decrease from early to late summer due to decreased complexity and increased seagrass habitat fragmentation.
METHODS

Study species

The blue crab, *Callinectes sapidus* Rathbun, is a ubiquitous decapod crustacean that inhabits shallow estuarine and coastal waters of the Eastern and Gulf coasts of North America (Williams 1984). In Chesapeake Bay, adult females release larvae at the bay mouth from June to September (Van Engel 1958, McConaugha et al. 1988). Larvae develop through 7 or 8 zoeal stages on the continental shelf and re-invade Chesapeake Bay as postlarvae in summer and fall (van Montfrans et al. 1990). These small, vulnerable postlarvae settle in seagrass and metamorphose to the juvenile form. Young juvenile crabs remain in seagrass where food is abundant, whereas late-instar crabs (i.e., > 7th instar, carapace width (CW) > 10.7 mm) often are found in unvegetated sediment, salt marshes or oyster reefs (Pile et al. 1996, Eggleston et al. 1998). Large juveniles have a relative size refuge from many predators (Orth and van Montfrans 1987, Pile et al. 1996, Schulman et al. 1996) but juvenile crabs of all sizes remain vulnerable to large finfish and conspecifics, their chief predators (Hines et al. 1990, Mansour 1992, Moody 1994, Moksnes et al. 1997).

Study site

This research was performed in *Z. marina* seagrass beds adjacent to the Goodwin Islands (76° 24' W x 37° 13' N), a group of small, unpopulated landforms within a Chesapeake Bay National Estuarine Research Reserve in the lower York River (Figure 1). The islands are separated from the shoreline by a narrow channel (approx. 0.5 km


wide). Depths at low tide within these seagrass beds are ca. 0.5 m. Mean water temperature and salinity in the lower York river vary annually from 4 - 28 °C and 16 - 22 psu, respectively. Seagrass at the Goodwin Islands is primarily *Z. marina*, though some widgeongrass, *Ruppia maritima* L., is present in the shallows.

*Selection of seagrass patches*

Seagrass meadows typically are mapped with ground-based point-intercept techniques (e.g. Fonseca and Bell 1998) or high-altitude aerial photography and GIS (e.g. Orth and Moore 1983, Orth et al. 1996) which do not resolve seagrass patches < 1 m² in size. However, small patches (< 1 m²) are common in many fragmented seagrass meadows (Robbins and Bell 1994, personal observation). I used low-altitude aerial photography and GIS to visualize and measure seagrass patches at the Goodwin Islands as small as 0.05 m² in size (see Chapter 1). Seagrass beds were photographed in May 1998 from a small plane flying at an altitude of 400 m. Individual 20 cm x 20 cm photographs, each covering ca. 240,000 m², were scanned at 300 dpi, rectified, and combined into a mosaic showing the entire seagrass meadow in ARC/INFO®.

Patches ranging from 0.05 m² to 30,000 m² were present in the meadow, and represented different degrees of seagrass fragmentation (Figure 2). Three patch sizes were common within this range, and were selected for crab survival experiments (Table 1): small patches ca. 0.25 m², medium patches ca. 8.0 m², and large patches ca. 3000 m².

Additionally, I quantified survival in the largest patch of seagrass in the meadow (continuous seagrass), ca. 30,000 m², and in artificial seagrass plots placed in unvegetated sediment, which represented the smallest patches at 0.05 m². The number and proportion
of patches in each of these five fragmentation types and their areas, perimeters, and perimeter to area ratios are shown in Table 1.

**Shoot density measurements**

To test if shoot density differed among fragmentation types and among seasons, I haphazardly took four 15 cm diameter x 20 cm deep cores in each of four randomly selected sites within continuous seagrass, large patches, medium patches and small patches in early summer (9-11 June 1998) and late summer (8-9 August 1998) and counted the number of *Z. marina* shoots in each core. I used a two-way, fixed-factor analysis of variance (ANOVA) to test if mean shoot density differed among fragmentation types and seasons. I tested for homogeneity of variance with Cochran’s C test, and based post-hoc multiple comparisons on Student-Newman-Keuls tests in this and all subsequent tests (Underwood 1997).

**Blue crab survival experiments**

**General methodology.** To test the effects of seagrass fragmentation and shoot density on crab survival, I tethered juvenile blue crabs (1.0 - 3.0 cm spine-to-spine carapace width, CW) in artificial seagrass plots of 0.25 m diameter (Schulman 1996). These plots maintained shoot density constant and precluded confounding effects of food and chemical cues associated with natural seagrass (Schulman 1996, Eggleston et al. 1998). Plots were constructed of Vexar mesh (a woven plastic material) that was sewn to circular steel frames. Segments of buoyant extruded polypropylene ribbon (0.5 cm wide x 50 cm long) were folded in two and tied to the Vexar to simulate seagrass shoots. A
brass snap swivel was affixed to the center of each plot so that one crab could be tethered in each plot per trial. Crabs were tethered by affixing them to 5 cm segments of monofilament line with cyanoacrylate glue. This technique is widely used to measure relative survival in crustaceans (e.g., Heck and Thoman 1981, Heck and Wilson 1987, Wilson et al. 1987, Eggleston et al. 1990, Pile et al. 1996, Shulman 1996, Ryer et al. 1997, Lipcius et al. 1998).

Crabs were collected by trawling seagrass beds adjacent to Allen’s Island in the lower York River (Figure 1), and were held in running seawater in an outdoor flume. No crab was held more than 48 h. Crabs were tethered in the lab, measured (CW) and acclimated to tethers for 24 h in running seawater before placement in the field.

Influence of fragmentation on survival. The influence of habitat fragmentation in the absence of covarying seagrass shoot density was tested in July, before seagrass defoliation and cownose ray invasion. Artificial plots containing 60 shoots (1200 shoots/m²) were held in running seawater for 2 wk. The chosen shoot density is within the natural range of shoot densities in the field (Orth and Moore 1986). On 29 June 1998 I placed one plot in each of four randomly selected sites within each fragmentation type. From 7 - 20 July 1998, I conducted five 24 h survival trials in each plot (N = (1 crab/plot) x (4 plots/fragmentation type • trial) x (5 trials) x (5 fragmentation types) = 100 crabs). After 24 h, tethered crabs were checked and categorized as live, eaten (fragments of the carapace remaining on the tether), molted (entire carapace remaining on the tether), or missing (no parts of the carapace remaining on the tether) (Pile et al. 1996). Crabs that molted or died on tethers were excluded from the analysis.
Missing crabs may have escaped from tethers, or may have been pulled off by predators. Adult blue crabs often carry off prey before consuming them (pers. obs.) and predatory fishes such as puffers also may remove crabs entirely from tethers. To assess the likelihood that missing crabs were pulled off tethers by predators, one plot containing a tethered crab was placed within a galvanized steel cage (1.0 cm mesh) in each fragmentation type in each 24 h trial (n = 5 crabs per fragmentation type total). After 24 h, all caged crabs remained tethered to plots. Additionally, no crabs escaped from tethers when held for 24 h before experiments. I therefore assumed that missing crabs had been taken off by predators.

Crab size may influence survival (Pile et al. 1996). I therefore first used logistic regression (Agresti 1990) to test if crab survival (live vs. eaten) was correlated with crab CW. Crab survival and CW were not related ($\chi^2 = 0.35$ with 1 df, $P = 0.55$). I then used a linear regression, with daily proportional survival as the dependent variable, and log10 patch size as the independent variable, to test if survival was related to seagrass patch size. The log10 transformation was used to linearize the relationship; statistical assumptions were checked through visual examination of residuals (Chatterjee and Price 1991).

Influence of fragmentation and shoot density on survival. A second tethering experiment was conducted in September to quantify the interactive effect of shoot density and fragmentation type on crab survival. Crabs were tethered in artificial plots to which 15, 30, or 60 shoots were tied (300, 600, and 1200 shoots/m$^2$, respectively). On 10 September 1998, one plot of each density was placed at each of four randomly selected sites within continuous seagrass, in four randomly selected large patches and four
randomly selected small patches (n = 4 plots/density • fragmentation type). A cage was placed over an additional fourth plot of a randomly selected density at each site to control for missing crabs; as above, no caged crabs were missing from tethers after 24 h. From 11-25 September 1998, I conducted ten 24 h survival trials in each plot (N = (1 crab/plot) x (4 plots/density • fragmentation type) x (3 fragmentation types) x (10 trials) = 120 crabs). I used a two-way, fixed-factor ANOVA to test if daily proportional survival (no. of surviving crabs / no. of crabs tethered per fragmentation type • day) differed among fragmentation types and shoot densities.

To examine the relationship between crab survival and seagrass shoot density among fragmentation types, I generated crab habitat-survival functions for continuous seagrass, large patches and small patches and examined approximations (i.e. Y/X vs. X) to the first derivatives (Lipcius et al. 1998). Plotting the first derivative of the habitat-survival function aids in visualization of the qualitative changes at low levels of shoot density.

I analyzed the form of each habitat-survival function with linear regression and a general functional response model (Lipcius et al. 1998). If the linear regression of proportional survival against seagrass shoot density was significant and residuals were random, I assumed the relation linear. If the linear regression was non-significant or residuals were non-random, I used the following model to distinguish sigmoid from hyperbolic curves:

\[ Y = \frac{AX^\beta}{(B + X^\beta)} \]
where $Y = \text{proportional crab survival}$, $X = \text{shoot density}$, $A = \text{asymptotic survival}$ (usually 1.0), $B = \text{the value of X at which } Y = 0.5A$, and $\beta = \text{the parameter associated with the form of the habitat-survival function}$. The habitat-survival function is sigmoid when $\beta > 1$, and hyperbolic when $\beta \leq 1$ but greater than zero (Lipcius et al. 1998).

The linear form of the above equation is

$$\log \left( \frac{Y}{[A - Y]} \right) = \log \left( \frac{1}{B} \right) + \beta \log(X)$$

Thus, a linear regression of $\log \left( \frac{Y}{[A - Y]} \right)$ on $\log(x)$ yields an estimate of $\beta$ that can be tested against hypothetical values of 0 or 1 with standard $t$-tests (Rawlings 1988, Chatterjee and Price 1991, Lipcius et al. 1998).

Analysis of the functional relationship between survival and shoot density may be spurious when only three levels of shoot density are used (Orth 1992, Schulman 1996). Therefore, my analysis of crab habitat-survival functions was intended only to supplement the ANOVA test for an interaction effect between fragmentation and shoot density.

**Predator abundance**

I quantified the abundance of potential predators in continuous seagrass, large patches, medium patches and small patches by trawling and suction sampling. On 21 - 22 August 1998, I conducted four replicate 2 min trawls in each fragmentation type with a 5 m otter trawl (2.5 cm mesh) towed behind a small boat. All crabs and fishes captured in the nets were measured (CW for crabs and total length (TL) for fishes) and released. I
used the number of blue crabs $\geq 50$ mm CW as an estimate of predator abundance in statistical analyses because adult and sub-adult blue crabs were the most common items captured in trawls (Table 2), and because they are a major predator on juvenile conspecifics (Darnell 1959, Tagatz 1968, Martin et al. 1989, Peery 1989, Hines et al. 1990, Mansour 1992, Moody 1994).

If large blue crabs are found only in seagrass, trawling may not have measured differences in predator abundance among fragmentation types because the percentage of bottom covered by Z. marina decreased as fragmentation increased. To test the assumption that predatory blue crabs are found in both seagrass and unvegetated sediment, and to further test for differences in predatory crab abundance among patch sizes, I suction sampled for large blue crabs in each fragmentation type. On 6 August 1998 we haphazardly deployed one 1.46 m diameter suction ring (see Pile et al. 1996 for description) in each of four large, medium, and small seagrass patches, and one ring in unvegetated sediment nearby each patch (N = 4 rings/bottom type · fragmentation type). All eight rings were deployed in seagrass in continuous seagrass. Each ring was sampled for crabs by suctioning for 6 min with an underwater suction dredge, followed by 3 min of dipnetting.

I pooled data from large, medium and small patches and then tested for a difference in the mean number of crabs per bottom type (vegetated vs. unvegetated) with a $t$-test. I then used the number of large crabs per tow (trawls), and the number of large crabs per m$^2$ (suctions) as dependent variables in separate one-way ANOVAs to test for differences in the abundance of large blue crabs among continuous seagrass, large patches, medium patches and small patches.
To find if the regional (i.e., lower York River area) abundance of large blue crabs differed between early and late summer, I calculated the mean number of large crabs (≥ 50 mm CW) captured per tow in both July (n = 4) and September (n = 5) 1998 by the Virginia Institute of Marine Science Juvenile Fish and Blue Crab Trawl Survey. We then tested for differences in mean crab abundance between July and September with a t-test.

Temporal changes in survival

I used a two-way, fixed factor ANOVA, with daily proportional survival as the dependent variable, and fragmentation type and time as independent variables, to test for temporal (early vs. late summer) differences in crab survival within continuous seagrass, large patches, and small patches. Temporal differences in survival could only be tested in high density plots within these three fragmentation types, as this was the only density used in both early and late summer.

Treatment-specific bias experiments

Though tethering is commonly used to measure relative predation rates among treatments, it may produce a biased measure of predation if tethering effects are not proportional across treatments (Peterson and Black 1994, Pile et al. 1996). This may be especially problematic when tethering is used to assess the influence of seagrass shoot density on survival, because crab tethers may get tangled with shoots in high seagrass densities, but not in low densities. Such treatment-specific bias would preclude interpretation of density effects on relative survival. I therefore conducted a full-factorial

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laboratory experiment to assess the effect of tethering upon bias in treatments involving artificial seagrass density and predator presence or absence.

Four artificial plots each of moderate seagrass density (600 shoots/m²) and high seagrass density (1200 shoots/m²) were placed in each of two 2000 l mesocosms filled with sand to a height of 0.25 m and York river water to a depth of 0.5 m. Each plot was encircled with a 1.0 m diameter x 0.75 m high mesh cage that was pushed into the sand, forming eight arenas in each mesocosm. For each artificial seagrass density, one arena in each mesocosm was chosen at random to receive one of the following treatment combinations: (1) tethered crab (10 - 30 mm CW) with predator, (2) tethered crab without predator, (3) untethered crab with predator, and (4) untethered crab without predator. Predators were adult blue crabs (80 - 120 mm CW) captured from trawls at Allen's Island, starved for 48 h before each 24 h trial, used once, and then released. Six 24 h trials were run in each mesocosm between 24 August and 1 September 1998 (n = 12 crabs per treatment combination). After 24 h, I recorded tethered crab status (live, eaten, missing, molted).

I used a G log-likelihood statistic to test if survival was independent of tethering (tethered vs. untethered) and shoot density. Treatment-specific bias is indicated by a significant interaction effect between tethering and shoot density (Peterson and Black 1994, Pile et al. 1996).

RESULTS


*Shoot density measurements*

As expected, there was a two-fold reduction in *Zostera marina* shoot density from early to late summer (Figure 3, Table 2). There was no difference in shoot density among continuous seagrass, large patches and medium patches in either early or late summer, though density was significantly higher in small patches than in large patches in both seasons (Figure 3, Table 2).

*Crab tethering*

**Influence of fragmentation on survival.** Contrary to my hypothesis, when artificial seagrass density was held constant in early summer there was a highly significant negative correlation between crab survival and patch size (Figure 10). Only 20% of tethered crabs survived in continuous seagrass, and 30, 48, 50, and 64 % survived in large patches, medium patches, small patches and plots placed in unvegetated sediment, respectively (Figure 10).

**Influence of fragmentation and shoot density on survival.** Patch size did not influence the relation between crab survival and shoot density. Seagrass fragmentation had no effect on crab survival in late summer, but crab survival differed with artificial shoot density within all three fragmentation types (Figure 11, Table 7). Only 15 – 30% of crabs survived in low density seagrass, whereas 40–52% of crabs survived in the intermediate density, and 61–65% of crabs survived in high density seagrass.

Variation in the form of the habitat-survival function was consistent with previous findings of a sigmoid-hyperbolic relationship. The linear regression of proportional survival on shoot density was significant for all three fragmentation types. In small
patches, residuals were random, and the curve therefore was considered linear. In continuous seagrass and large patches, however, residuals were non-random, with lower than average residuals in low- and high-density seagrass, and higher than average residuals in the intermediate density. When the general model was used to test between sigmoid and hyperbolic forms, $\beta = 2.3$ was significantly greater than both 0 and 1 in continuous seagrass, and the habitat-survival function was considered sigmoid. $\beta$ also was high (1.9) in large patches, but it was not significantly different from 1, and the habitat-survival function was considered hyperbolic (Figure 12, Table 8). Different functional forms also were evidenced in the approximations to the first derivatives (Figure 12). These results, however, must be viewed cautiously given that only three shoot densities were examined (Lipcius et al. 1998).

**Temporal effects on crab survival.** Contrary to my hypothesis, crab survival was higher in September than in July in continuous seagrass, large patches and small patches (Figure 13, Table 9). There was neither a difference in survival among the three fragmentation types nor an interaction effect of fragmentation type and time. Between 21 and 46% of crabs survived in early summer, whereas 61–65% of crabs survived in late summer (Figure 13).

**Predator abundance.** The mean number of large crabs ($\geq 50$ mm CW) captured in trawls differed significantly with fragmentation type (one-way ANOVA, df = 3, 12, $F = 5.2$, $P < 0.05$) (Figure 14). Crab abundance was significantly higher in continuous seagrass than in large patches and small patches, but abundance did not differ between continuous seagrass and medium patches, or between large patches, medium patches and small patches (Figure 14). Of the crabs collected in trawls, 48% were found in
continuous seagrass, 5% in large patches, 26% in medium patches, and 6% in small patches. Thus, the highest predatory crab densities were associated with the largest seagrass bed, either in the continuous core (continuous seagrass) or in the fringing patches (medium patches).

In the suction samples, large crab density was highest in continuous seagrass, intermediate in large patches and medium patches, and lowest in small patches. Forty four percent of crabs were captured in continuous seagrass, 28% in large patches, 25% in medium patches, and 3% in small patches. Differences in large crab density among fragmentation types were marginally significant (one-way ANOVA, df = 3, 28, F = 2.6, P = 0.06) due to high variance in crab density among replicate samples.

Large crab density did not differ significantly between seagrass and unvegetated sediment in the suction samples (t-test, df = 23, t = 1.2, P = 0.2; Figure 15) suggesting that trawls did not bias measures of crab abundance among patch sizes by sampling different proportions of seagrass in each fragmentation type. However, large crab density was more than two-fold greater in seagrass patches than in unstructured bottom. Thus, my sampling may have been too limited to detect a difference in predatory crab abundance between seagrass and unvegetated sediment. Greater crab abundance in seagrass than in unvegetated sediment would result in spuriously low measures of predatory crabs in patchy seagrass, because the proportion of area trawled that was covered by seagrass was lower than in continuous seagrass. Results of the predator surveys should therefore be interpreted with caution.
Though large crab abundance was somewhat higher in July (16.5 ± 7.7 crabs/tow) than in September (13.2 ± 3.2 crabs/tow SE) in trawls of the lower York River, the difference was not significant ($t$-test, $df = 7$, $t = -0.4$, $P = 0.7$; Figure 16).

**Treatment-specific bias experiments.** There was no significant interaction effect between tethering and shoot density on crab survival, demonstrating that a treatment-specific bias due to tethering was not present (Figure 17, Table 10). Additionally, no bias in relative predation was found for juvenile blue crabs tethered in low density seagrass (300 shoots/m$^2$) vs. unvegetated sediment in the lab (Pile et al. 1996). Though we did not test for differences in relative survival between low and intermediate artificial shoot density, we witnessed no tangling of tethers with artificial shoots in the lab. It is unlikely that crabs on tethers only 5 cm in length become tangled in shoots, especially at low and intermediate artificial shoot densities.

Survival was higher for untethered crabs than for tethered crabs. Though tethered crabs may swim, burrow, and hide behind seagrass shoots (Zimmer-Faust et al. 1994, Pile et al. 1996, personal observation), they cannot swim away from predators, or avoid them if predators are detected in advance of an encounter. Thus, tethering experiments may overestimate natural crab mortality (Zimmer-Faust 1994), but they provide an unbiased estimate of relative mortality among different seagrass densities.

**DISCUSSION**

In this experimental investigation of the effects of fragmentation in a marine ecosystem, the findings indicate that (1) blue crab survival is inversely related to patch size in fragmented seagrass beds, (2) the effect of fragmentation varies temporally, and
(3) a covarying feature of fragmentation – shoot density – strongly influences crab survival independently of fragmentation effects. Thus, in this seagrass system, habitat fragmentation, shoot density (i.e. habitat complexity) and temporal variation must be considered jointly when assessing the influence of habitat structure on faunal survival.

I removed the confounding effect of shoot density on survival and found an inverse relation between crab survival and patch size. This relation is opposite that for birds and mammals in agricultural landscapes, and highlights the need for empirical research on fragmentation effects in a variety of habitat types. Specifically, the influence of landscape structure on predator and prey behavior and abundance must be quantified if the effects of habitat fragmentation on faunal survival are to be understood.

Seagrass habitat fragmentation and crab survival

The effects of seagrass habitat fragmentation and shoot density on faunal survival have been difficult to distinguish because of their covariation and seasonality. For instance, increased hard clam (Mercenaria mercenaria L.) and bay scallop (Argopecten irradians Say) survival in large vs. small seagrass beds may have been due to differences in proportional edge among patch sizes, or to higher shoot densities in larger patches (Irlandi 1994, Irlandi et al. 1995). Hard clam survival, seagrass shoot density, and seagrass root biomass all were greater in large than in small seagrass patches in North Carolina (Irlandi 1997). Thus, confounding of complexity and patch size has precluded an effective test of how landscape configuration influences survival of seagrass fauna.

I eliminated the confounding effect of seagrass complexity and found that survival of blue crab juveniles was highest in small, isolated patches of seagrass. My
study is the first to demonstrate a negative correlation between prey survival and patch size in marine systems, and is comparable to that of Tewksbury et al. (1998) who found that songbird nest predation was greater in continuous than in fragmented forests in Montana.

My results contrast those demonstrating reduced songbird egg survival (Wilcove 1985, Small and Hunter 1988, Johnson and Temple 1990, Andrén 1992, Robinson et al. 1995) and increased nest parasitism (Brittingham and Temple 1983, Johnson and Temple 1990, Robinson et al. 1995) in small, isolated forest remnants relative to larger remnants. However, these studies describing negative effects of habitat fragmentation on fauna were conducted in midwestern America and Scandinavia, where forests are fragmented by farmland. In these agricultural landscapes, nest predators such as corvids (Andrén 1992) and mammals (Angelstam 1986), and nest parasites such as cowbirds (Robinson et al. 1995) prefer cropland to forest. These predators move freely in the landscape matrix with little risk of predation, and encounter their prey along patch edges as they move from open to forested habitats to depredate or parasitize nests. In contrast, predators were likely more abundant in continuous than in fragmented habitat in our study. Large blue crabs, a chief predator of juvenile conspecifics, were apparently more abundant, and juvenile blue crabs were eaten more often in continuous seagrass than in large or small patches of seagrass. Though large blue crabs may move over unvegetated bottom more safely than small juveniles, they are vulnerable to other crabs, birds, or fishes (Micheli 1997) and may be less willing to move among patches when no corridor of protective habitat is present (Micheli and Peterson 1999). Additionally, large blue crabs may seek refuge in seagrass when molting or mating (Ryer et al. 1997) and their bivalve prey may
be more abundant in continuous seagrass (Peterson 1982, Irlandi 1997). Thus, large blue crab predators may prefer continuous to fragmented seagrass, which may reduce predator-prey encounter rates in fragmented seagrass.

Some terrestrial predators also may prefer continuous to fragmented habitat, leading to positive effects of fragmentation on survival. For instance, forest fragmentation increased songbird breeding productivity in western Montana, because red squirrel nest predators preferred continuous to small forest patches (Tewksbury et al. 1998). Patchiness increases habitat heterogeneity, which influences predator–prey dynamics (Gause 1934, Huffaker 1958). Structure added to plain test tubes prevented predators (Didinium nasutum) from consuming all their prey (Paramecium caudatum) (Gause 1934). Similarly, prey mite (Eotetranychus sexmaculatus) populations persisted with predatory mites (Typhlodromus occidentalis) only when heterogeneity was high and habitat patches were randomly dispersed (Huffaker 1958). Goldenrod fragmentation caused local explosions of aphid populations, because goldenrod patchiness deterred predatory beetles from finding aphids (Kareiva 1987). In these examples, heterogeneity provided prey with habitat that predators could not colonize as quickly, or at all, thereby increasing prey survival. Generalizations about the effects of habitat fragmentation and heterogeneity on prey survival therefore may be difficult, because of species- and habitat-specific responses of predators and prey to landscape structure.

My results show that small seagrass patches hold significant refuge value for juvenile blue crabs. In contrast, bay scallop survival was lower in closely-spaced, small patches than in intermediate and large patches in Back Sound, North Carolina, though there was a trend for increased shoot densities with patch size (Irlandi et al. 1995).
Irlandi et al. (1995) proposed that unvegetated channels between closely-spaced, small seagrass beds facilitated the movement of large blue crabs, whelks, and other predators into beds, thereby increasing predation on scallops. Such corridors of unvegetated sediment between closely-spaced seagrass patches may enable mobile predators to remain near cover while efficiently moving among beds in search of prey. Unvegetated sediment channels were present in our medium patches (Figure 2), but had the opposite effect on survival in our seagrass landscape; 50% of juvenile blue crabs survived in these patches whereas only 26% survived in continuous seagrass.

The results of this experiment differed from those of Chapter 1, in which juvenile blue crab survival was lowest in large patches and but was higher in continuous seagrass, medium patches and small patches in June. Differences in predator abundance and distribution may have caused the difference in survival patterns among the two experiments. Large blue crab abundance may have been high in fragmented regions of the meadow in June, but may have been reduced in these regions by July, resulting in the inverse relationship between survival and patch size.

Alternatively, predators such as large blue crabs may not avoid fragmented areas, but their foraging efficiency may be reduced there. Crabs, fishes, or birds may have to search for appropriate feeding patches longer in fragmented seagrass, because patches are smaller and more dispersed. However, large mobile predators should frequently intercept many small seagrass patches because they have proportionally more edge than do continuous areas.

My experimental seagrass plots laid over unvegetated sediment differed from the other treatments because plots placed in unvegetated sediment represent an addition of
habitat, rather than a replacement of a portion of seagrass patches as in the other treatments. These artificial eelgrass plots closely resembled natural *Zostera marina* patches, but did not provide olfactory cues to crabs. These factors may have caused survival to be great in these plots due to treatment-specific bias. This is unlikely, however, because structural additions to marine sediment attract blue crabs effectively (Schulman 1996, Eggleston et al. 1998).

**Effects of fragmentation and shoot density on crab survival**

Unlike early summer, patch size (= fragmentation) had no influence on crab survival in September, probably due to alterations of the seagrass landscape in mid summer. Cownose rays foraged in the seagrass beds from mid July to late August, apparently concentrating their destructive feeding in large patches of seagrass. Continuous seagrass and large patches were pockmarked with numerous depressions, ca. 1 m wide x 0.3 m deep, that are characteristic of ray digging which fragments large patches into aggregations of smaller patches (Orth 1975, Smith and Merriner 1985). Differences in effective patch size among fragmentation treatments were therefore reduced in late summer, which may explain the lack of a significant difference in survival among these treatments.

Crab survival in September increased with shoot density in the artificial seagrass plots, irrespective of fragmentation treatment. Poor crab survival at low shoot densities was likely due to high detectability of small crabs by predators such as finfish and large blue crabs, which use chemical (Zimmer-Faust et al. 1994), tactile (Lipcius and Hines 1986, Eggleston 1990) and visual cues (Heck and Crowder 1991) when foraging.

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My findings suggest that the habitat-survival function differs by fragmentation type, though these results are limited due to the low number of shoot density treatments (n = 3). The apparently sigmoid (continuous seagrass), hyperbolic (large patches), and linear (small patches) habitat-survival functions likely were due to relative differences between plot (artificial) shoot density and the density of seagrass surrounding these plots. Specifically, predators may have easily found and captured crabs in artificial shoot densities lower than surrounding (patch) shoot densities. For instance, mean shoot density in continuous seagrass (1089 ± 181.1 shoots/m² SE) matched the high density treatment (1200 shoots/m²) resulting in poor crab survival in the low (300 shoots/m²) and medium (600 shoots/m²) treatments and an apparently sigmoid habitat-survival function. Juvenile blue crabs tethered in continuous seagrass in the lower York River exhibited a sigmoid habitat-survival function with an inflection point at approximately 600 shoots/m² (Schulman 1996). Low shoot density in large patches (665 ± 150.4 shoots/m² SE) raised crab survival in the low and intermediate shoot density treatments and may have caused the habitat-survival function to be hyperbolic. Finally, high shoot density in small patches (1500 ± 169.0 shoots/m² SE) reduced crab survival in the intermediate shoot density treatment, probably resulting in a linear habitat-survival function.

Though differences between patch and plot shoot densities varied somewhat among fragmentation types in early summer (range of difference = 816 to 1401 shoots/m² in large patches and small patches, respectively), this variation likely did not cause juvenile blue crab survival to be different among fragmentation types in July. Crab survival was high in small patches, where density differences between surrounding Z. marina and plots was greatest.
Temporal variation in crab survival

Juvenile blue crab survival increased from early to late summer despite seasonal increases in seagrass fragmentation and decreases in shoot density. This increase in survival contrasts the decreased survival of crabs tethered in naturally-occurring seagrass (Chapter 1) and may have been caused by differences between plot shoot densities and surrounding seagrass shoot densities. Zostera marina shoot density decreased from June to August, so that plot (= artificial) shoot densities were lower than surrounding seagrass in early summer but not in late summer. The relatively low plot shoot densities may have allowed predators to detect and capture crabs more easily in early than in late summer.

Alternatively, increased survival may have been caused by emigration of predators from seagrass beds or predator swamping by juvenile blue crabs. If large blue crabs or other predators prefer continuous to fragmented seagrass, they may have left seagrass beds for other habitats after cownose rays fragmented continuous seagrass and large patches areas in mid summer. Large blue crabs also may leave seagrass beds in late summer if rays deplete their bivalve prey. If ray fragmentation influenced predator distribution, disproportionate ray fragmentation of continuous seagrass and large patches should have resulted in larger increases in crab survival from early to late summer in continuous seagrass and large patches, relative to small patches. There was a trend for greater differences in survival between early and late summer as patch size decreased (difference in proportional survival in continuous seagrass = 0.42, large patches = 0.31, small patches = 0.18; Figure 7) but the interaction effect of shoot density and month was non-significant. Peak blue crab recruitment in late summer (August – November; Orth
and van Montfrans 1987, van Montfrans et al. 1990) often occurs as settlement pulses that may swamp predators, as evidenced by laboratory and field experiments demonstrating inverse density-dependent or density independent juvenile crab mortality in benthic habitats (Pile 1993, van Montfrans et al. 1995, Moksnes et al. 1997). Abundance of small juvenile blue crabs (3 – 30 mm CW) in seagrass beds at the Goodwin Islands was ca. 2.3 fold greater in September than in June, 1998 (Hovel, unpublished data) which may have reduced their overall mortality.

Temporal differences in survival likely were not due to changes in large blue crab (= predator) abundance. Large blue crab abundance typically declines through the summer due to predation by birds, fishes, conspecifics (Micheli 1997) and fishery exploitation (Lipcius and Van Engel 1990). There was no significant difference, however, in lower York River crab abundance between early and late summer, 1998.

Finally, I recognize that the temporal differences in survival as a function of fragmentation type were not necessarily due to time, but to other covarying factors or stochastic variation. These experiments require replication to determine whether the temporal patterns in survival are consistent seasonal phenomena.

**Implications for restoration and conservation**

Quantifying the joint effects of seagrass shoot density, fragmentation, and time on survival is necessary to predict the effectiveness of seagrass restoration and stock-enhancement efforts. Recent widespread loss of seagrass due to sediment and nutrient loading (Orth and Moore 1983, Dennison et al. 1993), fishing gear, and propeller scarring (Sargant et al. 1995) has prompted efforts to restore seagrass to many coastal areas by
seeding or shoot transplantation (Fonseca et al. 1999). However, seagrass transplanting is labor intensive, so that managers tasked with restoring seagrass often must choose between planting few large beds at low shoot densities, or many smaller beds at moderate or high shoot densities. My results suggest that both the size of planted patches and the spacing of planted shoots will be critical determinants of faunal survival. Specifically, planting one large continuous area of seagrass at low shoot densities may not enhance blue crab survival as effectively as planting many smaller beds at high shoot densities.

Patchy seagrass may hold value for other seagrass epifauna as well as juvenile blue crabs. Grass shrimp (Palaemonetes spp.) densities were significantly higher in small (0.25 m²) artificial seagrass patches than in intermediate and large patches (0.5 - 4.0 m²) in Back Sound, North Carolina (Eggleston et al. 1998). Small isolated seagrass beds in high energy sites of Core and Back Sounds in North Carolina supported substantial densities of pink shrimp (Penaeus duorarum), though densities were significantly higher in continuous seagrass (Murphey and Fonseca 1995). More importantly, patchy vs. continuous beds served different functions for shrimp among seasons and through ontogeny, suggesting that both patchy and continuous seagrass beds deserve protection from destruction (Murphey and Fonseca 1995). Seagrass restoration may only enhance faunal abundance if a variety of bed spatial configurations are present.

Simple relationships between patch size and faunal survival are unlikely in seagrass, because of the strong effect of co-varying complexity on survival. Relationships between seagrass habitat structure and faunal survival are made even more complex by dramatic temporal alterations in seagrass complexity and patch size, and the influence of juvenile conspecifics on survival (Chapter 1). These changes may make
spatial patterns in survival more difficult to quantify; however, seagrasses and other marine biogenic habitats provide excellent opportunities for determining how landscape change, which has received little attention, may influence landscape structure and function.
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Chapter 3

Modeling blue crab survival in a fragmented seagrass landscape
ABSTRACT

Seagrasses are highly fragmented subtidal habitats that serve as important nursery areas for many commercially- and ecologically-important species, including the blue crab *Callinectes sapidus* Rathbun. As in fragmented forests, loss of seagrass coverage may reduce blue crab survival. However, I found juvenile blue crab survival to be inversely related to seagrass patch size in Chapter 2. Thus, crab survival may be maximized at an intermediate level of fragmentation where the negative effects of low seagrass cover and large patch size both are reduced. I tested this hypothesis by constructing simple models for per capita blue crab survival in a simulated 10000 m² seagrass-unvegetated sediment landscape. I used GIS to measure seagrass landscape characteristics, and used data on blue crab survival and abundance from previous studies to generate empirical functions for the effects of seagrass percent cover, seagrass patch size, crab preference for seagrass and density-dependent predation on juvenile blue crab survival. Seagrass percent cover generally had a larger effect on modeled juvenile blue crab survival than did patch size. When predation on crabs was density-independent, crab survival varied between 13-32 % and was maximized at intermediate values of seagrass percent cover (ca. 40 %). However, under the more realistic scenario of density-dependent survival, per capita juvenile blue crab survival was relatively low (18-20 %) and varied little with percent cover. The results indicate that both continuous and fragmented seagrass landscapes may hold refuge value for juvenile blue crabs.
INTRODUCTION

The decline of faunal populations due to habitat fragmentation is a central concern for ecologists and conservation biologists today (Saunders et al. 1991, Andrén 1994, Meffe and Carroll 1994). Habitat fragmentation has three components: loss of original habitat, reductions in habitat patch size, and increased patch isolation (Andrén 1994). Fragmented habitats therefore typically consist of small, spatially-isolated patches embedded within an unstructured matrix. In forests fragmented by roads and cropland, reduced prey survival due to habitat loss is exacerbated by increased predation in small remnant patches due to their high edge-to-interior ratios (Small and Hunter 1988, Temple and Cary 1988, Andrén 1994, Paton 1994). Reduced species persistence in agricultural landscapes is well documented for birds (Brittingham and Temple 1983, Wilcove 1985, Small and Hunter 1988, Andrén 1992, Robinson et al. 1995; see review by Paton 1994) mammals (Fahrig and Merriam 1985, van Apeldoorn al. 1992) and insects (Elliot et al. 1998).

Seagrasses form fragmented, subtidal landscapes along estuarine shorelines throughout the world (Robbins and Bell 1994). Seagrass coverage generally has declined worldwide due to increased estuarine nutrient enrichment and suspended sediment loads associated with human population growth along coastlines (Orth and Moore 1983, Fonseca et al. 1999). At smaller scales (i.e., within a seagrass meadow) waves and currents, animal activity and humans fragment continuous stands of seagrass into discrete patches of various sizes and shapes, making seagrass habitat an aquatic analogue to fragmented terrestrial landscapes (Robbins and Bell 1994, Fonseca et al. 1999). Seagrass adds complexity to otherwise unstructured marine soft bottoms, providing critical refugia...
for a variety of species including many commercially-important crustaceans (e.g. crabs, shrimp) and bivalves (e.g. hard clams, scallops) (Heck and Crowder 1990, Orth 1992). Loss of seagrass is troublesome because survival of these species, as well as the fauna they consume, is greatly reduced in unvegetated sediments (Orth and van Montfrans 1982, Orth 1992, Heck and Coen 1995, Pile et al. 1996).

Though the negative effects of habitat fragmentation on fauna are evident in fragmented forests (but see Tewksbury et al. 1998, Friesen et al. 1999), the effects of habitat fragmentation on faunal survival and abundance in alternative habitats and at different scales largely are unknown. In seagrass, faunal survival may be low in small, isolated patches due to high edge-to-interior ratios, or to reduced habitat complexity (e.g. shoot density and below-ground biomass) which covaries with patch size (Irlandi 1994, 1997). Alternatively, higher-order predation may be great in unvegetated sediment, deterring predators such as large blue crabs (*Callinectes sapidus* Rathbun) from inhabiting regions of high fragmentation (Micheli 1997, Micheli and Peterson 1999) which raises prey survival rates in small, isolated patches (Chapter 2). Thus, spatial variation in habitat structure at multiple scales, combined with complex species interactions may result in dissimilar effects of habitat fragmentation on fauna in seagrass and terrestrial landscapes.

The blue crab is a ubiquitous, commercially-important decapod crustacean of the eastern and Gulf coasts of North America (Williams 1984). In Chesapeake Bay, adult females release larvae at the bay mouth from June to September (Van Engel 1958, McConaugha et al. 1988). Larvae develop through 7 or 8 zoeal stages on the continental shelf and re-invade Chesapeake Bay as postlarvae in summer and fall, primarily settling

In Chapter 1 and 2, I measured juvenile blue crab survival in a small, fragmented Chesapeake Bay seagrass meadow and found that (1) proportional crab survival is inversely related to seagrass patch size, (2) proportional crab survival is higher in seagrass than in unvegetated sediment, and (3) proportional crab survival decreases as juvenile blue crab density increases, suggesting that crab survival is density-dependent (Perkins-Visser et al. 1996, Pile et al. 1996, Moksnes et al. 1997). Thus, juvenile blue crab survival may decline as seagrass cover is reduced, due to poor survival in unvegetated sediment, or survival may increase as seagrass cover is reduced due to decreasing patch size. In this chapter, I quantify the relationship between seagrass patch size and proportional seagrass cover in this subtidal landscape using aerial photography and a geographic information system (GIS), and then develop simple models to investigate the relative effects of reduced seagrass patch size (positive effect) and reduced proportional seagrass cover (negative effect) on blue crab survival. I hypothesized that blue crab survival would be optimal at an intermediate level of seagrass habitat fragmentation, where the negative effects of large patch size and loss of seagrass habitat on crab survival both are lowest (Figure 18). Undertaking this modeling study allowed...
It enables me to predict more comprehensive effects of seagrass fragmentation on juvenile blue crab survival, via the incorporation of both patch size and seagrass cover effects. Additionally, the results of this study have implications for seagrass restoration and blue crab conservation efforts (see Discussion).

METHODS AND MATERIALS

Study site

I quantified the relationship between seagrass patch size and percent cover, and measured the effect of seagrass patch size on juvenile blue crab survival in Zostera marina seagrass beds adjacent to the Goodwin Islands (76° 24' W x 37° 13' N), a group of small islands forming a Chesapeake Bay National Estuarine Research Reserve in the lower York River. The islands are separated from the shoreline by a narrow channel (approx. 0.5 km wide). Depths at low tide within these seagrass beds are ca. 0.5 m. Mean water temperature and salinity in the lower York river vary annually from 4 - 28 °C and 16 - 22 psu, respectively. Seagrass at the Goodwin Islands is primarily Z. marina, though some widgeongrass, Ruppia maritima L., is present in the shallows.

Seagrass mapping

To find how seagrass patch size varies with seagrass percent cover, we constructed a digital map of the Goodwin Islands seagrass meadow from 1:4800 overhead photos taken in May of 1998 (for details see Hovel and Lipcius 1999b). Briefly, color 20 cm x 20 cm overhead photographs were taken from a small plane flying at an altitude of 400 m and then scanned at a resolution of 300 dpi with a Hewlett Packard 6100 C color scanner. Digital images then were rectified and combined into a
single mosaic showing the entire seagrass meadow using ARC/INFO® (Environmental Systems Research Institute, Redlands, CA). Digital images consisted of grid cells (pixels), each of which was classified as “seagrass” or “unvegetated sediment.” The 300 dpi resolution allowed us to measure seagrass patches as small as 0.05 m².

Patch size typically varies nonlinearly with habitat percent cover; mean patch area increases slowly at low levels of percent cover, and then increases rapidly at intermediate and high values of percent cover as patches coalesce into larger, continuous areas of habitat (Andrén 1994, Robinson et al. 1995). Thus, fragmented habitats typically consist of several small patches and one larger, continuous area of habitat at intermediate levels of fragmentation (Andrén 1994). I therefore measured (1) the area encompassed by the largest seagrass patch (hereafter known as “largest patch”), (2) the mean area of remaining patches (“hereafter known as “small patches”), and (3) the proportion of the quadrat covered by seagrass (“percent cover”) from 176 uniformly-spaced 100 m x 100 m quadrats laid over the map. I chose this quadrat size because it encompassed the entire range of patch sizes present at the study site (within an order of magnitude). Quadrats were grouped by percent cover (0-9 %, 10-19 %, etc). To find if trends in patch size vs. percent cover depended on quadrat size, I repeated this procedure with square quadrats measuring 25 m and then 50 m on a side. Additionally, I tested whether small patches and maximum patches were normally distributed in each group (n = 5 – 40 quadrats per group) with a Kolmogorov-Smirnov test. Departures from normality would indicate that mean maximum patch size or mean small patch size may be biased toward low or high values.
Patch size effects – empirical functions

The effect of seagrass patch size on juvenile blue crab (10–30 mm carapace width, 0 + year class) survival was measured by conducting crab tethering trials in naturally-occurring seagrass patches (for details see Chapter 2). Briefly, juvenile blue crabs were tethered by affixing them to 5 cm segments of monofilament line with cyanoacrylate glue; I then attached each crab to an artificial seagrass plot (0.25 m diameter) embedded within a naturally-occurring seagrass patch. The artificial seagrass plots consisted of segments of buoyant extruded polypropylene ribbon (0.5 cm wide x 50 cm long) folded in two and tied to a Vexar® mesh frame; plots maintained shoot density constant and precluded confounding effects of food and chemical cues associated with natural seagrass (Schulman 1996, Eggleston et al. 1998). From 7-20 July 1998, I conducted five 24 h survival trials in each plot (N = [1 crab/plot] x [4 plots/patch size • trial] x [5 trials] x [5 patch sizes] = 100 crabs). Patch sizes chosen for experiments (0.05, 0.25, 8, 3000 and 30000 m²) encompassed the entire range of sizes available at the study site. After 24 h, tethered crabs were checked and categorized as live or eaten. A linear regression of proportional crab survival (number found alive/number tethered) revealed that crab survival was inversely related to seagrass patch size by the equation:

\[ S = 0.52 - (0.06\times \log_{10}X) \]  

(1)

(n = 5, df = 1, 3, F = 53.3, P < 0.01, \( r^2 = 0.94 \); Chapter 2) where S = per capita (= proportional) crab survival and X = patch area (m²).
Crab survival models

Model structure and assumptions. I developed a simple deterministic model for per capita blue crab survival in a simulated 100 m x 100 m seagrass-unvegetated sediment landscape using our empirically-determined relationships among blue crab survival, seagrass patch size and seagrass percent cover. The simulated landscape consisted of three components in which crabs were allowed to “settle” (i.e. inhabit before being lost to predation): (1) the largest patch, (2) small seagrass patches, or (3) unvegetated sediment. Because the small patches did not include the largest patch, the sum of the areas covered by components 1 and 2 was equal to the total area of seagrass. I assumed that (1) juvenile blue crab survival was determined solely by predation; (2) there were a constant number of crabs in the landscape, regardless of the proportional cover of seagrass; (3) crab survival was determined only by seagrass patch size (models 1 and 2) or by patch size and crab density (model 3) when crabs were in seagrass; and (4) that either 0 or 10 % of crabs survived in unvegetated sediment. Survival of late-instar juvenile blue crabs tethered in unvegetated sediment varies between 0 % (Schulman 1996) and 12 % (Pile et al. 1996) in Chesapeake Bay.

The basic model has the form

\[
S = [(0.52 - 0.06\times A_{\text{small}})\times P_{\text{small}}] + [(0.52 - 0.06\times A_{\text{max}})\times P_{\text{max}}] + [S_{\text{un}}\times P_{\text{un}}] 
\] (2)

where \( S \) = per capita survival of crabs, \( A_{\text{small}} = \log_{10}(\text{small patch area}) \), \( A_{\text{max}} = \log_{10}(\text{large patch area}) \), \( P_{\text{small}} \) = the proportion of crabs settling in small patches, \( P_{\text{max}} \) = the proportion of crabs settling in the largest patch, \( P_{\text{un}} \) = the proportion of crabs settling in unvegetated

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sediment, and $S_{un}$ = the survival rate of crabs in unvegetated sediment (0 or 10%). Each term calculates the proportion of crabs that “settle” and subsequently survive in a given component of the landscape (= “patch-specific survival”; see Results: model 1 below). Thus, the average per capita survival of crabs, averaged across the landscape, is equal to the sum of the proportion that settle and survive in the largest patch, in patches of mean size, and in unvegetated sediment.

I used this basic formula to constructed three versions of the model, with each successive version incorporating a greater degree of realism concerning crab distribution and survival (Figure 19). By constructing simple and then more complex models, I was able to determine the relative effects of the processes known to influence juvenile blue crab survival. In the simplest version (“model 1”), I assumed that crabs were homogeneously distributed throughout the landscape. In the second version (“model 2”) I added crab preference for seagrass, and in the third (“model 3”) I incorporated both crab preference for seagrass and crab density-dependent survival. For each model, I present crab patch-specific survival for the large patch, the small patches (i.e. the first and second term on the right-hand side of equation 2), and total per capita crab survival.

**Model 1.** In model 1, I assumed that crabs settle homogeneously throughout the landscape; the proportion of crabs settling in each component of the landscape therefore is equal to the proportion of the landscape occupied by each component. For example, if 40% of the 100 m x 100 m landscape was covered by the largest patch, I assumed 40% of the crabs would settle in the largest patch, and $P_{max} = 0.4$.

**Model 2.** In model 2, I assumed that “settling” crabs preferred seagrass to unvegetated sediment so that crab densities were 10 fold greater in seagrass than in
unvegetated sediment. Given a constant number of crabs in the landscape, the proportion of crabs in seagrass is determined by a hyperbolic function (Appendix 1):

\[
P_s = \frac{PC_s}{PC_s + \alpha(1-PC_s)}
\]  

(3)

where \( P_s \) = the proportion of crabs in seagrass, \( PC_s \) = percent cover of seagrass, and \( \alpha \) = the ratio of crab density in unvegetated sediment to crab density in seagrass (= 0.1). Thus, if seagrass covers 50% of the landscape, 90.9% of crabs would be found in seagrass and 9.1% of crabs would be found in unvegetated sediment to yield a density ratio of 10:1. Thus,

\[
P_{\text{max}} = (PC_{\text{max}}/PC_s)*P_s
\]  

(4)

where \( PC_{\text{max}} \) = the percent of the landscape covered by the largest patch. Therefore

\[
P_{\text{small}} = P_s - P_{\text{max}}
\]  

(5)

**Model 3.** In model 3 I incorporated density-dependent crab survival, wherein proportional survival decreases as crab density increases (Perkins-Visser et al. 1996, Pile et al. 1996). To include density-dependent survival, I modeled crab survival as in Model 2 but added a density-dependent survival function (Chapter 1) to each term.

I used crab tethering and suction sampling (Chapter 1) to determine the relation between crab survival and crab density in seagrass. Briefly, from 6-16 September 1998 I tethered 200 juvenile blue crabs within naturally-occurring seagrass patches for 24 h to
determine crab survival rates (artificial plots were not used). The following week (24-25 September) I returned to the same sites and sampled for blue crabs with a suction dredge equipped with a 500 μm collecting bag to determine crab density. Crabs were suctioned from haphazardly deployed 0.24 m$^2$ (0.55 m diameter) cylindrical suction rings for 2 minutes, and blue crabs were enumerated in each sample. A linear regression of blue crab survival on blue crab density revealed that crab survival was inversely related to crab density by the equation:

\[ Y = 9.2 - 0.4D \]  
\[ (n = 5, \text{df} = 1, 3, F = 10.8, P < 0.05, r^2 = 0.78; \text{Chapter 1}) \]

where \( S \) = percent survival and \( D \) = crab density (no. m$^{-2}$). I used this function to factor in density-dependent survival for crabs in both seagrass and in unvegetated sediment.

Crab densities for the model were determined by assuming that a total of 10,000 crabs inhabited the landscape; this value was chosen because it yielded crab densities in seagrass and in unvegetated sediment that are comparable to those found in Chesapeake Bay seagrass beds for 0 + juveniles (i.e. 0–15 crabs m$^{-2}$; Pile et al. 1996). I then calculated crab density in the largest patch as

\[ D_{\text{max}} = \frac{S_{\text{max}}(M_2)}{P_{C_{\text{max}}}} \]

where \( D_{\text{max}} \) = the density of crabs in the largest patch and \( S_{\text{max}}(M_2) \) is crab patch-specific survival in the largest patch from model 2 (i.e. the middle term of the right-hand side of equation 2). \( D_{\text{max}} \) therefore is the density of surviving crabs in the largest patches from model 2. Similarly, I calculated crab density in small patches as

\[ D_{\text{small}} = \frac{S_{\text{small}}(M_2)}{P_{C_{\text{small}}}} \]
where $D_{\text{small}}$ = the density of crabs in patches of mean size and $S_{\text{small}(M2)}$ is crab patch-specific survival in small patches from model 2 (i.e. the first term of the right-hand side of equation 2). In the case that 10% of crabs in unvegetated sediment survive, the density of crabs in unvegetated sediment is

$$D_{\text{un}} = S_{\text{un}(M2)}/PC_{\text{un}}$$  \hspace{1cm} (9)

where $D_{\text{un}}$ = the density of crabs in unvegetated sediment and $S_{\text{un}(M2)}$ is the proportion of crabs surviving in unvegetated sediment from model 2 (i.e. the last term of the right-hand side of equation 2).

Model 3 therefore is

$$S = [9.2 - 0.4*D_{\text{small}}] + [9.2 - 0.4*D_{\text{max}}] + [9.2 - 0.4*D_{\text{un}}]$$  \hspace{1cm} (10)

Each term calculates the proportion of crabs that survive in a given component of the landscape, factoring in patch size effects, crab preference for seagrass, and crab density-dependent survival.

Statistical analysis

I quantified the relationships between per capita crab survival and seagrass percent cover with simple linear regression, with linear regression on log-transformed data, and with the Ricker function (Lipcius and Hines 1986, Pile et al. 1996). First, a linear regression was performed on untransformed per capita survival values; if the fit was significant and met the statistical assumptions of randomly distributed residuals, the relationship was determined to be linear. If the fit was non-significant or if the residuals were non-random, I performed a linear regression using (1) log-transformed data to fit a
hyperbolic curve (Chatterjee and Price 1991), or (2) the linearized form of the Ricker function to fit a parabolic curve (Lipcius and Van Engel 1990, Pile et al. 1996). The Ricker function is

\[ S = (A)(PC_s)e^{-\beta PC_s} \]  

(11)

where \( S \) = per capita survival, \( PC_s \) = percent cover of seagrass, \( A \) = a scaling parameter related to density dependent survival, and \( \beta \) = a parameter associated with the form of the function. The linearized form of the equation is

\[ \ln(S/PC_s) = \ln(A) - \beta PC_s \]  

(12)

When the fit of more than one function was significant and met all statistical assumptions, we selected the function with the highest \( r^2 \) value and the lowest \( P \) value (Pile et al. 1996).

RESULTS

Patch size vs. percent cover

Small patch size varied little with seagrass percent cover; small patch size was < 1 m\(^2\) at low values of percent cover, was ca. 2 m\(^2\) at intermediate values of percent cover, and then decreased to < 1 m\(^2\) at high values of percent cover (Figure 20). In contrast, the size of the largest patch increased by two orders of magnitude with percent cover in a hyperbolic fashion, so that the largest patch covered nearly the entire landscape at high values of percent cover (Figure 20).

Patch size vs. percent cover relationships were robust to quadrat size; trends for small and large patch size with percent cover were similar regardless of the size of our
quadrat (625 m$^2$, 2500 m$^2$, or 10000 m$^2$). In all percent cover groups, small and large patches were normally distributed (Kolmogorov-Smirnov tests, all $P > 0.1$).

**Crab survival**

**Patch size effects.** The effects of patch size on per capita crab survival are shown in Figure 21 for small patches and for the large patches. Per capita crab survival (1) was higher in small patches than in the large patches, (2) decreased slightly and then increased with percent cover in small patches, and (3) decreased with percent cover in the large patches.

**Model 1.** Average per capita crab survival increased with seagrass percent cover in a hyperbolic fashion when crabs were homogeneously distributed in the landscape (Figure 22, Table 11). Patch-specific crab survival (the product of the crab survival rate due to patch size and the proportion of crabs inhabiting each component) generally was low in small patches at all values of percent cover, but increased in a linear fashion in the large patches to a maximum of ca. 25 %. The relationship between average per capita survival and percent cover remained hyperbolic when we assumed that 10 % of crabs in unvegetated survived. At low values of percent cover, crab survival was ca. 10 % higher than when no crabs in unvegetated sediment survived, and the difference between curves decreased as percent cover increased (Figure 22).

**Model 2.** When crabs preferred seagrass to unvegetated sediment, the relationship between total per capita crab survival and seagrass percent cover was parabolic, with maximum survival at intermediate values of percent cover (Figure 23, Table 11). Total per capita crab survival increased rapidly from low (5 %) to
intermediate (35–45%) values of percent cover, and then decreased slowly from intermediate to high values of percent cover. Total per capita survival was higher than in model 1 at all values of percent cover, and maximum crab survival was ca. 7% higher than in model 1. Patch-specific survival increased rapidly in small patches and in the large patches from low to intermediate values of percent cover, accounting for the rapid increase in average per capita survival when seagrass percent cover was low. Thereafter, patch-specific survival decreased in small patches but increased slightly in the large patches, resulting in a moderate decrease in average per capita survival from intermediate to high values of percent cover (Figure 23).

**Model 3.** When I incorporated density-dependent crab survival into the model, average per capita crab survival varied little with percent cover, remaining at about 16-18% regardless of the proportion of the landscape covered by seagrass (Figure 24, Table 11). Juvenile blue crab densities were highest at low values of percent cover and decreased in a hyperbolic fashion with percent cover. Average per capita survival was lower than in model 2 at all but the lowest value of seagrass percent cover. Patch-specific survival in both patches of mean size and in the largest patch increased in a hyperbolic fashion with percent cover, but varied by only 1.5% from low to high values of seagrass percent cover.

**DISCUSSION**

In this modeling study of blue crab survival in a fragmented seagrass landscape, the results indicate that (1) functions for blue crab survival vs. seagrass fragmentation (= percent cover) generally are non-linear, (2) juvenile blue crab survival is maximized at
intermediate values of percent cover when crab survival is density-independent, and (3) juvenile blue crab survival is low and varies little with seagrass percent cover when survival is density-dependent. Under conditions most likely found in nature (i.e., crab preference for seagrass and density-dependent survival), therefore, seagrass fragmentation appears to have little influence on the per capita survival rate of juvenile blue crabs.

The proportion of the landscape covered by seagrass generally had a greater effect on per capita crab survival than did patch size *per se*; the addition of crabs to seagrass as percent cover increased outpaced crab losses due to increasing patch size. However, the relationship between total per capita blue crab survival and seagrass percent cover differed among the three versions of the model, indicating that crab preference for seagrass (model 2) and density-dependence (model 3) had large influences on the relationship between crab survival and seagrass fragmentation. In model 1, crabs were distributed homogeneously in the landscape, so the proportion of crabs inhabiting seagrass increased in a linear fashion with percent cover. Though the area of the large patches increased with percent cover, tending to reduce crab survival, the increasing proportion of crabs inhabiting seagrass resulted in a higher proportion of the total crab population surviving as percent cover increased. The slight increase and then decrease in crab survival in small patches caused the relationship to be slightly hyperbolic, but per capita crab survival did not reach an upper asymptote even when 95% of the landscape was covered by seagrass. Thus, under the assumption that crabs are distributed homogeneously throughout the landscape, juvenile blue crab survival increases with seagrass percent cover.
In model 2, I assumed that crab densities were 10-fold higher in seagrass than in unvegetated sediment. This condition is more realistic than model 1; seagrass is the primary settlement habitat for blue crab postlarvae in Chesapeake Bay (Orth and van Montfrans 1987, Pile et al. 1996) and juvenile crab densities (i.e. ≤ 25 mm carapace width) are higher in seagrass than in unvegetated sediment, often by an order of magnitude (Heck and Orth 1980, Orth and van Montfrans 1987, Williams et al. 1990, Hovel and Lipcius 1999b). This disparity likely is due to both post-settlement predation and habitat selection (Williams et al. 1990). Crab per capita survival was maximized at intermediate values (e.g. 25-45 %) of seagrass cover in model 2, and was higher than in model 1 for all values of percent cover. The results of this model therefore supported my original hypothesis that crab survival would be maximized at intermediate values of percent cover. This pattern resulted from the rapid increase in the proportion of crabs inhabiting seagrass as percent cover increased from low to intermediate values, due to the hyperbolic relationship between the proportion of crabs in seagrass and percent cover (Appendix 1). Though increasing patch size with percent cover had a negative influence on crab survival, this was greatly outweighed by the rapid decrease in the proportion of crabs lost to unvegetated sediment as percent cover increased. At intermediate to high values of percent cover, the rate at which crabs were added to seagrass slowed, and patch size increased, resulting in a gradual decline in crab per capita survival with percent cover.

In model 3, crab densities were 10-fold greater in seagrass than in unvegetated sediment, and crab survival was density-dependent. This is the most realistic of the three models, because juvenile blue crab survival decreases as crab density increases (Perkins-
Crab per capita survival was lower than in model 2 and varied little with seagrass percent cover. Crab densities were highest at low values of percent cover and decreased in a hyperbolic fashion as percent cover increased (Figure 23a) resulting in higher crab proportional mortality due to density-dependence when seagrass percent cover was low. Density-dependent survival therefore had the effect of dampening the variation in crab survival with seagrass percent cover.

Patterns were similar when we assumed that 10% of the crabs inhabiting unvegetated sediment survived. In all three models, increases in average per capita survival with 10% of crabs in unvegetated sediment surviving, compared to 0% surviving were greatest at low values of percent cover where the proportion of the landscape covered by unvegetated sediment was greatest. The effect of this added survival was greatest in models 1 and 2; the added 10% survival increased average per capita crab survival by ca. 10% and 8%, respectively, at low levels of percent cover. Because average per capita survival was relatively low, however, these increases represented a substantial increase in the amount of crabs surviving. In model 3, the addition of survivors in unvegetated sediment made little difference, due to the dampening effect of density-dependent survival.

It is interesting to note that, when crab survival was density-dependent, no more than 20% of crabs inhabiting the landscape survived, and seagrass percent cover had little effect on juvenile blue crab survival. However, this relationship may only be valid over the range of crab densities that I chose for the simulation, which were similar to densities of 0+ year class (≤ 30 mm carapace width) juvenile blue crabs in seagrass (Pile et al. 1996, Hovel and Lipcius 1999b). Densities of newly-settled and early-instar blue
crabs in seagrass typically are higher than for late-instars; densities of newly-settled crabs may be particularly high due to episodic settlement events (van Montfrans et al. 1995, Pile et al. 1996, Moksnes et al. 1997). Moreover, survival of newly-settled crabs may be inversely density-dependent (Moksnes et al. 1997), and blue crab survival rates differ with crab size (Pile et al. 1996). Effects of seagrass fragmentation on newly-settled crabs therefore may differ substantially from those presented here for older juveniles. Nonetheless, the results indicate that, given realistic crab densities, seagrass fragmentation had little effect on the survival of 0+ year class juvenile blue crabs.

My results differ from studies on survival of songbirds in agricultural landscapes, in which survival rates generally decline as forest fragmentation increases (Brittingham and Temple 1983, Wilcove 1985, Small and Hunter 1988, Andrén 1992, Robinson et al. 1995, Keyser et al. 1998). However, similar to my results, the relationship between forest cover and nest mortality is hyperbolic for many species (Robinson et al. 1995), suggesting that non-linear effects of habitat fragmentation on faunal survival may be common. Non-linearity may result from increased detrimental effects of decreasing patch size and increasing patch isolation on survival at low levels of percent cover; patch size and isolation effects are greatly reduced at high levels of percent cover, where patches tend to coalesce into large, continuous areas of habitat (Andrén 1994). Additionally, the density of songbird nests increases as forest cover and forest patch size are reduced, leading to further reductions in survival at low levels of percent cover due to density-dependent predation (Gates and Gysel 1978, Keyser et al. 1998) similar to my study.
The blue crab supports a substantial commercial and recreational fishery in Chesapeake Bay, but intensifying demand and loss of seagrass coverage baywide (Orth and Moore 1983) have put the blue crab in danger of decline. My results have clear implications for efforts to enhance blue crab stocks through seagrass restoration. In particular, my findings suggest that blue crab survival will be low (ca. 16-20 %) but relatively constant regardless of the proportion of the landscape covered by seagrass. Thus, a landscape composed of small, spatially-isolated patches may be equally valuable for preserving blue crab populations as a landscape completely covered by seagrass.

Though seagrass is amenable to restoration because it spreads rapidly and is easily transplanted, efforts to restore seagrass have met with variable success; time-consuming, labor-intensive plantings may produce only patchy seagrass coverage if beds are disrupted by waves, currents and storms (Fonseca et al. 1999). Additionally, digging predators such as cownose rays (*Rhinoptera bonasus*) are particularly disruptive to seagrass beds in Chesapeake Bay (Orth 1975, *personal observation*). Planting seagrass in discrete patches therefore may save time and energy while resulting in an equally effective habitat as would planting a continuous stand of seagrass that likely would become fragmented. Moreover, pre-existing patchy seagrass beds should not be thought of as expendable. Isolated seagrass patches are rapidly colonized by mobile epifauna such as blue crabs (Sogard 1989) and patch-based sub-populations may constitute a significant fraction of total epifaunal populations (Murphey and Fonseca 1995).

However, such restoration strategies may not be optimal for other stages of the blue crab life cycle (e.g. postlarvae and newly-settled crabs) because the influence of seagrass fragmentation on abundance and survival may differ through ontogeny. For instance,
early-instar blue crab survival may be low in small seagrass patches due to high densities of grass shrimp (*Palaemonetes* spp.) predators (Eggleston et al. 1998). Additionally, patch size and shape may influence settlement rates of blue crab postlarvae and therefore the abundance of juvenile blue crabs (Eggleston et al. 1998).

The scope of this study was restricted in several ways. First, my data on landscape characteristics and on blue crab survival and abundance was collected at only the Goodwin Islands, and relationships among these variables may not hold for other seagrass landscapes. Though aerial surveys suggest that seagrass fragmentation patterns at this site are representative of other seagrass landscapes in Chesapeake Bay (*personal observation*), factors that structure seagrass landscape pattern (e.g. currents, waves, and bioturbators) may differ among sites, altering relationships between seagrass fragmentation and patch size. My experiments require replication to confirm that fragmentation patterns and their influence on juvenile blue crab survival and abundance hold for other locations. Second, I used only one quadrat size (100 m x 100 m) to quantify seagrass landscape characteristics. Though relationships between seagrass cover and patch size were robust to quadrat size, this is set an upper limit to seagrass patch size of 10,000 m², and correspondingly limited patch size effects on crab survival and crab densities. Third, crab survival rates were determined by tethering crabs in seagrass. Though widely used to measure crustacean relative survival rates (e.g. Heck and Thoman 1981, Heck and Wilson 1987, Wilson et al. 1987, Eggleston et al. 1990, Pile et al. 1996, Shulman 1996, Lipcius et al. 1998) tethered crabs cannot flee from predators and tethering therefore underestimates actual survival rates. Per capita survival rates presented here therefore are conservative. Fourth, I assumed that seagrass shoot density
did not vary among patch sizes. Though differences in *Z. marina* shoot density among patch sizes were slight at the Goodwin Islands (e.g. 800 shoots m$^{-2}$; Chapter 1), seagrass shoot density often positively covaries with patch size (e.g. Irlandi et al. 1995, Irlandi 1997). Juvenile blue crab survival typically increases with seagrass shoot density (Orth and van Montfrans 1982, Pile et al. 1996, Schulman 1996); thus, low shoot densities in small patches may lower blue crab survival and reduce differences in crab survival with patch size. Finally, my study was restricted on an ecological scale. The effects of seagrass fragmentation on other factors influencing blue crab population dynamics, such as food sources, were not included in the model. Moreover, I modeled only short-term effects of seagrass fragmentation on juvenile blue crabs; the influence of fragmentation on long-term population dynamics, and on different phases of blue crab life history was not considered, nor were effects of seagrass fragmentation at larger (e.g. baywide) scales. Limitations such as these identify avenues for further research that must be addressed before applying my results to conservation efforts.

My results suggest that both fragmented and continuous seagrass habitats may be valuable to juvenile blue crabs. Though requiring replication, my results are encouraging for blue crab conservation because fragmented seagrass habitats that are present along many Chesapeake Bay shorelines may provide important habitat for juvenile blue crabs. Moreover, planting seagrass in discrete patches may allow a greater area of the seafloor to be restored while still providing useful habitat. Conservation strategies that both preserve existing habitat and restore habitat are necessary to counter the effects of habitat fragmentation and loss on species in terrestrial (Sinclair et al. 1995, Dobson et al. 1997) and marine (Allison et al. 1997) ecosystems.
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Williams, A.B. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the Eastern United States, Maine to Florida. Smithsonian Institute Press, Washington, DC, USA


Chapter 4

Dissertation conclusions
Habitat fragmentation alters predator-prey dynamics, and reduces the survival and abundance of many species in terrestrial ecosystems. Loss of original habitat, reductions in habitat patch size, and increased patch isolation all act to raise predation rates on fauna and lower species diversity within the original habitat (Andrén 1994). Landscape-scale studies measuring fragmentation effects have been restricted primarily to agricultural landscapes in the American midwest and Scandinavia; the effects of habitat fragmentation on faunal survival and abundance in alternative habitats and at different scales largely are unknown. In this study, I measured the effect of seagrass habitat fragmentation on juvenile blue crab survival and abundance. The major conclusion of my study is that simple relationships between blue crab survival and seagrass habitat fragmentation do not exist. Instead, a mix of deterministic processes that vary both spatially and temporally influence the survival and abundance of juvenile blue crabs. For instance, seagrass patch size, seagrass complexity, time, and the density of juvenile conspecifics all influenced the survival of juvenile blue crabs.

The effects of seagrass patch size and complexity on faunal survival have been difficult to distinguish because of their covariation (e.g. Irlandi 1994) and seasonality (Orth and Moore 1986). One of the major goals of this study was to determine the singular effect of seagrass habitat fragmentation on juvenile blue crab survival; that is, to distinguish between the effects of seagrass complexity and patch size on survival. I did this by standardizing seagrass complexity around tethered crabs with artificial seagrass plots placed in natural seagrass patches. In this experiment, crab relative survival and patch size were inversely related. This pattern appears to have been due to low abundance of large blue crabs, the chief predator of juvenile conspecifics, in fragmented
regions of the meadow. These relationships between prey survival, predator abundance and seagrass habitat fragmentation are fundamentally different than in fragmented forests (but see Tewksbury et al. 1998). The replacement of forest habitat with cropland increases both the abundance of songbird nest predators (Andrén 1992, Robinson et al. 1995) and their access to nests (Paton 1994). In contrast, the increased risk of higher-order predation may deter predators of juvenile blue crabs, such as large conspecifics, from inhabiting the more fragmented portions of the seagrass meadow. However, a more definitive test of the influence of seagrass fragmentation on predator behavior and abundance in a variety of sites will be required to confirm this hypothesis.

Juvenile blue crab survival and seagrass patch size were not inversely related when crabs were exposed to predators without using artificial seagrass to equalize shoot densities among patch sizes (Chapter 1). In this case, the relationship between crab survival and seagrass patch size nonlinear; survival was lowest in large patches and generally higher in the remaining fragmentation types. This pattern may in part have been due to low shoot densities in the large patches, but shoot density did not entirely explain differences in survival with patch size. Variation in juvenile blue crab survival with patch size likely was due to a complex interaction between a number of environmental variables, such as patch size, patch isolation, seagrass complexity and crab density, all of which influence predator distribution and abundance and therefore juvenile blue crab survival. Seagrass habitats are temporally and spatially dynamic, and faunal survival patterns may be equally dynamic. Though interactions among these factors may be complex, my experiments showed that none of these factors has an overriding
influence on survival. Further experimentation is needed to disentangle the various influences of these factors on juvenile blue crab survival.

The fact that several environmental variables influence juvenile blue crab survival may account for the conflicting results of the two tethering experiments. Though seagrass shoot density was standardized in Chapter 2 and not in Chapter 1, the results suggest that the distribution and abundance of predators (and perhaps prey) caused crab survival to differ between the two experiments. Crabs were tethered in naturally-occurring seagrass in June (Chapter 1), and in artificial plots in July (Chapter 2). Predators of juvenile blue crabs may have been more abundant in the fragmented regions of the landscape in early summer but not in mid-summer when the second tethering experiment was performed. Further experimentation is required to determine the persistence of both of these patterns (i.e. the non-linear relationship between survival and patch size, or the inverse relationship between survival and patch size).

Seagrass habitats are characterized by rapid changes in habitat structure at large and small scales. I conducted my experiments in both early and late summer and found that differences in habitat structure and differences in juvenile blue crab density likely altered blue crab survival rates through time. For example, increased fragmentation by cownose ray bioturbation likely caused the lack of a patch size effect on crab survival in late summer in artificial seagrass plots (Chapter 2). In “natural” seagrass (Chapter 1), higher densities of juvenile conspecifics in late summer, and perhaps seagrass defoliation, likely reduced juvenile blue crab survival from early to late summer. Crab survival was higher in late than in early summer in artificial seagrass plots, likely due to differences between plot shoot densities and artificial shoot densities between time periods. These
results further indicate that factors influencing juvenile blue crab survival may vary temporally and interact in a complex manner.

The blue crab supports a substantial commercial and recreational fishery in Chesapeake Bay, but intensifying demand for crabs and loss of seagrass coverage baywide have put the blue crab in danger of decline. My results have implications for efforts to enhance blue crab stocks through seagrass conservation and restoration. Specifically, my results indicate that (1) both the size of planted patches and the spacing of planted shoots will influence juvenile blue crab survival, and (2) patchy seagrass beds may hold value for juvenile blue crabs. The take-home message from my study should not be that habitat fragmentation benefits the blue crab, but that both fragmented and continuous seagrass habitats should be considered important. Quantifying the joint effects of seagrass fragmentation, seagrass shoot density, crab density and time on crab survival is necessary to predict the effectiveness of seagrass restoration and stock-enhancement efforts.

The negative effects of habitat fragmentation on many species of birds in agricultural landscapes is well documented (reviewed by Paton 1994). However, as ecologists increasingly apply landscape-scale questions to alternative ecosystems, and to a greater variety of species, it is becoming clear that generalizations about the effects of habitat fragmentation on prey survival are not possible, because of species- and habitat-specific responses of predators and prey to landscape structure (e.g. Kareiva 1987, McGarigal and McComb 1995, Eggleston et al. 1998, Tewksbury et al. 1998, Friesen et al. 1999, this study). These studies highlight the need for empirical research on fragmentation effects in a variety of habitat types and at different scales. Seagrass
habitats are ideal for applying landscape ecology principles, and offer a unique challenge to landscape ecologists (Robbins and Bell 1994) because they exhibit temporal and spatial variation over a variety of scales. An application of these principles to seagrass habitats and other marine ecosystems is timely, because they allow ecologists to answer fundamental scale-related questions, and to contribute to the conservation of marine species.
LITERATURE CITED


Table 1. Mean patch area, mean patch perimeter, perimeter-to-area ratio (P/A) and percent of the landscape covered by each fragmentation type at the Goodwin Islands.

Numbers in parentheses = 1 SE.

<table>
<thead>
<tr>
<th>Fragmentation type</th>
<th>Patch area (m$^2$)</th>
<th>Patch perimeter (m)</th>
<th>P/A (m$^{-1}$)</th>
<th>% total area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Continuous seagrass</td>
<td>30,105*</td>
<td>24,202*</td>
<td>0.8*</td>
<td>26.6</td>
</tr>
<tr>
<td>Large patches</td>
<td>3,148 (607)</td>
<td>4,563 (996)</td>
<td>1.47 (0.13)</td>
<td>44.6</td>
</tr>
<tr>
<td>Medium patches</td>
<td>8.3 (5.5)</td>
<td>16.9 (6.7)</td>
<td>10.23 (0.05)</td>
<td>28.1</td>
</tr>
<tr>
<td>Small patches</td>
<td>0.3 (0.01)</td>
<td>2.3 (0.3)</td>
<td>15.4 (0.07)</td>
<td>0.7</td>
</tr>
<tr>
<td>TOTAL</td>
<td>35,155*</td>
<td>32,391*</td>
<td>2.07*</td>
<td>100</td>
</tr>
</tbody>
</table>

* Only one continuous patch was present in the meadow, precluding calculation of means and standard errors.
Table 2. (A) Two-way ANOVA and (B) Student-Newman-Keuls (SNK) results for the shoot density measurements. Treatments are arranged in decreasing order of shoot density and are not significantly different if sharing an underline.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>1</td>
<td>9,921,282.3</td>
<td>63.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Fragmentation type (FT)</td>
<td>3</td>
<td>2,032,266.5</td>
<td>4.3</td>
<td>0.015</td>
</tr>
<tr>
<td>Time · FT</td>
<td>3</td>
<td>562,648.1</td>
<td>1.2</td>
<td>0.33</td>
</tr>
<tr>
<td>Residual</td>
<td>24</td>
<td>3,741,761.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>31</td>
<td>524,450.3</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(B)

**Fragmentation type**

| SP | CS | MP | LP |

CS = continuous seagrass, LP = large patches, MP = medium patches, and SP = small patches.
Table 3. (A) Two-way ANOVA and (B) SNK results for blue crab survival. Treatments are arranged in decreasing order of survival and are not significantly different if sharing an underline.

(A)  

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>1</td>
<td>0.39</td>
<td>15.6</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Fragmentation type (FT)</td>
<td>4</td>
<td>0.05</td>
<td>1.9</td>
<td>0.11</td>
</tr>
<tr>
<td>Time • FT</td>
<td>4</td>
<td>0.11</td>
<td>4.5</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Residual</td>
<td>89</td>
<td>0.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>98</td>
<td>0.03</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(B)  

<table>
<thead>
<tr>
<th>Month</th>
<th>June</th>
<th>September</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MP</td>
<td>CS</td>
</tr>
<tr>
<td>Fragmentation type</td>
<td>CS</td>
<td>LP</td>
</tr>
</tbody>
</table>

CS = continuous seagrass, LP = large patches, MP = medium patches, SP = small patches, ES = early summer, LS = late summer.
Table 4. (A) Two-way ANOVA and (B) SNK results for blue crab density (ln transformed) in early and late summer 1998. Treatments are arranged in decreasing order of crab density and are not significantly different if sharing an underline.

(A)

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>$F$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>1</td>
<td>8.2</td>
<td>4.5</td>
<td>0.04</td>
</tr>
<tr>
<td>Fragmentation type (FT)</td>
<td>3</td>
<td>20.6</td>
<td>3.8</td>
<td>0.02</td>
</tr>
<tr>
<td>Time · FT</td>
<td>3</td>
<td>0.9</td>
<td>0.5</td>
<td>0.65</td>
</tr>
<tr>
<td>Residual</td>
<td>20</td>
<td>1.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>27</td>
<td>2.6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(B)

*Fragmentation type*

<table>
<thead>
<tr>
<th>SP</th>
<th>CS</th>
<th>MP</th>
<th>LP</th>
</tr>
</thead>
</table>

CS = continuous seagrass, LP = large patches, MP = medium patches, and SP = small patches, ES = early summer, LS = late summer.
Table 5. (A) Two-way ANOVA results for blue crab size (carapace width, square root transformed) in early and late summer 1998.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>1</td>
<td>21.2</td>
<td>9.8</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Fragmentation type (FT)</td>
<td>3</td>
<td>2.5</td>
<td>1.2</td>
<td>0.35</td>
</tr>
<tr>
<td>Time · FT</td>
<td>3</td>
<td>0.4</td>
<td>0.2</td>
<td>0.89</td>
</tr>
<tr>
<td>Residual</td>
<td>18</td>
<td>2.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>25</td>
<td>2.7</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 6. Regression results for mean juvenile blue crab density as a function of seagrass shoot density and time (early vs. late summer). (A) Multiple regression with both factors; (B) simple regressions for each time period.

(A)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regression</td>
<td>2</td>
<td>70.1</td>
<td>55.4</td>
<td>&lt;0.001</td>
<td>0.95</td>
</tr>
<tr>
<td>Error</td>
<td>5</td>
<td>1.3</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(B)

<table>
<thead>
<tr>
<th>Time period</th>
<th>Coefficient</th>
<th>df</th>
<th>t</th>
<th>P</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early summer</td>
<td>0.008</td>
<td>1</td>
<td>3.5</td>
<td>0.07</td>
<td>0.86</td>
</tr>
<tr>
<td>Late summer</td>
<td>0.02</td>
<td>1</td>
<td>7.6</td>
<td>&lt;0.05</td>
<td>0.96</td>
</tr>
</tbody>
</table>
Table 7. (A) Two-way ANOVA and (B) Student-Newman-Keuls (SNK) results for the late summer tethering experiment in artificial seagrass plots.

(A)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fragmentation type (FT)</td>
<td>2</td>
<td>0.009</td>
<td>0.2</td>
<td>0.8</td>
</tr>
<tr>
<td>Shoot density</td>
<td>2</td>
<td>0.651</td>
<td>14.5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>FT • Shoot density</td>
<td>4</td>
<td>0.425</td>
<td>0.95</td>
<td>0.4</td>
</tr>
<tr>
<td>Residual</td>
<td>48</td>
<td>0.04</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>56</td>
<td>0.07</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(B)

<table>
<thead>
<tr>
<th>Comparison</th>
<th>SNK difference</th>
<th>g</th>
<th>D’</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low vs. High</td>
<td>0.38</td>
<td>3</td>
<td>0.19</td>
<td>**</td>
</tr>
<tr>
<td>Low vs. Medium</td>
<td>0.22</td>
<td>2</td>
<td>0.16</td>
<td>**</td>
</tr>
<tr>
<td>Medium vs. High</td>
<td>0.17</td>
<td>2</td>
<td>0.16</td>
<td>*</td>
</tr>
</tbody>
</table>

‘D = (EMS/n)^{1/2} \cdot Q_A$, with n = 15, Error Mean Square = 0.054 with 18 df, Q_{18,3.0.05} = 3.61, Q_{18,2.0.05} = 2.97. * P < 0.05, ** P < 0.01.
Table 8. (A) Linear regression results of daily proportional survival as a function of artificial shoot density. (B) Survival response analyses for continuous seagrass and large patches, which exhibited non-random residuals in linear regressions. CS = continuous seagrass, LP = large patches, and SP = small patches.

(A)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>$r^2$</th>
<th>Residuals random?</th>
</tr>
</thead>
<tbody>
<tr>
<td>CS Regression</td>
<td>1</td>
<td>0.65</td>
<td>22.1</td>
<td>&lt;0.001</td>
<td>0.57</td>
<td>no</td>
</tr>
<tr>
<td>Error</td>
<td>17</td>
<td>0.03</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LP Regression</td>
<td>1</td>
<td>0.28</td>
<td>4.63</td>
<td>0.05</td>
<td>0.21</td>
<td>no</td>
</tr>
<tr>
<td>Error</td>
<td>17</td>
<td>0.06</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SP Regression</td>
<td>1</td>
<td>0.29</td>
<td>6.12</td>
<td>0.02</td>
<td>0.27</td>
<td>yes</td>
</tr>
<tr>
<td>Error</td>
<td>17</td>
<td>0.05</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(B)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>$r^2$</th>
<th>$\beta$</th>
<th>$\beta&gt;0$?</th>
<th>$\beta&gt;1$?</th>
</tr>
</thead>
<tbody>
<tr>
<td>CS Regression</td>
<td>1</td>
<td>30.1</td>
<td>22.4</td>
<td>&lt;0.001</td>
<td>0.57</td>
<td>2.31</td>
<td>***</td>
<td>**</td>
</tr>
<tr>
<td>Error</td>
<td>17</td>
<td>1.35</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LP Regression</td>
<td>1</td>
<td>21.9</td>
<td>7.02</td>
<td>0.02</td>
<td>0.29</td>
<td>1.97</td>
<td>**</td>
<td>ns</td>
</tr>
<tr>
<td>Error</td>
<td>17</td>
<td>3.12</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 9. Two-way ANOVA results for crabs tethered in continuous seagrass, large patches, and small patches in early and late summer.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fragmentation type (FT)</td>
<td>2</td>
<td>0.06</td>
<td>0.63</td>
<td>0.54</td>
</tr>
<tr>
<td>Season</td>
<td>1</td>
<td>1.26</td>
<td>14.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>FT · Season</td>
<td>2</td>
<td>0.07</td>
<td>0.76</td>
<td>0.47</td>
</tr>
<tr>
<td>Residual</td>
<td>30</td>
<td>0.08</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>35</td>
<td>0.12</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 10. *G* test analysis for the laboratory experiment testing for tethering (= tethered vs. untethered crabs) treatment-specific bias for two shoot densities (600 and 1200 shoots/m²).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>( \chi^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density</td>
<td>1</td>
<td>0.01&lt;sup&gt;ns&lt;/sup&gt;</td>
</tr>
<tr>
<td>Tether</td>
<td>1</td>
<td>0.01&lt;sup&gt;ns&lt;/sup&gt;</td>
</tr>
<tr>
<td>Density x tether</td>
<td>1</td>
<td>0.01&lt;sup&gt;ns&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
Table 11. Results of the linear regressions of per capita crab survival on seagrass percent cover for Models 1, 2 and 3. Log transformations were used to fit hyperbolic curves, and the Ricker function was used to fit parabolic curves.

<table>
<thead>
<tr>
<th>Model</th>
<th>Function</th>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>P</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model 1</td>
<td>hyperbolic</td>
<td>Regression</td>
<td>1</td>
<td>692.4</td>
<td>&lt;0.001</td>
<td>0.98</td>
</tr>
<tr>
<td>0 %</td>
<td>$S = 0.55(PC_s)^{0.86}$</td>
<td>Error</td>
<td>8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Regression</td>
<td>1</td>
<td>1746.5</td>
<td>&lt;0.001</td>
<td>0.99</td>
</tr>
<tr>
<td>10 %</td>
<td>$S = 6.98(PC_s)^{0.29}$</td>
<td>Error</td>
<td>8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model 2</td>
<td>parabolic</td>
<td>Regression</td>
<td>1</td>
<td>175.4</td>
<td>&lt;0.001</td>
<td>0.95</td>
</tr>
<tr>
<td>0 %</td>
<td>$S = 2.42(PC_s)e^{(-0.02*PC_s)}$</td>
<td>Error</td>
<td>8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Regression</td>
<td>1</td>
<td>102.9</td>
<td>&lt;0.001</td>
<td>0.92</td>
</tr>
<tr>
<td>10 %</td>
<td>$S = 3.02(PC_s)e^{(0.02*PC_s)}$</td>
<td>Error</td>
<td>8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model 3</td>
<td>hyperbolic</td>
<td>Regression</td>
<td>1</td>
<td>140.4</td>
<td>&lt;0.001</td>
<td>0.94</td>
</tr>
<tr>
<td>0 %</td>
<td>$S = 14.8(PC_s)^{0.04}$</td>
<td>Error</td>
<td>8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Regression</td>
<td>1</td>
<td>146.8</td>
<td>&lt;0.001</td>
<td>0.94</td>
</tr>
<tr>
<td>10 %</td>
<td>$S = 15.7(PC_s)^{0.04}$</td>
<td>Error</td>
<td>8</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

S = total per capita survival; PCs = percent cover of seagrass.
Appendix 1. Derivation of the hyperbolic function describing the proportion of crabs found in seagrass under the assumption that crab density is 10 fold greater in seagrass than in unvegetated sediment.

For a landscape composed only of seagrass and unvegetated sediment, we have:

\[ P_s = \frac{D_s A_s}{D_s A_s + (D_u A_u)} \]  

where \( P_s \) = the proportion of crabs inhabiting seagrass, \( D_s \) = crab density in seagrass, \( A_s \) = area of seagrass, \( D_u \) = crab density in unvegetated sediment, and \( A_u \) = the area of unvegetated sediment. Simplifying, we have

\[ P_s = \frac{1}{1 + (D_u A_u)/(D_s A_s)} \]  

The density of crabs in unvegetated sediment is related to the density of crabs in seagrass by a constant

\[ D_u = \alpha D_s \]  

where \( \alpha = 0.1 \). The percent cover of seagrass is simply the area of seagrass divided by total area of the landscape

\[ P_{cs} = \frac{A_s}{A_{tot}} \]  

so that

\[ A_s = (P_{cs})(A_{tot}) \]  

Additionally, the percent cover of unvegetated sediment is

\[ A_u = (1 - P_{cs})(A_{tot}) \]
Substituting equations 3, 5 and 6 into equation 2 yields

\[ P_s = \frac{1}{1 + \left[ \left( \frac{\alpha D_s (1-PC_s)(A_{tot})}{(D_s)(PC_s)(A_{tot})} \right) \right]} \]  

(7)

Simplifying, we have

\[ P_s = \frac{1}{1 + \left( \frac{\alpha (1-PC_s)}{PC_s} \right)} \]  

(8)

Rearranging the equation yields

\[ P_s = \frac{PC_s}{PC_s + \alpha (1-PC_s)} \]  

(9)
Figure 1. Map of the Chesapeake Bay, Virginia, showing the study site in the lower York River. Tethering experiments and predator trawls were conducted at the Goodwin Islands (1), and crabs were held at the Virginia Institute of Marine Science in Gloucester Point, five miles NW of the Goodwin Islands (2).
Figure 2.1: 4800 scale overhead aerial photograph showing patches from the different fragmentation types in seagrass meadow adjacent to the Goodwin Islands. Continuous seagrass (CS), large patches (LP), medium patches (MP), and small patches (SP) are all shown.
Figure 3. Mean (+ 1 SE) *Zostera marina* shoot density in the four vegetated fragmentation types in June and August 1998. Abbreviations as in Figure 2.
Mean seagrass shoot density (number m\(^{-2}\) + SE)

Fragmentation type

- Early summer
- Late summer

<table>
<thead>
<tr>
<th>Fragmentation type</th>
<th>Early summer</th>
<th>Late summer</th>
</tr>
</thead>
<tbody>
<tr>
<td>CS</td>
<td>2500 ± 500</td>
<td>1000 ± 200</td>
</tr>
<tr>
<td>LP</td>
<td>2000 ± 100</td>
<td>500 ± 50</td>
</tr>
<tr>
<td>MP</td>
<td>1500 ± 75</td>
<td>1250 ± 250</td>
</tr>
<tr>
<td>SP</td>
<td>1000 ± 150</td>
<td>1500 ± 300</td>
</tr>
</tbody>
</table>
Figure 4. Mean (+ 1 SE) percent blue crab survival in the five fragmentation types in June and September 1998. Abbreviations as in Figure 2.
Percent blue crab survival (+ SE)

Fragmentation type

Early summer
Late summer
Figure 5. Blue crab survival vs. Zostera marina shoot density in June and September 1998. Note different scales on both axes.
A

$P = 0.2$

$r^2 = 0.11$

B

$Y = 13.5 - (0.007X)$

$P < 0.01$

$r^2 = 0.38$

Percent survival

Shoot density (no. m$^{-2}$)
Figure 6. Mean (+ 1 SE) density of juvenile blue crabs in the four vegetated fragmentation types in June and September 1998. No crabs were found in unvegetated sediment. Abbreviations as in Figure 2.
Mean no. of crabs m$^{-2}$ (+ SE)

- **Early summer**
- **Late summer**

<table>
<thead>
<tr>
<th>Fragmentation type</th>
<th>Early summer</th>
<th>Late summer</th>
</tr>
</thead>
<tbody>
<tr>
<td>CS</td>
<td>6.5 ± 1.2</td>
<td>5.3 ± 0.8</td>
</tr>
<tr>
<td>LP</td>
<td>1.2 ± 0.5</td>
<td>3.1 ± 0.9</td>
</tr>
<tr>
<td>MP</td>
<td>15.7 ± 2.3</td>
<td>18.9 ± 3.4</td>
</tr>
<tr>
<td>SP</td>
<td>12.1 ± 1.7</td>
<td>20.3 ± 4.2</td>
</tr>
</tbody>
</table>

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Figure 7. Mean density of juvenile blue crabs vs. *Zostera marina* shoot density in June and September 1998.
Number of blue crabs $m^{-2}$

- Early summer:
  - $Y = -2.4 + 0.01X$
  - $P < 0.05$
  - $r^2 = 0.98$

- Late summer:
  - $Y = -20.0 + 0.01X$
  - $P = 0.07$
  - $r^2 = 0.93$

Shoot density (number $m^{-2}$)
Figure 8. Mean (+ 1 SE) density of juvenile blue crabs in the interior and in the edge of large seagrass patches in late summer 1997.
Figure 9. Blue crab survival vs. blue crab density in June and September 1998.
Mean blue crab density (number m$^{-2}$)
Figure 10. Linear regression of crab proportional survival (no. of crabs remaining alive / no. of crabs tethered) in artificial seagrass plots placed in the five different seagrass fragmentation types in July 1998. CS = continuous seagrass, LP = large patches, MP = medium patches, and SP = small patches, US = plots placed in unvegetated sediment.
$Y = 0.52 - 0.06(X)$

$r^2 = 0.94$

$p = 0.005$

Proportional survival

\[ \log_{10} \text{(patch size)} \]
Figure 11. Mean crab daily proportional survival in low (300 shoots/m², black bars), intermediate (600 shoots/m², light gray bars) and high density (1200 shoots/m², dark gray bars) artificial seagrass plots placed in continuous seagrass (CS), large patches (LP), and small patches (SP) in September 1998.
Mean proportional survival (+ SE)

Fragmentation type

300 shoots/m²
600 shoots/m²
1200 shoots/m²

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Figure 12. Habitat-survival functions (a, c, e) for juvenile blue crabs tethered in low, medium, and high density artificial eelgrass plots embedded within continuous seagrass (CS), large patches (LP), and small patches (SP), and approximations to their first derivatives (b, d, f).
Figure 13. Survival of juvenile blue crabs tethered in high density (1200 shoots/m²) artificial eelgrass plots placed in continuous seagrass (CS), large patches (LP), and small patches (SP) in early and late summer, 1998.
Figure 14. Mean (+ SE) number of blue crabs > 30 mm CW captured in (A) otter trawls (mean = crabs per trawl) and (B) suction samples (mean = crabs per m²) in each fragmentation type in August 1998. Unlike letters above bars denote means that are significantly different at p < 0.05.
Mean number of predatory crabs per tow or m$^2$ (+ SE)

Fragmentation type

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Figure 15. Mean density (+ SE) of large blue crabs (≥ 50 mm carapace width) captured in suction samples in vegetated and unvegetated bottom. LP = large patches, MP = medium patches, and SP = small patches.
Figure 16. Number of crabs captured in trawls of the lower York river in June and September, 1998. Means (+ SE) for each month were calculated from the mean number of crabs > 50 mm captured per tow (n = 12 to 16 tows/month in the Virginia Institute of Marine Science Trawl Survey.)
Mean number of crabs per tow (+ SE)

<table>
<thead>
<tr>
<th>Sampling month</th>
<th>Mean</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>July</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>12</td>
<td></td>
</tr>
</tbody>
</table>

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Figure 17. Proportional survival of juvenile blue crabs placed in arenas with adult blue crabs in the laboratory experiment. Crabs were either tethered to plots that were 600 or 1200 shoots/m², or free to move about the arena (untethered). All crabs placed in arenas without adult blue crab predators were recaptured (see text for more information).
Figure 18. Graphical representation of the hypothesized separate and combined effects of seagrass percent cover and seagrass patch size on juvenile blue crab survival.
Figure 19. Graphical representation of the three models. Crabs “settled” into the largest patches (“largest”), into patches of mean size (“mean”), or into unvegetated sediment. Predation rates depended on patch size and crab density. Thicker arrows in models 2 and 3 denote the ten-fold difference in crab density in seagrass vs. unvegetated sediment.
Model 1

STARTING POPULATION

Largest → Mean → Unvegetated

settlement

predation (patch size)

survivors + survivors + survivors = Total per capita survival

Model 2

STARTING POPULATION

Largest → Mean → Unvegetated

settlement

predation (patch size)

survivors + survivors + survivors = Total per capita survival

Model 3

STARTING POPULATION

Largest → Mean → Unvegetated

settlement

predation (patch size)

predation (crab density)

survivors + survivors + survivors = Total per capita survival
Figure 20. Size of the largest patches, small patches, and percent of the landscape covered by the largest patch (line) vs. percent cover of seagrass in 100 m x 100 m quadrats at the Goodwin Islands.
The graph shows the relationship between percent seagrass cover and patch size, along with the percent coverage of the largest patch. The x-axis represents percent seagrass cover, ranging from 0 to 100. The y-axis on the left shows patch size in square meters, ranging from 0.1 to 10,000. The y-axis on the right shows percent coverage of the largest patch, ranging from 0 to 100.

The graph includes two lines:
- The line for largest patches increases as percent seagrass cover increases.
- The line for mean patches decreases as percent seagrass cover increases.

This data suggests that as seagrass cover increases, the size of the largest patches also increases, while the mean patch size decreases.
Figure 21. Crab proportional survival in small patches and in the largest patch vs. seagrass percent cover.
Percent survival

Mean patches

Largest patches

Seagrass percent cover

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Figure 22. (A) Patch-specific crab survival (proportion of crabs "settling" and subsequently surviving) in small patches ("small") and in the largest patch ("largest"), and (B) average per capita crab survival vs. seagrass percent cover for model 1. "Total" in B is the sum of the two lines in A, and assumes that 0 % of the crabs in unvegetated sediment survive; "total + 10 %" assumes that 10 % of the crabs in unvegetated sediment survive.
A

Patch-specific survival (% of total crabs)

Largest

Mean

B

Total per capita survival

Total + 10%

Total

Percent seagrass cover

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Figure 23. (A) Patch-specific crab survival in small patches ("small") and in the largest patch ("largest"), and (B) average per capita crab survival vs. seagrass percent cover for model 2. See Figure 22 and text for explanation.
Figure 24. (A) Density of juvenile blue crabs in small patches ("small") and in the largest patch ("largest"). (B) patch-specific crab survival, and (C) average per capita crab survival vs. seagrass percent cover for model 3. Note different scales on the Y axes. See Figure 22 and text for explanation.
VITA

Kevin Alexander Hovel