Habitat quality and prey size as determinants of survival in post-larval and early juvenile instars of the blue crab *Callinectes sapidus*

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ABSTRACT: Habitat structure and prey size are important determinants in the outcome of predator-prey interactions. We investigated the role of simulated habitat type and density (simulated *Zostera marina* [hereafter referred to as '*Zostera*']: 500 and 1500 shoots m^{-2}, and simulated *Spartina alterniflora* [hereafter referred to as '*Spartina*']: 97 and 291 shoots m^{-2}) in mediating predator-prey interactions. Proportional survival during predation by the piscene predator *Fundulus heteroclitus* on 2 successive life-history stages (post-larvae and first juvenile instars) of the blue crab *Callinectes sapidus* (Rathbun), was quantified under laboratory conditions that closely approximated field conditions. We also examined the effects of juvenile crab size (equal biomass and equal numbers of 2 or 3 prey-size categories, respectively) on survival during adult *F. heteroclitus* predation in the absence of vegetation. Crab size categories included small (first juvenile instars; 2.1 mm carapace width [cw]), medium (fourth and fifth crab stage juveniles; 6.0 to 9.1 mm cw), and large (sixth and seventh stage juveniles; 9.2 to 12.6 mm cw) in the equal numbers experiments and small and medium crabs for the equal biomass experiment. Mean proportional survival was higher for both life-history stages in simulated *Zostera*, with first-instars exhibiting higher proportional survival than post-larvae at the experimental densities tested (post-larvae: no grass = 0.23, low-density grass = 0.44, high-density grass = 0.57; first-instars: no grass = 0.47, low-density grass = 0.87, high-density grass = 0.87). Mean proportional survival did not differ significantly among life-history stages in the simulated *Spartina* treatments, although proportional survival between treatments was higher for first-instars than post-larvae (post-larvae: no *Spartina* = 0.17, low-density *Spartina* = 0.18, high-density *Spartina* = 0.19; first-instars: no *Spartina* = 0.46, low-density *Spartina* = 0.43, high-density *Spartina* = 0.48). Finally, size-refuge experiments with equal numbers or biomass of prey demonstrated significant differences between each size or/and biomass category tested. Crabs exhibited increasing proportional survival with increasing crab size (small = 0.34, medium = 0.66, large = 0.97) or weight (small = 0.18, medium = 0.67) in the presence of *F. heteroclitus*, suggesting that *C. sapidus* attains a refuge in size from predation by adult *F. heteroclitus* at approximately 9.2 to 12.6 mm. Our findings suggest that the influence of habitat structure on crab survival (possibly as a function of surface area) varies with simulated habitat type, crab density and crab stage (post-larvae versus first-instar), providing additional evidence of the importance of seagrasses in the early life-history stages of blue crabs.

KEY WORDS: *Zostera* · *Spartina* · Blue crab · Post-larvae · Juvenile instars · Post-larvae · Survival

INTRODUCTION

The ability of a prey species to avoid predation is a function of a complex set of temporally variable interactions involving behavior, size and density relationships of predator and prey, and habitat quality (Main 1985, 1987, Sih 1985, 1987, Kneib 1995, Lipcius et al. 1998). The importance of habitat structure in ameliorating predation is complex (Bell et al. 1991). Structural quality associated with biological or physical attributes of

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the marine environment ranges from less complex structures, such as shell fragments or gravel (Sponaugle & Lawton 1990), to highly complex systems like seagrass beds (Heck & Crowder 1991). Such components of the habitat interact with the size and behavior of both prey and predator to ultimately determine the degree of prey survival (Paine 1976, Heck & Crowder 1991, Rooker et al. 1998a).

Various habitats in estuaries and coastal lagoons, such as seagrass beds, salt marshes, macroalgae and oyster reefs, provide biogenic structure (Marx & Herrnkind 1985, Orth & van Montfrans 1990, Sogard & Able 1991, Eggleston & Armstrong 1995, Kneib 1995, Eggleston et al. 1998, Rooker et al. 1998b). These habitats support a diverse and dense assemblage of animals, and are generally considered critical nurseries for numerous species of vertebrates and invertebrates (Boesch & Turner 1984, Kneib 1984, Orth et al. 1984, Rozas & Minello 1998, Minello 1999, Beck et al. 2001). Structural complexity is determined by morphology, biomass, density, and the spatial configuration of these structural attributes, which influences habitat value (Stoner 1980, 1982, Rader 1984, Summerson & Peterson 1984, Ryer 1988, Irlandi & Peterson 1991, James & Heck 1994, Lee & Kneib 1994, Irlandi 1995, Irlandi et al. 1995).

Salt marshes (e.g. *Spartina alterniflora*) and submersed aquatic vegetation (e.g. *Zostera marina*) are 2 major structural components in the estuarine systems of North America. Several species, including the blue crab *Callinectes sapidus*, have been linked to these habitats (Minello 1999). The life cycle of the blue crab involves ontogenetic shifts in habitat use. After hatching, planktonic larvae (zoeae) develop through 7 to 8 stages on the nearshore continental shelf, eventually resulting in the post-larva (megalopa) stage. Megalopae reinvade coastal bays and estuaries (Rabalais et al. 1995, van Montfrans et al. 1995) and settle into shallow nursery habitats such as marsh and seagrass beds (Zimmerman & Minello 1984, Orth & van Montfrans 1987, 1990, Thomas et al. 1990, Heck & Coen 1995, Kneib 1995, Morgan et al. 1996). Later-stage juveniles and adults re-distribute to different habitats based on size, sex, molt stage, salinity, and food availability (Hines et al. 1987, Mansour & Lipcius 1991).

Quantitative sampling in a variety of shallow-water habitats along the latitudinal range of the blue crab (seagrass, mud, sand, marsh creeks) has demonstrated that abundance is significantly higher in structured (both marsh and seagrass) than unstructured habitats; among vegetated habitats, abundances are generally higher in seagrass beds (Heck & Orth 1980a, Orth & van Montfrans 1987, Mense & Wenner 1989, Thomas et al. 1990, Wilson et al. 1990, Heck & Coen 1995, Orth et al. 1996), although in the Gulf of Mexico densities

can be higher in marsh than seagrass habitats (Rozas & Minello 1998). In Chesapeake Bay, such abundance relationships hold true, particularly for early-instar juvenile crabs, which are often up to 2 orders of magnitude more abundant in seagrass beds than in adjacent marsh creeks or unvegetated habitats (Orth & van Montfrans 1987).

Comparisons of first and second instar crab densities in a seagrass bed and marsh creek in Chesapeake Bay revealed an absence of these stages in the marsh creek and relatively high densities in the seagrass bed (Orth & van Montfrans 1987), even though post-larvae were found to settle on artificial substrates placed in the marsh creek (R.J.O. & J.v.M. unpubl. data). Third- and later instar crabs were increasingly more abundant in the marsh creek, although at significantly lower densities than in the adjacent seagrass bed. A reduction in the density of later-stage crabs (size range 11 to 25 mm carapace width) in the seagrass bed and increasing abundance in the marsh creek suggested that blue crabs may undergo shifts in habitat use triggered by attainment of a size refuge from predation (Orth & van Montfrans 1987) analogous to those by juvenile spiny lobster, which shift from algae to sponges and finally to coral reefs or ledges (Smith & Herrnkind 1992). Evidence from a field-tethering experiment in seagrass and adjacent unvegetated habitats which utilized first-through ninth-instar juvenile crabs demonstrated that predation rates diminished significantly between the fifth (size range 7.5 to 9.1 mm) and ninth (14.2 to 16.1 mm) juvenile instars (Pile et al. 1996).

We postulated that predation limits abundance of the earliest juvenile instars in marsh creek, and that later-stage crabs (larger than the third-instar, 4.25 mm) increase in abundance due to movement of crabs from seagrass to the marsh creek coupled with a size refuge from predation as crabs grow larger. This study addresses 2 issues: survival of post-larvae and first-instar crabs as a function of different densities of simulated habitat types (*Zostera* and *Spartina*), and the attainment of a refuge in size from predation in the absence of vegetation. Although seagrass and marsh creeks support a diverse number of predators to test these 2 issues, we chose the abundant benthic omnivore which is *Fundulus heteroclitus*, often found in both habitats.

MATERIALS AND METHODS

Animal collection. *Callinectes sapidus* post-larvae were collected from stationary plankton nets deployed during nighttime hours (Olmi 1995) from a pier located at the Virginia Institute of Marine Science, Gloucester Point. Post-larvae were collected immediately prior to

experimentation and held in aerated aquaria until use (within 48 h). First-instar and older juveniles were derived from plankton-collected megalopae that were subsequently held in the laboratory until metamorphosis to the first-juvenile instar. These were fed and grown to the size appropriate for experimentation.

Fundulus heteroclitus were collected using minnow traps placed in marsh creeks prior to conducting experiments. Fish (size range 80 to 100 mm standard length) were acclimated in aerated aquaria and fed live food from daily plankton collections supplemented with 'Purina' fish pellets. Fish were starved for 24 h prior to the initiation of each experiment. New predators were used for each experimental trial.

Laboratory experiments. All experiments described below were conducted in 160 l cylindrical fiberglass tanks (42 cm high × 68 cm wide, area of bottom = 0.36 m^2). The tank bottoms were filled to approximately 4 cm with sieved beach sand (grain size < 1.0 mm). Aeration of the tanks was adjusted to ensure a minimal water circulation considerably below the swimming capability of post-larvae (Luckenbach & Orth 1992) and juvenile crabs. Upon termination of an experiment, the tank contents were sieved through a 1.0 mm sieve and the surviving animals were enumerated. Water and sediment were replaced between each experimental trial.

Expt 1. Effects of simulated habitat type and plant density on post-larvae and first-instar crab survival: We first tested the hypothesis that proportional survival of post-larvae and first-instar crabs was positively correlated with plant density. We used simulated habitat types to eliminate the complicating effects of alternative prey on live plants or leachates from live plants that might affect prey or predator behavior (Forward et al. 1994), and mimics that were most similar to the natural habitats we were testing: *Zostera* and *Spartina*. As simulated habitat types have been used frequently in marine ecological field (e.g. Eggleston et al. 1998) and laboratory (Gotceitas & Colgan 1989, Nelson & Bonsdorff 1990, Olmi & Lipcius 1991, James & Heck 1994) research over the past 2 decades, it seemed appropriate to use simulated habitats to investigate predator-prey interactions in our laboratory experiments.

Green polypropylene ribbon was used to simulate *Zostera* leaves, while green ribbon material inserted into translucent plastic soda straws was used to simulate bases of *Spartina* marsh shoots. The green ribbon simulated the color of epiphytic algae that grow along the bases of *Spartina* plants. We did not attempt to simulate the aerial portion of *Spartina* (i.e. the leaves), because organisms are unlikely to be exposed to any but the basal area of the shoots during high tide. Straws measuring 6 mm diameter × 34 cm long were used to simulate a marsh plant stalk. While not recre-

ating all features of marsh plants, straws best mimic *Spartina*'s most obvious habitat features and are similar to the wooden dowels (6 mm diameter, 30 cm length) used by Nelson & Bonsdorf (1990) to simulate *Phragmites* habitat in their predator-prey experiments.

Two shoot-density treatments were used in the experiments to provide an ecologically meaningful comparison of natural conditions: (1) low; low-density shoots similar to natural densities, (2) high; high-density shoots and 3 times denser than in the low-density treatment. We used data from Orth & Moore (1986) for seagrass shoot density and width. *Spartina* shoot width and density were representative of plants from the York River system (5.1 mm, 44 to 432 shoots m^{-2} width and density, respectively: R. N. Lipcius unpubl. data).

Low- and high-density (3×) *Spartina* treatments comprised tanks with 35 shoots (97 shoots m^{-2}) and 105 shoots (292 shoots m^{-2}) per tank, respectively. Straws were inserted into the sand such that their tops extended above the water surface. The water depth was approximately 25 cm. The straws were placed randomly in the tanks in groups of 3, 4, or 5 straws, reflecting natural clumping of *Spartina* shoots. Low-density treatments had 3 groups of 3 straws, 4 of 4 straws, and 2 of 5 straws. These conditions were increased 3-fold in high-density treatments.

Low- and high-density (3×) *Zostera* treatments comprised tanks with 180 (500 shoots m^{-2}) and 540 shoots (1500 shoots m^{-2}) per tank, respectively. Simulated *Zostera* shoots were constructed with either 3 or 4 leaves (leaf width = 5 mm), per shoot. Low-density treatments had 108 shoots with 4 leaves and 72 shoots with 3 leaves while in high-density treatments these parameters were increased 3-fold. *Zostera* shoots were constructed by tying the polypropylene ribbon to a plastic mesh mat buried under the sediment surface; simulated shoots extended to the water surface.

Prey densities represented the high range of natural densities for early juvenile crabs (Orth & van Montfrans 1987) and post-larvae (R.J.O. & J.v.M. unpubl. data). Thirty first-instar crabs and 60 post-larvae were used in the respective experiments.

We used 16 tanks in an experimental trial to test either simulated seagrass or marsh structure, with 4 tanks each randomly assigned to high-density, low-density, or no grass treatments, and controls (devoid of fish predators). Treatment assignments were re-randomized among tanks for each trial. Prior to each experiment, the tanks were filled with 1 µm-filtered estuarine water from the York River and allowed to acclimate to room temperature (approx. 22 to 24°C) for 24 h. Four separate trials (n = 16 for each of the 4 treatments) were conducted using post-larvae or first-instar crabs in simulated *Zostera*, while 2 trials (n = 8 for each of the 4 treatments) were conducted in the simulated
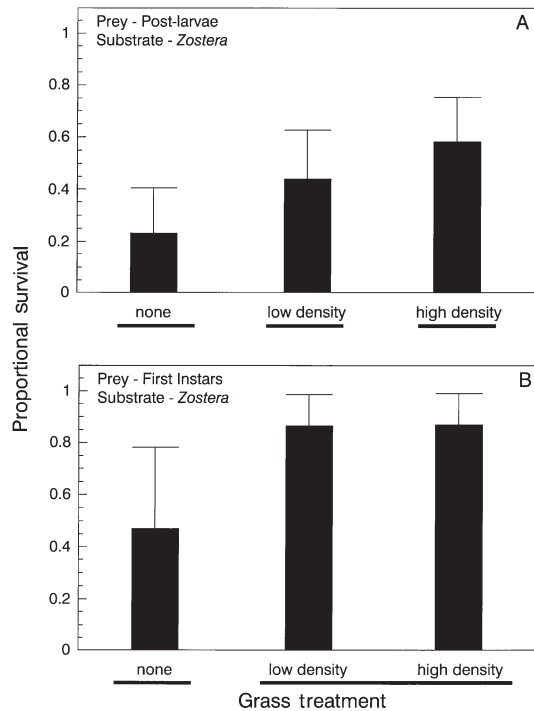
Fig. 1. *Callinectes sapidus.* Proportional survival (mean ± 1 SD) of (A) post-larvae, and (B) first-instar blue crabs in the low- and high-density and in the no *Zostera* treatments. Horizontal lines below treatment designations indicate those treatments that are statistically similar

Spartina habitat. All experiments were conducted between 7 September and 4 October, 1988.

Experimental trials were commenced at 17:30 h by placing either post-larvae or first-instar crabs into the tanks. Two *Fundulus heteroclitus* were placed in fine, plastic mesh baskets suspended in the tank overnight to allow predators and prey to acclimate to the experimental conditions while concurrently preventing the fish from foraging. The following morning at 05:00 h, the fish were released from the baskets and overhead fluorescent lights turned on at 06:00 h. The fish were allowed to forage for 8 h until termination of the experiment at 14:00 h. Substrates were carefully removed from the tanks at the conclusion of each experimental trial and rinsed in fresh water to ensure the collection of all remaining prey; fish were removed by dipnetting.

Exp 2. Crab-size effects on survival without habitat structure; equal numbers versus equal biomass: We tested the hypothesis that juvenile *Callinectes sapidus* attain a size refuge from predation by quantifying effects of *Fundulus heteroclitus* predation on different sizes of juvenile crabs in bare sand. Young-of-the-year crabs in 3 size classes, comprising 30 small (first-instar crabs 2.5 mm in carapace width), 30 medium (6.0 to 9.1 mm wide crabs equivalent to fourth- and fifth-in-

star juveniles), and 30 large (9.2 to 12.6 mm wide individuals which reached the sixth- and seventh-juvenile instar) crabs were used as prey in 3 experimental trials. Crabs from the individual size categories were randomly assigned to 1 of 9 tanks, with each tank having only 1 size class; 2 predators were later added after acclimation procedures similar to those described above. Sampling protocols for this experiment ('equal numbers experiment') also followed those described above.

Subsequently, we tested the effect of predation on prey survival by using either small or medium crabs in separate treatments with the same total crab biomass (equal biomass experiment). We did not use large crabs because a high proportion of these survived in the equal numbers experiments. For both treatments, 3 replicates, utilizing either 80 small crabs or 10 medium crabs, were randomly assigned to 1 of 6 tanks containing sand substrate, to which 6 *F. undulus heteroclitus* were added after acclimation, as described earlier.

Statistical analysis. Two sets of analyses were run as follows:

Survival of post-larvae and first-instars in simulated Zostera and Spartina: After angular transformation to meet the assumption of homogeneity of variance, statistical analyses were made of the proportional survival of crabs. Analysis of variance was performed using simulated grass density as the main effect and trial as a blocking factor. Four separate analyses examined each combination of grass type (simulated *Zostera* and *Spartina*) and prey type (post-larvae and first-instar crabs). Ryan's *Q* multiple-range test was used to make comparisons between levels of the main effect.

Survival under conditions of equal numbers and equal biomass of prey: Statistical analyses were performed on survival determined as the proportion of prey recovered from each experimental trial. Analysis of variance used prey size as the main effect and trial as a blocking factor. Separate analyses were made for each experiment (equal numbers and equal biomass). Ryan's *Q* multiple-range test was used to make comparisons between levels of the main effect in each experiment.

RESULTS

Survival of post-larvae and first-instars in simulated *Zostera* and *Spartina* trials

The proportional survival of post-larvae and first-instar crabs in the no-grass treatments for the simulated *Zostera* and *Spartina* tests was similar. This suggests that the following results were a function of simulated vegetation type and density.
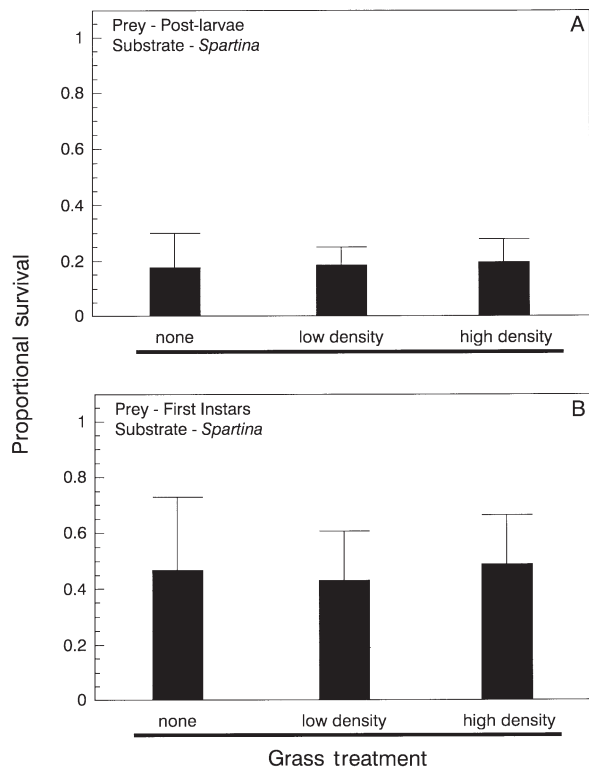
Fig. 2. *Callinectes sapidus.* Proportional survival (mean ± 1 SD) of (A) post-larvae, and (B) first-instar blue crabs in the low- and high-density and in the no *Spartina* shoot treatments. Horizontal lines below treatment designations indicate those treatments that are statistically similar

In the simulated *Zostera* trials, proportional survival of post-larvae differed significantly among grass-density treatment levels (Fig. 1A) ($F = 34.30$, df = 2,15, p = 0.0001). Survival was highest in the high-density grass (0.57) treatment, intermediate in the low-density (0.44) treatment, and lowest in the no-grass treatment (0.23).

The proportional survival of first-instar crabs also differed significantly among grass-density levels in the simulated *Zostera* trials (Fig. 1B) $F = 21.31$, df = 2,15, p = 0.0001), with survival in low-density grass (0.87) similar to that in high-density treatments (0.87) but differing significantly from the no-grass treatment (0.47). Survival of crabs in the controls averaged 0.96 for all simulated *Zostera* trials.

In the simulated *Spartina* treatments, proportional survival of both post-larvae and first-instar crabs did not differ significantly among shoot-density treatment levels (Fig. 2) (post-larvae: $F = 0.21$, df = 2,15, p = 0.8111; first-instar crabs: $F = 0.12$, df = 2,15, p = 0.8870). Survival in the no-, low- and high-*Spartina* shoot treatments was 0.17, 0.18, and 0.19 for post-larvae, and 0.46, 0.43, and 0.48 for first-instar crabs, respectively.

Crab survival in the controls averaged 0.97 for all simulated *Spartina* trials.

Survival under conditions of equal numbers and equal biomass of prey

The proportional survival of crabs differed significantly among the 3 size classes in the equal numbers experiment (Fig. 3A) ($F = 17.60$, df = 2,8, p < 0.0001). Survival was greatest for large crabs (0.97), lower for intermediate-sized crabs (0.66), and lowest for small crabs (0.34). The survival of crabs in the controls averaged 0.97 for all 3 sizes.

In the equal biomass experiments, proportional survival differed significantly (Fig. 3B) ($F = 14.77$, df = 1,5, p = 0.018) between small and medium-sized crabs being greatest for the medium-sized class (0.67) and lowest for the small-sized class (0.18). Proportional survival of crabs in the controls averaged 0.93 and 0.96 for the medium and small crabs, respectively.
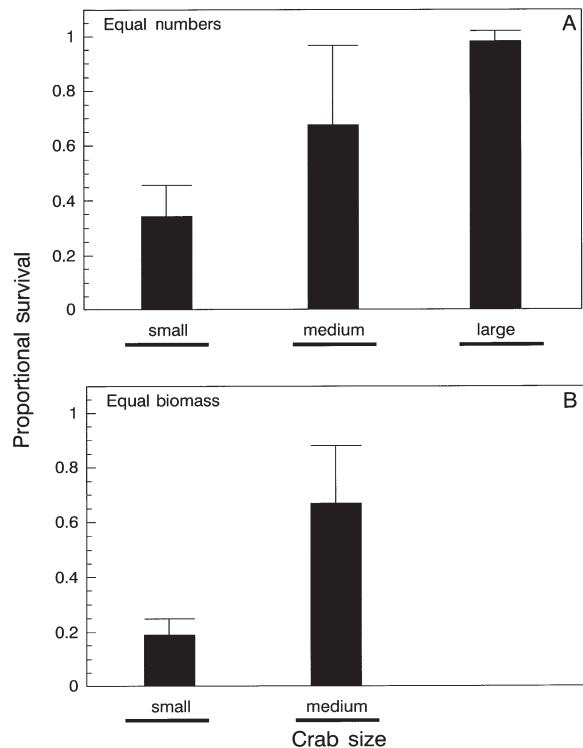

Fig. 3. *Callinectes sapidus.* Proportional survival in (A) equal numbers experiment for 3 different crab sizes (small = 2.5 mm; medium = 6.0 to 9.1 mm; large = 9.2 to 12.6 mm), and (B) equal biomass experiment for 2 different crab sizes (small = 2.5 mm; medium = 6.0 to 9.1 mm). Horizontal lines below treatment designation indicate those treatments that are statistically similar

DISCUSSION

Differential survival of early life-history stages of the blue crab appears to depend upon both life-history stage (post-larvae vs first-instars) and habitat, thereby supporting earlier perspectives on habitat-specific size distribution patterns documented in nature (Orth & van Montfrans 1987). Whereas our findings corroborate those of other predator-prey investigations regarding the importance of habitat structure and prey size as determinants of prey survival (Heck & Crowder 1991, Rooker at al 1998a, Stunz & Minello 2001), we also have demonstrated that life-history stage significantly influences predator-prey dynamics.

Although simulated seagrass reduced predation in both post-larvae and first-instar crabs, no refuge was afforded crabs by the simulated marsh shoots for either life-history stage. In addition, proportional survival in the simulated seagrass treatments was higher than in the simulated marsh treatments for each of the 2 plant-density treatments. The absence of any refuge in the simulated marsh structure was surprising, but may in
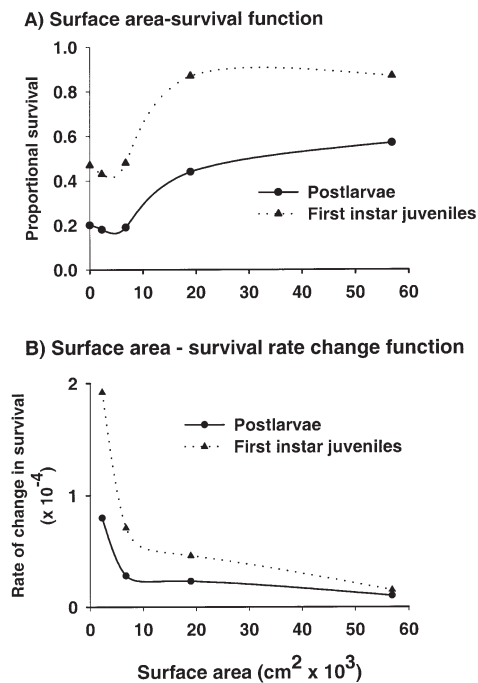

Fig. 4. *Callinectes sapidus.* Post-hoc analysis of (A) survival and (B) survival rate change of post-larvae and first-juvenile instars as a function of treatment surface area (sensu Lipcius et al. 1998). Prey survival is directly related to increased surface area, whereby the rate of change in survival (B, first derivative) decreases with increasing surface area and converges at the highest value tested. (Note that in A, control survival at a surface area of 0 falls on the *y*-axis followed by the 2 *Spartina* and *Zostera* surface area values, respectively; these data are confounded by treatment: see 'Discussion')

part explain some of the abundance patterns noted in our field sampling. While first-stage instars were generally abundant in the seagrass habitat, we rarely found them in the marsh creek habitat (Orth & van Montfrans 1987). Although post-larvae are known to enter the marsh area we sampled on nighttime flood tides (R.J.O. & J.v.M. unpubl. data), neither post-larvae nor early juvenile stages were found in pit traps deployed among *Spartina alterniflora* shoots on the marsh surface. The absence or paucity of these life-history stages in *S. alterniflora* marshes may be due to increased risk of predation in these habitats. Thomas et al. (1990) and Rozas & Minello (1998) also found fewer small crabs in marsh habitats compared to nearby seagrass beds.

The differences in surface area between simulated seagrass and marsh may be a confounding influence that could also explain some of the differences in proportional survival. We attempted to reproduce natural plant densities in our experimental treatments, although the total surface area of *Spartina*, even in the highest-density treatment, was approximately 3 times lower than that simulated by the low density *Zostera* treatment. Prey survival appears to be a function of quantifiable habitat structure such as biomass (Lipcius el al. 1998) or surface area. The first derivative of the relationship illustrates the consequences of predator-prey dynamics (Lipcius et al. 1998). A post-hoc examination of our results suggests that the surface area of various treatments may have influenced survival of both post-larvae and first-instar juvenile crabs (Fig. 4). Proportional survival was low for post-larvae (approx. 0.20) in the 3 lowest surface area treatments (0, 2244, and 6731 cm^2), increasing by more than 2-fold (0.44 and 0.57) in the highest surface-area treatments (18 965 and 56 894 cm^2), although these results were confounded by habitat type (low survival was associated with the low surface area of the simulated *Spartina* treatments, and higher survival with the increased surface area of the simulated *Zostera* treatments) (Fig. 4A).

Although the same treatment biases apply to first-instar crabs, these displayed a similar relationship with lowest survival (0.43 to 0.47) in the 3 lowest surface area (zero and *Spartina*) treatments and an almost 2-fold increase in survival (0.87) in the highest density *Zostera* treatments (Fig. 4A). Survival of both post-larvae and first-instar juvenile crabs followed a similar pattern, although juvenile crabs exhibited a higher overall survival with increasing surface area than did post-larvae (Fig. 4A). Furthermore, the rate of change in survival for both post-larvae and first-instar juvenile crabs decreased with increasing surface area and converged at the highest surface area tested (56 894 cm^2: Fig. 4B). These data suggest a possible threshold effect of surface area on survival (Heck & Orth 1980b, Got-

ceitas & Colgan 1989, Nelson & Bonsdoff 1990, Heck & Crowder 1991), although definitive resolution of such patterns awaits more experimentation.

Despite the absence of a refuge benefit for post-larvae and first-instar crabs in the simulated marsh plants in the present study, blue crabs are abundant both as post-larvae and juveniles in marshes along the Atlantic and Gulf coasts, where seagrasses are absent or rare (e.g. South Carolina [Mense & Wenner 1989], Georgia [Wrona et al. 1995], Louisiana [Zimmerman & Minello 1984]). Recent studies suggest that factors other than a refuge from predation may be important in determining prey abundances, e.g. density-dependent processes, marsh physiography, various physical factors (e.g. frequency and duration of tidal inundation) and their biological interactions (Kneib 1984, 1995, Zimmerman & Minello 1984, Orth & van Montfrans 1990, Rozas & Minello 1998, Minello 1999, Cicchetti & Diaz 2000). However, in experimental mesocosms, Stunz & Minello (2001) found that more structurally complex habitats such as oyster shell and seagrasses provided young red drum *Sciaenops ocellatus* with more protection than did *Spartina alterniflora*. Perhaps features of structure such as surface area are the contributing factors in the refuge value of various habitats for associated species.

On sand bottoms, the proportional survival from predation by *Fundulus heteroclitus* increased with increasing crab size in both the equal numbers and equal biomass experiments. A size refuge was attained at about 12 to 15 mm carapace width (sixth- and seventh-instar crabs), a size refuge that is smaller than that postulated earlier (Orth & van Montfrans 1987) or indicated by field-tethering experiments (Pile et al. 1996). However, our results are based on the restricted conditions imposed by the experimental laboratory setting, whereby 1 predator species with a limited gape was allowed to feed on 3 size categories of blue crab prey in the absence of a structured habitat. We would expect the size at which a prey attains a refuge from natural predation to be a function of the foraging strategy and gape size of the predator (Heck & Orth 1980b, Ryer 1988), behavioral responses of the prey in the presence of the predator (Main 1985, 1987), and characteristics of the habitat (e.g. degree of fragmentation [Hovel & Lipcius 2001], distance from shoreline or other habitats such as marsh [Micheli & Peterson 1999, Raposa & Oviatt 2000], and aspects of habitat structure, e.g. leaf width, biomass, or surface area [Ryer 1988, Lipcius et al. 1998, Rooker et al 1998a, Attrill et al. 2000]). Rooker et al. (1998a) found mortality rates for juvenile red drum lower in a seagrass habitat than over bare sand, and that mortality from predation decreased with increasing prey size in both habitat types.

Olmi & Lipcius (1991) found no effect of simulated *Zostera marina* on the survival of blue crab post-larvae in the presence of both sand shrimp *Crangon septemspinosa* and grass shrimp *Palaemonetes pugio*. The lack of effect may have been the smaller containers used by Olmi & Lipcius compared to those used in our experiments (0.06 m² vs 0.36 m²), the relatively longer experimental period (40 h vs 8 h), and the lower simulated *Zostera* shoot density (145 shoots m⁻² [surface area = 175 cm²] vs 500 shoots m⁻² [surface area = 18 965 cm²]), coupled with differences in the foraging strategies of the predators used.

Factors affecting the survival of early juvenile blue crabs may be similar to those influencing the survival and distribution of other species with complex life cycles (Roughgarden et al. 1988) exhibiting strong swimming capabilities. Pueruli (post-larvae) of the spiny lobster *Panuliris argus* settle in structurally complex macroalgae, remain there for several months while foraging, and thereafter shift to small crevices or other cover during daytime (Marx & Herrnkind 1985, Herrnkind & Butler 1986, Marx 1986). Algal-dwelling juveniles are extremely susceptible to predation, while slightly larger juveniles emerging from the settlement habitat attain a partial size refuge from predation (Herrnkind & Butler 1986, Smith & Herrnkind 1992) similar to that seen for blue crabs. Dungeness crabs *Cancer magister*, which recruit into oyster shells as post-larvae from offshore plankton and have strong swimming abilities, may exhibit similar ontogenetic shifts once they have gained a refuge in size in oyster-shell areas (Fernandez et al. 1993, 1994, Eggleston & Armstrong 1995).

Our experiments provide additional evidence for the importance of seagrasses in the survival of post-larval and juvenile blue crabs, possibly as a result of increased surface area (Stoner 1980, Stoner & Lewis 1985). For the blue crab, the value of seagrass as a refuge may be restricted to a relatively narrow range of crab sizes (in this study from the post-larvae to the first-instar juvenile). If surface area is important, then management efforts should focus on increasing habitats that provide the greatest surface area to benefit associated fauna. However, other structural features of seagrassess (e.g. blade width: Ryer 1988, Rooker et al. 1998a) have also been shown to influence the survival of other animals, so multiple features of habitat complexity may need to be considered in habitat protection and enhancement programs. If vegetated areas (or other structured habitats featuring similar levels or types of complexity) comprise higher quality refuges producing disproportionately greater numbers of individuals that enter the adult population relative to other habitats (i.e. the concept of the nursery area defined by Beck et al. 2001), management efforts should focus on implementing strategies to preserve and/or enhance these nursery habitats and the extrinsic variables (e.g. water quality: Dennsion et al. 1993) that ultimately determine their long-term survival.

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