

Influence of seagrass landscape structure on the juvenile blue crab habitat-survival function

Kevin A. Hovel^{1,2,*}, Mark S. Fonseca¹

¹NOAA/NOS Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Road, Beaufort, North Carolina 28516, USA

²Present address: Department of Biology, San Diego State University, 5500 Campanile Drive, San Diego, California 92182-4614, USA

ABSTRACT: Organismal survival in marine habitats is often positively correlated with habitat structural complexity at local (within-patch) spatial scales. Far less is known, however, about how marine habitat structure at the landscape scale influences predation and other ecological processes, and in particular, how these processes are dictated by the interactive effect of habitat structure at local and landscape scales. The relationship between survival and habitat structure can be modeled with the habitat-survival function (HSF), which often takes on linear, hyperbolic, or sigmoid forms. We used tethering experiments to determine how seagrass landscape structure influenced the HSF for juvenile blue crabs *Callinectes sapidus* Rathbun in Back Sound, North Carolina, USA. Crabs were tethered in artificial seagrass plots of 7 different shoot densities embedded within small (1–3 m²) or large (>100 m²) seagrass patches (October 1999), and within 10 × 10 m landscapes containing patchy (<50% cover) or continuous (>90% cover) seagrass (July 2000). Overall, crab survival was higher in small than in large patches, and was higher in patchy than in continuous seagrass. The HSF was hyperbolic in large patches and in continuous seagrass, indicating that at low levels of habitat structure, relatively small increases in structure resulted in substantial increases in juvenile blue crab survival. However, the HSF was linear in small seagrass patches in 1999 and was parabolic in patchy seagrass in 2000. A sigmoid HSF, in which a threshold level of seagrass structure is required for crab survival, was never observed. Patchy seagrass landscapes are valuable refuges for juvenile blue crabs, and the effects of seagrass structural complexity on crab survival can only be fully understood when habitat structure at larger scales is considered.

KEY WORDS: Habitat structure · Blue crab · Habitat fragmentation · Seagrass · Habitat-survival function

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Habitat structure strongly influences patterns of prey survival in marine systems (Bell et al. 1991, Bartholomew et al. 2000). At relatively fine spatial scales (i.e. cm to m, or the scale of many individual organisms), the ability of predators to find and capture their prey is often inhibited by structural elements of marine habitats, such as seagrass blades (Heck & Crowder 1991, Hovel & Lipcius 2002), kelp fronds and blades (Carr 1994, Anderson 2001), cobble and

boulders (Connell & Jones 1991, Wahle & Steneck 1991, 1992), and living or dead coral (Hixon & Carr 1997). Structure at landscape scales (i.e. 10 to >1000 m) also influences predator–prey dynamics. As in fragmented forests (e.g. Andr n 1994, Paton 1994, Robinson et al. 1995) and grasslands (Karieva 1987, Diffendorfer et al. 1995), the size of habitat patches (Irlandi 1997, Hovel & Lipcius 2001), distance from the patch edge (Bologna & Heck 1999), patch spacing (Micheli & Peterson 1999), and proportional habitat cover (Irlandi et al. 1995, Hovel 2003) all may influence

*Email: hovel@sciences.sdsu.edu

predator foraging behavior, and therefore prey survival, in marine systems.

Seagrasses, which form structured habitats in otherwise unstructured shallow marine and estuarine soft bottoms worldwide (Hemminga & Duarte 2000), provide refuge from predators for many invertebrates (e.g. blue crabs *Callinectes sapidus*: Pile et al. 1996, Hovel & Lipcius 2001, 2002; hard clams *Mercenaria mercenaria*: Peterson 1982, Irlandi 1997; pink shrimp *Penaeus duorarum*: Murphey & Fonseca 1995) and fishes (e.g. red drum *Sciaenops ocellatus*: Rooker et al. 1998). At local scales (= within seagrass patches), prey survival varies with the density, biomass, or surface area of seagrass shoots (see reviews by Heck & Crowder 1991 and Orth 1992). Few studies, however, have evaluated how structure at the landscape scale influences prey survival. Seagrass landscapes exhibit high variability in habitat patch size, patch spacing, and proportional cover due to the actions of waves, currents, and bottom-feeding animals (Robbins & Bell 1994, Fonseca & Bell 1998, Townsend & Fonseca 1998), and continuous areas of seagrass are increasingly being fragmented by boating, fishing, and coastal development (Sargent et al. 1995, Fonseca et al. 1998), all of which may strongly influence predator-prey dynamics and therefore prey survival. For instance, juvenile hard clam survival increased with seagrass patch size (Irlandi 1997) and with seagrass proportional cover (Irlandi et al. 1995) in North Carolina, whereas juvenile crab survival decreased with seagrass patch size (Hovel & Lipcius 2001) and seagrass proportional cover (Hovel 2003) in Chesapeake Bay and California, respectively.

Thus, to comprehensively address how the structure of marine habitats influences prey survival and abundance, the relationship between organismal survival and habitat structure needs to be quantified at multiple spatial scales. In this study we examine how seagrass structure at the landscape scale influences the relationship between juvenile blue crab survival and seagrass shoot density, a prominent element of habitat structure that varies within and among seagrass patches. We model the influence of shoot density on blue crab survival using the habitat-survival function (HSF), which defines the relationship between prey survival and habitat structure at relatively small spatial scales (Lipcius et al. 1998). This relationship may be linear (e.g. Olmi & Lipcius 1991), but in seagrass prey survival typically increases with habitat structure in a non-linear fashion (Heck & Crowder 1991, Orth 1992, Schulman 1996). Common non-linear forms for the HSF are (1) hyperbolic, in which at low levels of habitat structure prey survival increases rapidly with small increases in structure before reaching an upper asymptote (e.g.

Lipcius et al. 1998); and (2) sigmoid, in which a threshold level of structure is required before prey survival begins to increase with habitat structure to an upper asymptote (Gotceitas & Colgan 1989, Schulman 1996). Prey survival may also be inversely related to habitat structure (in a linear or non-linear manner) if, for instance, predator density is positively correlated with habitat structure (e.g. Schulman 1996, Hovel & Lipcius 2002).

The blue crab *Callinectes sapidus* Rathbun (Decapoda: Brachyura: Portunidae) supports one of the most valuable single-species fisheries in the United States, and is a ubiquitous and abundant member of estuarine and coastal soft-bottom communities along the east and gulf coasts (Williams 1984). Adult female blue crabs release larvae from June to September (McConaugha et al. 1983) and larvae develop through 7 to 8 stages on the continental shelf. Postlarval blue crabs re-invade estuaries in summer and fall, with settlement peaks in September to October in Chesapeake Bay and North Carolina (van Montfrans et al. 1990). Postlarval blue crabs preferentially settle in seagrass and subsequently metamorphose to the juvenile form. Seagrass habitat provides small, vulnerable crabs with cover from predators, which include larger conspecifics (Mansour 1992, Moody 1994), birds, and fishes (e.g. striped bass *Marone saxatilis*, Atlantic croaker *Micropogonias undulatus*, and flounder *Paralichthys* spp.).

Juvenile blue crab survival is influenced by seagrass shoot density and biomass (Schulman 1996, Hovel & Lipcius 2002), seagrass patch size (Hovel & Lipcius 2001, Hovel 2003), crab size, and conspecific density (Pile et al. 1996). However, the interactive effect of seagrass structure at different scales on survival has not been considered. Moreover, the influence of seagrass habitat fragmentation on juvenile blue crab survival is unclear, because juvenile blue crab survival decreased with patch size in Chesapeake Bay (Hovel & Lipcius 2001) but increased with seagrass patch size in North Carolina (Hovel 2003). Using juvenile blue crabs, we specifically address the following questions: (1) Does survival increase or decrease with seagrass patch size and with seagrass patchiness at the landscape scale? (2) Does the HSF differ between small and large seagrass patches, and between patchy seagrass and continuous seagrass?

MATERIALS AND METHODS

Study sites and landscape selection. Blue crab survival experiments were conducted in October 1999 and June 2000 in seagrass landscapes found in Back Sound, North Carolina, USA (Fig. 1). October survival

experiments were conducted at Harkers Island (34° 42' N, 76° 34' W) and June survival experiments were conducted at Middle Marsh (34° 41' N, 76° 36' W), ca. 2 km from Harkers Island. Mean daily water temperatures in Back Sound are ca. 21°C in October and 23°C in June, salinity levels are ca. 32 to 33 psu throughout the year, and the tidal range is ca. 1 m. Three seagrass species (eelgrass *Zostera marina*, shoalgrass *Halodule wrightii*, and widgeongrass *Ruppia maritima*) are found in Back Sound. *Z. marina* abundance peaks in late spring to early summer, whereas *H. wrightii* abundance peaks in fall (Irlandi et al. 1999). *R. maritima* was not found in appreciable amounts in the subtidal areas where our experiments were conducted.

The seagrass landscape at Harkers Island (HI) is characterized by patchy eelgrass and shoalgrass beds surrounded by mud and sand sediment at depths of ca. 0.5 to 1.5 m. Patch sizes range from ca. 0.05 to 3000 m² (Hovel 2003). Seagrass patches used in experiments were on the leeward side of HI and therefore were protected from high wave and current activity (Fonseca & Bell 1998). At Middle Marsh, 2 sites (ca. 2 km apart) differing in relative exposure to prevailing wind-generated waves were used for experiments: middle marsh west (MMW: low hydrodynamic activity, comparable to HI) and middle marsh east (MME: high hydrodynamic activity). Relative wave exposure is

ca. 6-fold higher, and maximum current speeds are ca. 2-fold higher at MME than at MMW (Fonseca & Bell 1998, Townsend & Fonseca 1998). Patches ranging from <1 to ca. 5000 m² are located at each site (authors' pers. obs.).

Seagrass structural complexity measurements. To find if seagrass above-ground structural complexity (shoot density and shoot biomass) and seagrass species composition varied with patchiness and site, and to determine the natural range of shoot densities found in Back Sound seagrass landscapes, we quantified seagrass shoot density and biomass for all species present within small and large patches at HI (October 1999) and within patchy and continuous seagrass at MME and MMW (June 2000). At HI, we haphazardly chose 10 small (1 to 3 m²) and 10 large (≥100 m²) seagrass patches, and took one 15 cm diameter × 20 cm deep core from the center of each patch. At Middle Marsh, we selected 3 patchy seagrass areas and 3 continuous areas in MME and MMW (see 'Middle Marsh survival experiments' below for description of how these were selected) and took 1 core in a haphazardly chosen spot in each area. Core samples were frozen and returned to the laboratory, where we counted the number of short shoots of each species in each core, measured the length of the longest blade per shoot to the nearest mm, and weighed shoots that had been dried at 60°C for 48 h to obtain shoot biomass per unit area for each species. We used separate 2-tailed *t*-tests to test for differences in total shoot density and total biomass between small and large patches at HI, and used separate 2-way, fixed factor ANOVAs to test for differences in total shoot density and total shoot biomass between MME and MMW and patchy and continuous seagrass at Middle Marsh. Cochran's *C*-test was used to test for heterogeneity of variances for each analysis, and data were log₁₀-transformed when necessary to meet test assumptions in this and all subsequent analyses. We also used the procedures outlined in Graham & Edwards (2001) to calculate the proportion of the model fit (ω^2) accounted for by each factor and their interaction.

Effects of seagrass landscape structure on the juvenile blue crab habitat-survival function. Methodology: To test for interactive effects of seagrass patchiness and structural complexity on the juvenile blue crab habitat-survival function, we tethered crabs in artificial seagrass plots which were embedded within naturally occurring small and large seagrass patches. Tethering is widely used to measure relative survival among treatments for crustaceans (e.g. Heck & Thoman 1981, Wilson et al. 1987, Pile et al. 1996, Lipcius et al. 1998, Heck et al. 2001, Hovel & Lipcius 2001) and other species (e.g. snails: Warren

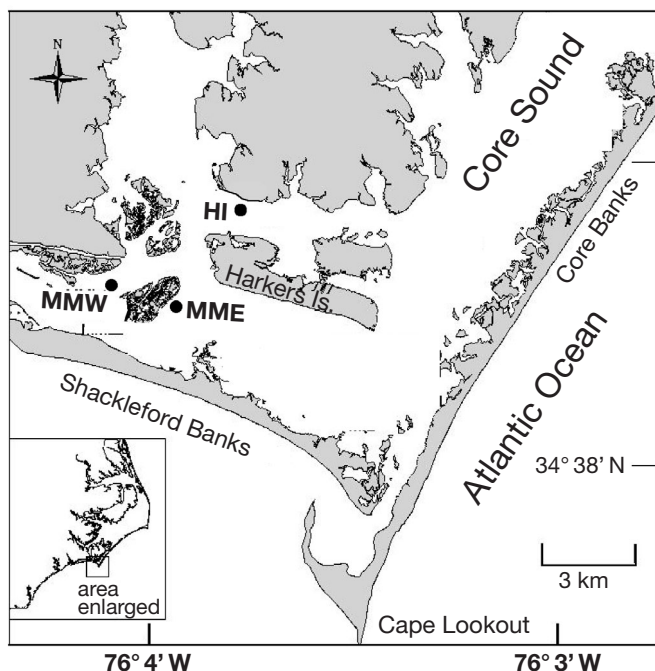


Fig. 1. Location of the study sites in Back Sound, North Carolina, USA. HI = Harkers Island, MME = Middle Marsh East, MMW = Middle Marsh West

1985). Artificial seagrass plots were used to precisely control the density of simulated seagrass shoots around tethered crabs (Schulman 1996, Hovel & Lipcius 2001). Plots were 0.05 m² in area and were constructed of 2 cm high sections of 25 cm diameter PVC pipe. Monofilament fishing line (80 lb test) was strung across plots at right angles, forming squares ca. 2 cm on a side within the PVC ring. Monofilament was used as a point of attachment for simulated shoots and to simulate seagrass rhizomes (below-ground structure). Simulated shoots were 50 cm sections of green polypropylene ribbon folded in 2 and tied to intersections of monofilament line. A brass snap swivel was affixed to the center of each plot so that 1 crab could be tethered in each plot on each trial day. We exposed tethered crabs to predators in plots of 7 different shoot densities: 0, 100, 200, 400, 800, 1600, and 2400 shoots m⁻².

Juvenile blue crabs were collected by dipnetting in seagrass beds and were held in outdoor running seawater flumes at the NOAA/NOS Center for Coastal Fisheries and Habitat Research in Beaufort, NC. No crab was held for >48 h. Crabs were tethered in the laboratory by affixing them to 5 cm segments of 20 lb test monofilament with cyanoacrylate glue (Pile et al. 1996). Crabs were measured (spine-to-spine carapace width, CW) to the nearest tenth of a millimeter, and acclimated to tethers in the laboratory for 24 h before being placed in the field.

Tethering may produce treatment-specific bias when habitat structure is varied around tethered organisms, because tethers may become tangled when shoots are dense but not when shoots are sparse (Peterson & Black 1994). However, no treatment-specific bias was detected between shoot density treatments for juvenile blue crabs exposed to predators in laboratory mesocosms (Pile et al. 1996, Hovel & Lipcius 2001). Additionally, we limited tethers to 5 cm in length, which allowed crabs to exhibit natural burrowing behavior in sediment, but limited the propensity for tethers to become tangled in surrounding shoots.

Harkers Island survival experiments: Beginning on 19 October 1999, we tethered 1 juvenile blue crab per plot and placed each plot in 1 haphazardly chosen small (<1 to 3 m²) or large (≥100 m²) seagrass patch at HI (Fig. 1). Crab CW ranged from 5.1 to 24.7 mm (mean ± SE = 10.4 ± 0.17 mm, N = 252 crabs). Three replicate plots of each shoot density × patch size combination were used per day for 6 d from 19 October to 3 November 1999 [N = (1 crab per plot) × (3 plots per shoot density per patch size) × (7 shoot densities) × (2 patch sizes) × (6 trials) = 252 crabs]. Plots were placed no less than 5 m apart. After 24 h, we checked crabs and categorized them as live, eaten (fragments

of the carapace remaining on the tether), missing (no parts of the carapace remaining on the tether) or molted (entire carapace remaining on the tether: Pile et al. 1996). Ten crabs that either molted on the tether or went missing were eliminated from the analysis. To test for the possibility that tethers with carapace fragments could result from sources of mortality other than predation, we placed 10 tethered crabs within predator exclusion cages for 24 h over the course of the experiment. All were alive and remained glued to tethers after 24 h.

We used 2 statistical analyses for the HI survival experiments. First, we determined how crab survival (live vs eaten) varied with shoot density, patch size, and crab CW with a multiple logistic regression (SAS 1990, Proc LOGISTIC). We used the Akaike Information Criterion to select the best fit model from competing models in which individual explanatory variables were added and removed from the analysis (Stokes et al. 1995, Cody & Smith 1997). Any model not meeting the goodness-of-fit criteria of Hosmer & Lemeshow (1989) was rejected in this and subsequent tests. Second, we followed the procedures outlined in Lipcius et al. (1998) to analyze the form of the habitat-survival function for crabs exposed to predators in small and in large seagrass patches. We used linear regression and a general functional response model to determine if the HSF was linear, hyperbolic or sigmoid in each patch size (Lipcius et al. 1998). We first calculated proportional crab survival for each patch size × shoot density combination by dividing the number of crabs remaining alive by the number of tethered crabs pooled over the 6 trial days. Proportional survival was then regressed on seagrass shoot density separately for crabs tethered in small and large patches. If the linear regression of proportional survival against seagrass shoot density was significant and residuals were random (as assessed by visually comparing standardized residuals to normal probability plots), we assumed the relation linear. If the linear regression was non-significant or residuals were non-random, we used the following model to distinguish sigmoid from hyperbolic curves:

$$Y = AX^\beta / (B + X^\beta)$$

where Y = proportional crab survival, A = asymptotic survival, X = shoot density, B = the value of X at which $Y = 0.5A$, and β = the parameter associated with the form of the HSF. 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:

$$\log(Y / [A - Y]) = \log(1/B) + \beta \log(X)$$

Thus, a linear regression of $\log(Y / [A - Y])$ on $\log(X)$

yields an estimate of β that can be tested against hypothetical values of 0 or 1 with standard *t*-tests (Chatterjee & Price 1991, Lipcius et al. 1998).

Middle Marsh survival experiments: Juvenile blue crab survival experiments were also conducted at 2 sites adjacent to Middle Marsh, ca. 2 km from HI. We tethered juvenile blue crabs (6.8 to 36.5 mm CW, mean \pm SE = 20.3 \pm 0.57, N = 168 crabs) in patchy and continuous seagrass at MME and MMW in June 2000 (Fig. 1). On 1 June 2000 we visually chose three 10 \times 10 m areas of seafloor with patchy seagrass (\leq 50% cover) and 10 \times 10 m areas with continuous seagrass (\geq 90% cover) at each site (MME and MMW). We then marked the corners of these areas with PVC poles and used a 10 m lead line to visually estimate the amount of seagrass within each of the 100 contiguous 1 \times 1 m squares within each 100 m² area. The amount of seagrass in each quadrat was placed into one of 8 categories: 0 (no seagrass), 0.1 (few, solitary shoots), 0.5 (few shoots at <5% cover), 1 (numerous shoots but <5% cover), 2 (5 to 25% cover), 3 (25 to 50% cover), 4 (50 to 75% cover), or 5 (>75% cover). From these data we calculated 2 measures of landscape structure: (1) mean seagrass cover per quadrat (sum of values for all quadrats/100) and (2) total percent cover (number of quadrats with >5% cover/100). We used separate 2-way, fixed-factor ANOVAs to test for differences in mean seagrass cover per quadrat and total percent cover between patchy and continuous seagrass and between MME and MMW at Middle Marsh.

We captured juvenile blue crabs by dipnetting at HI, and on each of 6 days between 8 and 30 June 2000 we placed one plot of each shoot density (containing a randomly chosen tethered blue crab) in continuous and patchy seagrass at MME and MMW. Zero shoot density plots could not be recovered on several occasions due to thick seagrass cover, and were eliminated from the final analysis. Plots were randomly assigned to 1 of the three 100 m² areas in patchy seagrass and continuous seagrass in each site on each day [N = (1 crab per plot) \times (1 plot per shoot density per patchiness treatment per site) \times (6 shoot densities) \times (2 patchiness treatments) \times (2 sites) \times (6 trials) = 144 crabs]. We tested how crab survival varied with shoot density, patchiness treatment, site, and crab CW with a multiple logistic regression, and determined the HSF for juvenile blue crabs in patchy and continuous seagrass as described above for experiments at HI. Tethering results from the 2 sites (MME and MMW) were combined for HSF analysis to increase replication and because the multiple logistic regression revealed no significant interactive effect of site and patchiness treatment on survival (see 'Results: Seagrass fragmentation and the blue crab HSF' below).

RESULTS

Seagrass habitat structure

At HI in October, shoalgrass biomass per unit area was ca. 10-fold higher than that of eelgrass and widgeongrass, whereas at Middle Marsh in June, eelgrass biomass per unit area was ca. 4-fold higher than that of shoalgrass, and no widgeongrass was found. Seagrass shoot density and seagrass shoot biomass per unit area did not differ significantly between small and large patches at HI (Table 1). At Middle Marsh, seagrass shoot density was significantly greater at MME than at MMW, and model error and site accounted for most of the variance in the model (67.5 and 20.8% of the total variance for error and site, respectively) whereas patchiness treatment accounted for only 7.8% of the total variance (Table 2a). Seagrass shoot biomass per unit area was significantly lower in patchy seagrass at MMW than in continuous seagrass at MMW and patchy and continuous seagrass at MME. Most of the total model variance was accounted for by the patchiness \times site interaction term and model error (46.7 and 38.1%, respectively) whereas only 12.6% of the total variance was attributable to patchiness treatment (Table 2b).

There was a significant interactive effect of patchiness treatment and site on mean seagrass cover per quadrat and on total percent cover at Middle Marsh (Table 3, Fig. 2). The effect of site on mean seagrass cover per quadrat and on total percent cover depended on the patchiness treatment: there was no difference for either dependent variable between sites in continuous seagrass, but both variables were significantly greater in patchy seagrass at MME than in patchy seagrass at MMW. For both variables, however, differences between patchiness treatments were high and accounted for most of the variance in the model. For mean seagrass cover per quadrat, patchiness treatment accounted for 76% of the variance whereas

Table 1. Seagrass shoot density (shoots m⁻²) and shoot biomass (g m⁻²) and results of *t*-tests for small vs. large seagrass patches at Harkers Island (October 1999)

	N	Mean	SE	df	<i>t</i>	p
Shoot density						
Small patches	10	3557	310	18	0.53	0.6
Large patches	10	3778	275			
Shoot biomass						
Small patches	10	41.6	6.5	18	0.16	0.8
Large patches	10	43.0	5.2			

Table 2. Results of 2-way ANOVAs and Student-Newman-Keuls tests (SNKs) for differences in seagrass shoot density (shoots m^{-2}) and shoot biomass ($g m^{-2}$) in patchy vs. continuous seagrass at MME and MMW (June 2000). Treatments are arranged in decreasing order and are not significantly different if sharing an underline. Parentheses = ± 1 standard error (SE). ω^2 = the percent of the total variance in the response variable due to each variance component

Source	df	MS ^a	F	p	ω^2
(a) Shoot density					
Patchiness	1	0.19	3.8	0.09	7.8%
Site	1	0.42	8.6	0.02	20.8%
Patchiness \times Site	1	0.12	2.5	0.15	3.9%
Error	8	0.05			67.5%
Total	11				
MME continuous	MME patchy	MMW continuous	MMW patchy		
4284 (1973)	3227 (535)	2547 (723)	887 (236)		
(b) Shoot biomass					
Patchiness	1	0.18	8.0	0.02	12.6%
Site	1	0.05	2.4	0.16	2.4%
Patchiness \times Site	1	0.61	27.7	<0.001	46.7%
Error	8	0.02			38.1%
Total	11				
MMW continuous	MME patchy	MME continuous	MMW patchy		
232.8 (52.8)	179.5 (35.9)	109.7 (20.1)	44.9 (5.7)		
^a Values were \log_{10} -transformed for analysis					

only ca. 6.7% of the variance was due to differences between sites and 9.2% was due to patchiness \times site interaction. Similarly, ca. 80% of the variance in total percent cover was due to patchiness treatments, 5.4% was due to differences between sites and 6.5% was due to patchiness \times site interaction.

Table 3. Results of 2-way ANOVAs for differences in mean seagrass cover per quadrat and mean total percent cover in patchy vs. continuous seagrass at MME and MMW (June 2000). ω^2 = the percent of the total variance in the response variable due to each variance component

Source	df	MS	F	p	ω^2
Cover per quadrat					
Patchiness	1	21.8	221.7	<0.001	76.0%
Site	1	2.2	22.4	0.002	6.7%
Patchiness \times site	1	2.76	28.1	<0.001	9.2%
Error	8	0.09			7.6%
Total	11				
Total percent cover					
Patchiness	1	9520.3	264.5	<0.001	80.7%
Site	1	675.0	18.8	0.003	5.4%
Patchiness \times Site	1	800.3	22.2	0.002	6.5%
Error	8	36.0			7.4%
Total	11				

Blue crab survival

Seagrass patch size, seagrass shoot density, and crab size (CW) all significantly influenced juvenile blue crab survival at HI (Table 4a). Crab survival was higher in small patches than in large patches, and increased with seagrass shoot density and with crab CW. The odds that a juvenile blue crab of average size would survive exposure to predators were ca. twice as great in small patches than in large patches (Table 4a, Fig. 3). At Middle Marsh, juvenile blue crab survival was significantly higher in patchy seagrass than in continuous seagrass, was higher at MMW than at MME, and was positively correlated with crab CW (Table 4b, Fig. 3). There was also a significant fragmentation type \times simulated shoot density interaction. The odds that a juvenile blue crab of average size would survive exposure to predators were ca. 1.5 times greater in patchy seagrass than in continuous seagrass at Middle Marsh, and 2.7 times greater in MMW than in MME.

Seagrass fragmentation and the blue crab HSF

At HI, proportional crab survival was significantly correlated with simulated seagrass shoot density in both small and large seagrass patches (Table 5a, Fig. 4). In

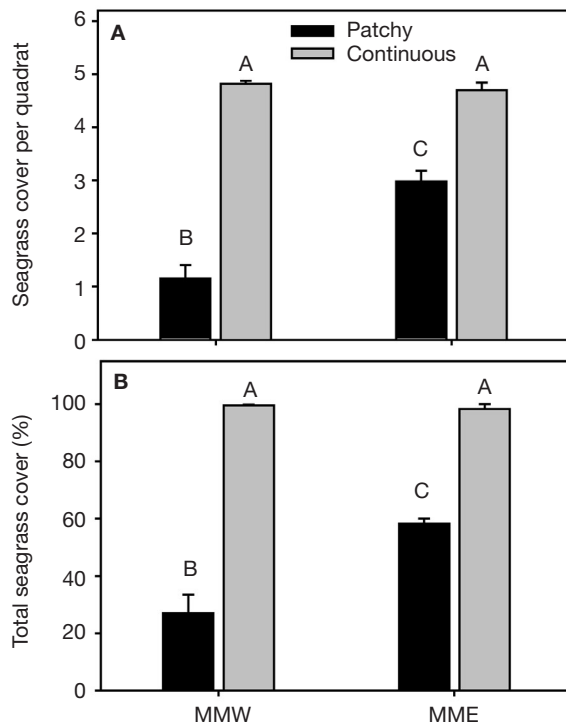


Fig. 2. (A) Mean seagrass cover per quadrat and (B) mean total percent seagrass cover (+SE) in June 2000 in patchy and continuous seagrass at Middle Marsh sites MME and MMW, North Carolina, USA (see Fig 1. for abbreviations). Unlike letters above bars denote means that were significantly different in SNK tests at $p < 0.05$

small patches, residuals were random, and a linear relationship explained 83 % of the variation in proportional crab survival. The relation was therefore deemed linear. In large patches, residuals appeared non-random, with lower than average residuals at low and high shoot densities, and higher than average residuals at intermediate shoot densities. We therefore used the general model to determine if the HSF could be considered hyperbolic or sigmoid. β for the general model was 0.14, and was significantly less than 1, and significantly greater than zero, indicating that the blue crab HSF for continuous seagrass at HI is hyperbolic (Fig. 5).

At Middle Marsh, there was no significant linear relationship between juvenile blue crab proportional survival and shoot density in patchy seagrass (Table 5b, Fig. 5). The general model also indicated no relationship between proportional survival and shoot density. However, residuals were non-random and suggested a parabolic fit to the data. The fit of a standard quadratic model to the data was not significant, but the parabolic Ricker function ($A \times X \times \exp^{(r \times X)}$; Ricker 1954) significantly fitted the data and explained 68 % of the variance in proportional crab survival (Fig. 5). Thus, in patchy seagrass at Middle

Table 4. *Callinectes sapidus*. Logistic regression results for crab survival. Numbers in parentheses are 95 % Wald confidence limits for odds ratios

Source	df	Parameter	p	Odds ratio
(a) Harkers Island				
Intercept	1	-1.85	0.003	
Shoot density ^a	1	0.0006	<0.001	1.06 (1.03, 1.10)
Patch size	1	-0.34	0.01	0.5 (0.3, 0.9)
Crab size ^b	1	0.15	0.01	1.2 (1.03, 1.3)
(b) Middle Marsh				
Intercept	1	-1.5	0.01	
Shoot density (SD) ^a	1	0.0004	0.08	0.99 (0.97, 1.008)
Patchiness (P) ^c	1	-0.68	0.01	0.67 (0.42, 0.85)
Site ^c	1	-0.51	0.007	0.36 (0.17, 0.75)
Crab size ^b	1	0.05	0.04	1.67 (1.01, 2.81)
SD \times P	1	-0.0005	0.02	0.98 (0.97, 0.99)

^aOdds ratio for survival calculated for an increase of 100 shoots
^bOdds ratio for survival calculated for an increase in crab CW of 10 mm
^cSurvival was higher in MMW than MME, and higher in patchy than in continuous seagrass (see Fig 1. for abbreviations)

Marsh, proportional crab survival increased rapidly to an intermediate value of shoot density (ca. 800 shoots m^{-2}), and then decreased with shoot density. In continuous seagrass, there was a significant linear relationship between proportional crab survival and shoot density, but residuals were non-random. β for the general model was 1.2, and was significantly greater than zero but not significantly different from 1, indicating that the blue crab HSF in continuous seagrass at Middle Marsh is hyperbolic.

DISCUSSION

Organismal survival and abundance are commonly positively correlated with habitat structural complexity. Far less is known, however, about how habitat structure at the landscape scale influences predator-prey interactions and other ecological processes, particularly in marine systems. We found that, in North Carolina seagrass beds, (1) juvenile blue crab relative survival was higher in smaller seagrass patches and in patchier seagrass landscapes than in larger patches and less fragmented landscapes, and (2) habitat structure at the landscape scale influenced relationships between juvenile blue crab survival and seagrass structural complexity (simulated shoot density). In large patches at HI, and in continuous seagrass at Middle Marsh, juvenile blue crab survival increased rapidly with shoot density at

low levels of structure but then quickly reached an upper asymptote (a hyperbolic habitat-survival function). In small patches at HI there was a positive linear correlation between crab survival and seagrass shoot density, whereas in patchy seagrass at Middle Marsh crab survival was highest at intermediate levels of shoot density (a parabolic HSF). Thus, the effects of seagrass structural complexity on epifaunal survival can only be fully understood when habitat structure at larger scales is considered.

Blue crab survival and seagrass landscape structure

Juvenile blue crab survival was greater in smaller than in larger patches at HI, and was greater in patchy seagrass than in continuous seagrass at Middle Marsh. Similarly, when seagrass structural complexity was standardized among patches, juvenile blue crab survival increased as seagrass patch size decreased in

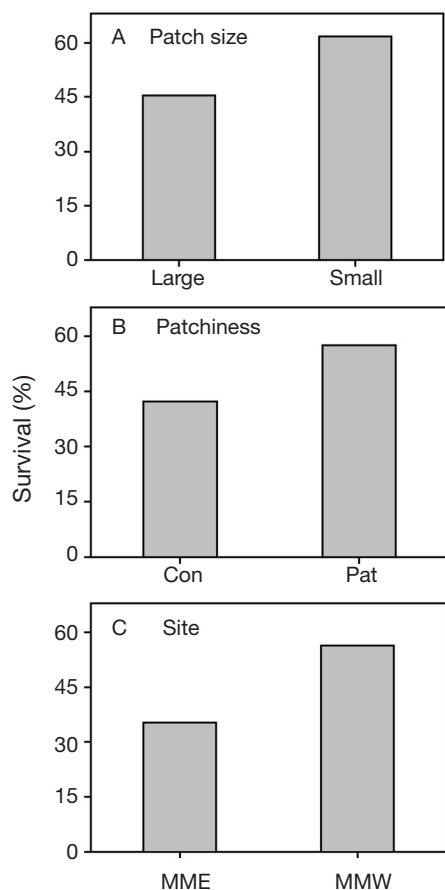


Fig. 3. *Callinectes sapidus*. Percent of tethered crabs remaining alive in June 2000 (A) in large vs. small seagrass patches at Harkers Island, (B) in continuous (Con) vs. patchy (Pat) seagrass landscapes at Middle Marsh, and (C) at MME and MMW, North Carolina, USA. For abbreviations see Fig. 1

Chesapeake Bay (Hovel & Lipcius 2001) as did juvenile rock crab *Cancer productus* survival in seagrass landscapes in Bodega Harbor, California (Hovel 2003). In Chesapeake Bay, greater juvenile blue crab survival in small patches corresponded to reduced densities of their chief predator (larger conspecifics: Moody 1994, Moksnes et al. 1997) in small patches (Hovel & Lipcius 2001). Predators such as large blue crabs may be reluctant to cross expanses of unvegetated sediment among small, isolated seagrass patches because they may be vulnerable to larger predators (e.g. birds, large fishes, and larger conspecifics: Micheli 1997, Micheli & Peterson 1999). Alternatively, predators may remain within large expanses of seagrass because their prey are abundant there. In Bodega Harbor, California, wading birds foraged primarily in large seagrass patches at low tides, which may have contributed to low juvenile *C. productus* survival in large patches (Hovel 2003).

Our results here contrast with several other studies examining relationships between organismal survival and seagrass landscape structure (bivalves: Irlandi 1994, 1997, Irlandi et al. 1995; crabs: Hovel & Lipcius 2002, Hovel 2003). In these studies, crabs, clams or scallops were exposed to predators by holding them in naturally occurring seagrass, and variation in seagrass structural complexity among patch sizes and landscape configurations may have strongly influenced trends in survival within each landscape. Indeed, Irlandi (1994) found that juvenile hard clam survival no longer varied with seagrass patch size when artificial seagrass was used to standardize shoot density between patch sizes. In Chesapeake Bay, differences in juvenile blue crab survival among seagrass patch sizes corresponded closely to differences in shoot densities among patches (Hovel & Lipcius 2002). Additionally, seagrass habitat structure is temporally dynamic at multiple spatial scales, such that even within a single landscape, the time at which experiments are conducted may strongly influence how seagrass patchiness influences survival (Hovel & Lipcius 2001; see also Villard et al. 1999 for a terrestrial analogue).

Differences in seagrass structural complexity between sites may also help explain why the odds of juvenile blue crab survival were substantially higher at MMW than at MME. Seagrass shoot density was significantly higher at MME than at MMW (Table 2a), such that our plot shoot densities were low relative to surrounding seagrass densities at MME but not at MMW. This may have increased predation rates on tethered crabs at MME if predators preferentially forage in structurally simpler areas within a patch because prey are easier to find and capture. Alternatively, the higher mean wave height and current speeds at MME compared to MMW may have reduced crab survival rates at MME, if larger waves and faster

currents increase predator mobility, more rapidly carry olfactory cues to predators, or make it more difficult for juvenile crabs to hide themselves in the sediment. Finally, it is also possible that predator abundance was simply higher at MME than at MMW during our experiments.

In a broader sense, in both marine and terrestrial systems the effects of habitat fragmentation on organismal survival and abundance are often inconsistent among landscapes (Bell et al. 2001, Hovel 2003), habitat types, and even among species or studies within landscapes (e.g. birds: Trzcinski et al. 1999, Villard et al. 1999; see review by McGarigal & Cushman 2002). Elements of marine or terrestrial landscape context such as predator species (Tewksbury et al. 1998), predator and prey life-history characteristics and behavior (Donovan et al. 1997), and the scale at which patches exist and at which studies are conducted (McGarigal & McComb 1995) all may lead to variable effects of habitat fragmentation on organismal survival and persistence (McGarigal & Cushman 2002). This suggests that elucidating the effects of habitat fragmentation on faunal abundance and survival, whether in terrestrial or marine landscapes, will require researchers to coordinate experimental techniques among studies in which repeated sampling and manipulations are conducted at several spatial scales across a variety of locations.

Seagrass fragmentation and the juvenile blue crab habitat-survival function

The HSF describes the relationship between 1 or more elements of habitat structure and organismal survival. In seagrass habitat the HSF is often positive (but see Schulman 1996) because denser, wider or longer blades (i.e. increasing structural complexity) interfere with predator search and capture of prey (Heck and Crowder 1991). In its simplest form (a linear HSF), survival increases in proportion to increases in habitat structure. A non-linear HSF is more common, however; a hyperbolic HSF indicates that at low levels of structure, organismal survival increases rapidly with small increases in habitat structure, and a sigmoid HSF indicates that a threshold level of structure must be reached before survival is enhanced.

Table 5. *Callinectes sapidus*. Habitat-survival function analyses for juvenile blue crabs in small and large seagrass patches at Harkers Island, and in patchy and continuous seagrass at Middle Marsh. * $p > 0.05$; na = not applicable; ns = not significant

Treatment	Source of variation	df	MS	p	r ²	β	$\beta > 0?$	$\beta > 1?$
(a) Harkers Island								
Small patches ^a	Regression	1	0.12	<0.01	0.83	na	na	na
	Error	5	0.20					
Large patches	Regression	1	0.15	0.02	0.63	0.14	*	ns
	Error	5	0.01					
(b) Middle Marsh								
Patchy seagrass ^b	Regression	1	12.5	<0.01	0.68	na	na	na
	Error	5	0.50					
Continuous seagrass	Regression	1	3.9	0.03	0.34	1.2	*	ns
	Error	10	0.60					
^a General model not evaluated because data met assumptions of linear model								
^b Tests for β not done because general model non-significant. Statistics refer to fit of Ricker function								

Though many studies have addressed how organismal survival varies with seagrass structural complexity, our study is the first to test whether the shape of the HSF varies with seagrass landscape structure. We found that the juvenile blue crab HSF varied between small and large seagrass patches, and between patchy and continuous seagrass landscapes. Juvenile blue crab survival increased linearly with simulated shoot density when seagrass patches were small at HI, and peaked at intermediate levels of shoot density when seagrass was patchy at Middle Marsh. However, crab survival increased rapidly with increases in simulated shoot density and then leveled out at an upper asymptote when seagrass patches were large and when seagrass landscapes were continuous. Thus, in relatively unfragmented seagrass landscapes, small increases in shoot density at low levels of habitat structure led to rapid increases in juvenile blue crab survival.

Similarly to our study, small increases in mixed algal and seagrass biomass resulted in dramatic increases in juvenile spiny lobster *Panulirus argus* survival in Bahía de la Ascensión, Mexico (Lipcius et al. 1998). Schulman (1996) found that the HSF for juvenile blue crabs in continuous Chesapeake Bay eelgrass beds varied with crab size. The HSF was hyperbolic for juvenile blue crabs of intermediate size (ca. 13 mm CW), was sigmoid for larger juveniles (ca. 20 mm CW), but was inversely hyperbolic for small juvenile blue crabs (ca. 4 mm CW). Schulman (1996) suggested that larger crabs have no cover from predators until surrounded by a relatively high number of seagrass blades, and that the inverse relationship between survival and habitat structure

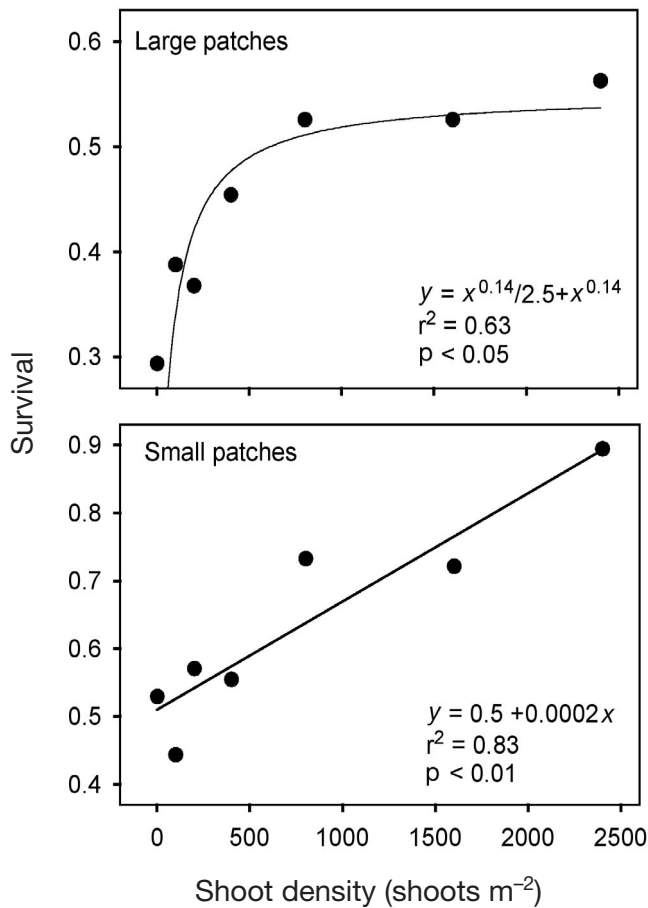


Fig. 4. *Callinectes sapidus*. Proportional survival of juvenile blue crabs vs. simulated seagrass shoot density in October 1999 in large and small seagrass patches at Harkers Island, North Carolina, USA

for small crabs may have been due to a high abundance of larger, cannibalistic conspecifics in plots of high shoot density. Though we did not measure predator abundance in our plots, juvenile blue crab abundance increases with seagrass shoot density (Williams et al. 1990, Hovel & Lipcius 2002) and thus the decreasing crab survival from intermediate to high levels of simulated shoot density in patchy seagrass at Middle Marsh may have been caused by high abundance of larger conspecifics in plots of high shoot density.

Predator behavior and predator foraging ability may change with seagrass patchiness, which may lead to variable survival and a variable HSF among landscape types. While we did not monitor predator behavior during our experiments, we speculate that if predators of juvenile blue crabs such as larger conspecifics and fishes are vulnerable to higher-order predators outside of seagrass, they would likely visit small, isolated

patches less often than larger patches, promoting juvenile blue crab survival in patchy seagrass. However, the cost of traveling to small, isolated patches (in terms of mortality risk) may cause predators to more extensively search a small seagrass patch for prey than an equivalent area of a larger seagrass patch, including areas of the small patch with moderate to high shoot density in which foraging may be relatively difficult. Thus, in small or isolated patches, prey survival should be high only at very high levels of shoot density (i.e. a linear or sigmoid HSF should be exhibited). In contrast, in continuous seagrass and in large patches, predators have a greater choice of foraging sites, and they may skip over or cursorily examine areas of high shoot density in favor of areas in which prey are more visible and easier to catch. Thus, even relatively small increases in shoot density could increase prey survival (i.e. the HSF should be hyperbolic), as was true in large patches at HI and in continuous seagrass at Middle Marsh.

Variability in the HSF among patch sizes could also have been due to differences in the ability of visually oriented predators to detect their prey. Within a large patch, a prey organism hiding among seagrass shoots is viewed in front of a 'backdrop' of other shoots that offer additional camouflage. Therefore, a small increase in shoot density could result in a disproportionate decrease in a predator's ability to see its prey. In a small patch, where prey are more likely to be near an edge, this additional camouflage may be missing and therefore a greater number of seagrass shoots may be necessary to effectively hide an organism from its predators.

Evaluating the relationship between structural complexity and organismal survival is a common theme in marine ecology, particularly in seagrass habitats (e.g. Stoner 1979, Heck & Thoman 1981, Peterson 1982, Heck & Wilson 1987; see reviews by Heck & Orth 1980, Heck & Crowder 1991, Orth 1992). Our results indicate that patchy seagrass beds hold refuge value for juvenile blue crabs (see also Hovel & Lipcius 2001), and in fact, the probability that juvenile blue crabs will survive exposure to predators is highest in small patches and in patchy seagrass beds. Both continuous and patchy seagrass landscapes therefore should be conserved. Our results also indicate that effects of structural complexity on survival depend on seagrass landscape context. Juvenile blue crab survival increased with relatively small additions of habitat structure when seagrass shoot density was low (a hyperbolic HSF) only when seagrass landscapes were continuous or when patches were large. In small patches, crab survival did not increase as rapidly with additions of structure, and in patchy seagrass at Middle Marsh,

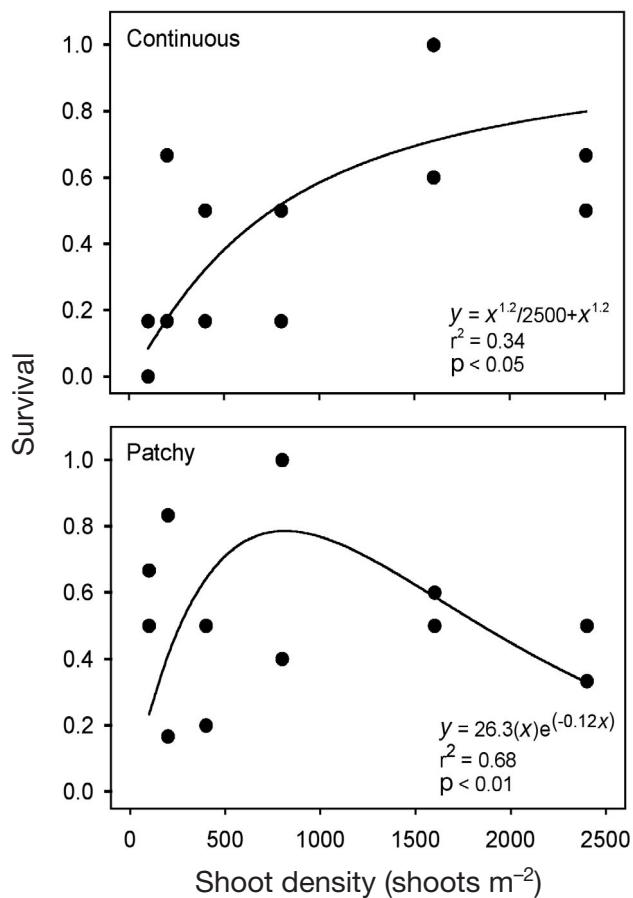


Fig. 5. *Callinectes sapidus*. Proportional survival of juvenile blue crabs vs. simulated seagrass shoot density in June 2000 in continuous and patchy seagrass landscapes at Middle Marsh, North Carolina, USA

crab survival was optimal at intermediate levels of habitat structure. All 4 experiments indicated that a threshold level of seagrass structure is not required for blue crab survival (see also Lipcius et al. 1998), at least for the sizes of juvenile blue crabs that we used in tethering experiments. Given the strong positive influence of seagrass structural complexity on blue crab density (Williams et al. 1990, Hovel & Lipcius 2002), and that blue crab mortality is density-dependent (Perkins-Visser et al. 1996, Pile et al. 1996, Moksnes et al. 1997), we postulate that juvenile blue crab survival in seagrass will primarily be dictated by interactive effects of structural complexity, landscape structure, and crab density on predator foraging behavior, rather than by the singular effects of any one of these factors. Juvenile blue crab survival in seagrass may be difficult to predict because all 3 of these factors change rapidly in seagrass landscapes.

Acknowledgements. We thank G. Thayer, W. J. Kenworthy, K. Hammerstrom, and J. Parker for support and advice over the course of the project. Funding for this research was provided by the NOAA/NOS Center for Coastal Fisheries and Habitat Research in Beaufort, NC, by way of a National Research Council Postdoctoral Associateship to K.A.H.

LITERATURE CITED

- Anderson T (2001) Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology* 82: 245–257
- Andrén H (1994) Effect of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355–366
- Bartholomew A, Diaz R, Cicchetti G (2000) New dimensionless indices of structural habitat complexity: predicted and actual effects on a predator's foraging success. *Mar Ecol Prog Ser* 206:45–58
- Bell S, McCoy E, Mushinsky H (1991) Habitat structure: the physical arrangement of objects in space. Chapman & Hall, London
- Bell SS, Brooks RA, Robbins BD, Fonseca MS, Hall MO (2001) Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. *Biol Conserv* 100: 115–123
- Bologna PAX, Heck KL Jr (1999) Differential predation and growth rates of bay scallops within a seagrass habitat. *J Exp Mar Biol Ecol* 239:299–314
- Carr M (1994) Effects of macroalgal dynamics on recruitment of a temperate reef fish. *Ecology* 75:1320–1333
- Chatterjee S, Price B (1991) Regression analysis by example. John Wiley, New York
- Cody R, Smith J, (1997) Applied statistics and the SAS programming language, 4th edn. Prentice-Hall, Upper Saddle River, NJ
- Connell S, Jones G, (1991) The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. *J Exp Mar Biol Ecol* 151:271–294
- Diffendorfer J, Gaines M, Holt R (1995) Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). *Ecology* 76:827–839
- Donovan TM, Jones PW, Annand EM, Thompson FR III (1997) Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78:2064–2075
- Fonseca MS, Bell SS (1998) Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Mar Ecol Prog Ser* 171:109–121
- Fonseca MS, Kenworthy WJ, Thayer GW (1998) Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters. National Oceanic and Atmospheric Administration Decision Analysis Series 12. NOAA, Silver Spring, MD
- Gotceitas V, Colgan P (1989) Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. *Oecologia* 80:158–166
- Graham M, Edwards M (2001) Statistical significance versus fit: estimating the importance of individual factors in ecological analysis of variance. *Oikos* 93:505–513
- Heck KL Jr, Crowder LB (1991) Habitat structure and predator-prey interactions. In: Bell SS, McCoy E, Mushinsky H (eds) Habitat complexity: the physical arrangement of objects in space. Chapman & Hall, New York, p 281–299
- Heck KL Jr, Orth RJ (1980) Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assem-

- blages. In: Kennedy VS (ed) Estuarine perspectives. Academic Press, New York, p 449–464
- Heck K Jr, Thoman T (1981) Experiments on predator–prey interactions in vegetated aquatic habitats. *J Exp Mar Biol Ecol* 53:125–134
- Heck KL Jr, Wilson KA (1987) Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. *J Exp Mar Biol Ecol* 107:87–91
- Heck KL Jr, Coen L, Morgan S (2001) Pre- and post-settlement factors as determinants of juvenile blue crab *Callinectes sapidus* abundance: results from the north-central Gulf of Mexico. *Mar Ecol Prog Ser* 222:163–176
- Hemminga MA, Duarte CM (2000) Seagrass ecology. Cambridge University Press, Cambridge
- Hixon M, Carr M (1997) Synergistic predation, density dependence, and population regulation in marine fish. *Science* 277:946–948
- Hosmer DW, Lemeshow S (1989) Applied logistic regression. John Wiley, New York
- Hovel K (2003) Habitat fragmentation in marine landscapes: relative effects of habitat cover and configuration on juvenile crab survival in California and North Carolina seagrass beds. *Biol Conserv* 110:401–412
- Hovel KA, Lipcius RN (2001) Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. *Ecology* 82:1814–1829
- Hovel KA, Lipcius RN (2002) Effects of seagrass habitat fragmentation on juvenile blue crab survival and abundance. *J Exp Mar Biol Ecol* 271:75–98
- Irlandi EA (1994) Large- and small-scale effects of habitat structure on rates of predation: how percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. *Oecologia* 98:176–183
- Irlandi EA (1997) Seagrass patch size and survivorship of an infaunal bivalve. *Oikos* 78:511–518
- Irlandi EA, Ambrose WG Jr, Orlando BA (1995) Landscape ecology and the marine environment: how spatial configuration of seagrass habitat influences growth and survival of the bay scallop. *Oikos* 72:307–313
- Irlandi EA, Orlando BA, Ambrose WG Jr (1999) Influence of seagrass habitat patch size on growth and survival of juvenile bay scallops, *Argopecten irradians concentricus* (Say). *J Exp Mar Biol Ecol* 235:21–43
- Kareiva P (1987) Habitat fragmentation and the stability of predator–prey interactions. *Nature* 326:388–390
- Lipcius RN, Eggleston DB, Miller DL, Luhrs TC (1998) The habitat-survival function for Caribbean spiny lobster: an inverted size effect and non-linearity in mixed algal and seagrass habitats. *Mar Freshw Res* 49:807–816
- Mansour R (1992) Foraging ecology of the blue crab, *Callinectes sapidus* Rathbun, in lower Chesapeake Bay. PhD thesis, College of William and Mary, Gloucester Point, VA
- McConaughy J, Johnson D, Provenzano A, Maris R (1983) Seasonal distribution of larvae of *Callinectes sapidus* (Crustacea: decapoda) in the waters adjacent to Chesapeake Bay. *J Crustac Biol* 3:582–589
- McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecol Appl* 12:335–345
- McGarigal K, McComb WC (1995) Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecol Monogr* 65:235–260
- Micheli F (1997) Effects of predator foraging behavior on patterns of prey mortality in marine soft bottoms. *Ecol Monogr* 67:203–224
- Micheli F, Peterson CH (1999) Estuarine vegetated habitats as corridors for predator movements. *Conserv Biol* 13:869–881
- Moksnes PO, Lipcius RN, Pihl L, van Montfrans J (1997) Cannibal–prey dynamics in juveniles and postlarvae of the blue crab. *J Exp Mar Biol Ecol* 215:157–187
- Moody KE (1994) Predation on juvenile blue crabs, *Callinectes sapidus* Rathbun, in lower Chesapeake Bay: patterns, predators, and potential impacts. PhD thesis, College of William and Mary, Gloucester Point, VA
- Murphey PL, Fonseca MS (1995) Role of high and low energy seagrass beds as nursery areas for *Penaeus duorarum* in North Carolina. *Mar Ecol Prog Ser* 121:91–98
- Olmi E III, Lipcius RN (1991) Predation on postlarvae of the blue crab, *Callinectes sapidus* Rathbun, by sand shrimp *Crangon septemspinosa* and grass shrimp *Palaemonetes pugio* Holthuis. *J Exp Mar Biol Ecol* 151:169–183
- Orth RJ (1992) A perspective on plant–animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. In: John DM, Hawkins SJ, Price JH (eds) Plant–animal interactions in the marine benthos. Clarendon Press, Oxford, p 147–1164
- Paton PWC (1994) The effect of edge on avian nest success: how strong is the evidence? *Conserv Biol* 8:17–26
- Perkins-Visser E, Wolcott TG, Wolcott DL (1996) Nursery role of seagrass beds: growth of juvenile blue crabs (*Callinectes sapidus* Rathbun). *J Exp Mar Biol Ecol* 198:155–173
- Peterson CH (1982) Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. *Mar Biol* 66:159–170
- Peterson CH, Black R (1994) An experimentalist's challenge: when artifacts of intervention interact with treatments. *Mar Ecol Prog Ser* 111:289–297
- Pile AJ, Lipcius RN, van Montfrans J, Orth RJ (1996) Density-dependent settler–recruit–juvenile relationships in blue crabs. *Ecol Monogr* 66:277–300
- Ricker WE (1954) Stock and recruitment. *J Fish Res Board Can* 11:559–623
- Robbins BD, Bell SS (1994) Seagrass landscapes: a terrestrial approach to the marine subtidal environment. *Trends Ecol Evol* 9:301–304
- Robinson SK, Thompson FR III, Donovan TM, Whitehead DR, Faaborg J (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990
- Rooker J, Holt G, Holt S (1998) Vulnerability of newly settled red drum (*Sciaenops ocellatus*) to predatory fish: is early-life survival enhanced by seagrass meadows? *Mar Biol* 131:145–151
- Sargent FJ, Leary TJ, Crewz DW, Krueger CR (1995) Scarring of Florida's seagrasses: assessment and management options. FMRI Tech Rep TR-1. Florida Marine Research Institute, St. Petersburg, FL
- Schulman JL (1996) Habitat complexity as a determinant of juvenile blue crab survival. MS thesis, College of William and Mary, Gloucester Point, VA
- Stokes M, Davis C, Koch G (1995) Categorical data analysis using the SAS system. SAS Institute, Cary, NC
- Stoner A (1979) Species-specific predation on amphipod crustacea by the pinfish *Lagodon rhomboides*: mediation by macrophyte standing crop. *Mar Biol* 55:201–207
- Tewksbury JJ, Heil SJ, Martin TE (1998) Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* 79:2890–2903
- Townsend EC, Fonseca MS (1998) Bioturbation as a potential mechanism influencing spatial heterogeneity of North Carolina seagrass beds. *Mar Ecol Prog Ser* 169:123–132
- Trzcinski MK, Fahrig L, Merriam G (1999) Independent

- effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecol Appl* 9:586–593
- van Montfrans J, Peery CA, Orth RJ (1990) Daily, monthly and annual settlement patterns by *Callinectes sapidus* and *Neopanope sayi* on artificial collectors deployed in the York River, Virginia. *Bull Mar Sci* 46:214–228
- Villard M, Trzcinski MK, Merriam G (1999) Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conserv Biol* 13:774–783
- Wahle RA, Steneck RS (1991) Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck? *Mar Ecol Prog Ser* 69:231–243
- Wahle RA, Steneck RS (1992) Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. *J Exp Mar Biol Ecol* 157:91–114
- Warren J (1985) Climbing as an avoidance behaviour in the salt marsh periwinkle, *Littorina irrorata* (Say). *J Exp Mar Biol Ecol* 89:11–28
- Williams A, Coen L, Stoetling M (1990) Seasonal abundance, distribution, and habitat selection of juvenile *Callinectes sapidus* (Rathbun) in the northern Gulf of Mexico. *J Exp Mar Biol Ecol* 137:165–183
- Williams AB (1984) Shrimps, lobsters, and crabs of the Atlantic coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, DC
- Wilson K, Heck KL Jr, Able K (1987) Juvenile blue crab, *Callinectes sapidus*, survival: an evaluation of eelgrass, *Zostera marina*, as refuge. *Fish Bull* 85:53–58

Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

*Submitted: October 6, 2004; Accepted: April 28, 2005
Proofs received from author(s): August 22, 2005*