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AJ Pile
Virginia Institute of Marine Science

R Lipcius
Virginia Institute of Marine Science

J Van Montfrans
Virginia Institute of Marine Science

R J. Orth
Virginia Institute of Marine Science

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DENSITY-DEPENDENT SETTLER–RECRUIT–JUVENILE RELATIONSHIPS IN BLUE CRABS[1]

ADELE J. PILE, ROMUALD N. LIPCIUS, JACQUES VAN MONTFRANS, AND ROBERT J. ORTH
The College of William and Mary, School of Marine Science, Virginia Institute of Marine Science, Gloucester Point, Virginia 23062 USA

Abstract. Current theory on the population dynamics of marine species with complex life history patterns posits that a suite of physical and biotic forces (e.g., habitat structure and density-dependent predation or emigration) control survival and abundance in early life history, particularly after settlement. We have conducted a long-term sampling effort accompanied by a series of field and laboratory experiments examining the joint effects of habitat type, body size, and population density upon abundance and survival of early juveniles of the blue crab, *Callinectes sapidus.* In addition, the chance occurrence of a tropical storm during one set of experiments provided an opportunity to assess the impact of a physical disturbance upon newly settled blue crab survival and abundance. In the 10-yr sampling effort, we quantified relationships between sequential life history stages (juvenile crab instars) in seagrass beds, the initial nursery habitat for blue crabs in the lower Chesapeake Bay. Inter-instar relationships were defined as the densities of larger instars as dependent on the densities of smaller instars. Inter-instar relationships for the youngest instars are described by hyperbolic functions until crabs begin to emigrate to unvegetated habitats at approximately the fifth instar. Inter-instar relationships between crabs larger than the fifth instar and smaller crabs become either parabolic or linear functions and decay as the number of instars between sequential life history stages increases. While both the hyperbolic and parabolic functions are indicative of populations regulated by density-dependent processes, either predation or emigration, the decay in the functions describing the inter-instar relationships for crabs larger than the fifth instar indicates that the suite of processes regulating this segment of the population changes qualitatively.

In laboratory and field experiments, the effects of vegetated and unvegetated habitats and size-specific predation on newly settled juveniles were tested. Tethering was used to quantify relative rates of predation, and a laboratory study was conducted to determine if tethering induced treatment-specific bias. We found no statistically significant interactions between the tethering treatment and the factor treatments of crab size and habitat during the laboratory study, indicating that tethering did not produce treatment-specific bias. Thus, tethering provided a relative measure of predation that allowed comparisons between treatments of habitat and crab size on crab survival. In both laboratory and field experiments, survival was significantly higher in vegetated habitats and with increasing size until the ninth instar, when survival did not differ by habitat. This difference explains the dispersal from vegetated to unvegetated habitats that occurred between the fifth and seventh instars. In addition, survival of all crabs was significantly increased both during and after Tropical Storm Danielle compared to pre-storm conditions.

A model is developed that describes juvenile survival as a function of crab size and habitat type. Survival curves in both habitats are represented by similar sigmoid functions with survival higher in vegetated habitats. Subsequently, the survival of newly settled blue crabs is likely dependent on the availability of complex habitat. Thus, a suite of biotic and physical processes, both density-dependent and density-independent, control the early life history after settlement for the blue crab.

Key words: blue crabs; Callinectes sapidus; *Chesapeake Bay; experimental bias; predation; recruits; settlers; tethering; tropical storms.*

INTRODUCTION

Ecologists have long tried to understand the causes of fluctuations in populations and define the processes mitigating these changes (e.g., Krebs et al. 1995). Population fluctuations are basically losses or additions to the population and result from mortality (losses), reproduction (additions), or migration (losses and additions). The functions that describe the relationships of abundance between subsequent life history stages within a population can have substantial consequences on the population. These relationships are either linear or exponential functions and are typically characterized using linear regression (Real 1977, 1979, Holm 1990). The characterization of these functions is essential to

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understanding population dynamics since the major difference between them is that exponential population models have more extensive regions of stability than models based on linear declines (May and Oster 1976, Bellows 1981).

A more comprehensive approach to understanding the population dynamics of organisms with complex life history patterns hypothesizes that stochastic forces and density-dependent processes jointly regulate populations during various phases of the life history (Paulik 1973, Fogarty and Idoine 1986, Lipcius and Cobb 1994). Such theory postulates that larvae are primarily influenced by stochastic variation (e.g., meteorological or oceanographic processes) resulting in density-independent survival and dispersal, whereas juveniles and adults are regulated by density-dependent processes such as predation and emigration. In general, relationships representative of density-dependent processes will have an exponential, as opposed to linear, decline as a function of density.

Recruitment is a critical period in the life history of marine organisms, with survival of early juveniles linked to adult populations and mediated by processes such as competition, predation, and availability of suitable habitat (e.g., Connell 1961*a*, *b*, Paine and Levin 1981, Roughgarden et al. 1988). Researchers define recruitment as the survival of individuals that settle to an arbitrarily selected point. This results in two distinct life history phases during the recruitment process: settlers and recruits. In organisms with pelagic larvae, settlers are the first adult-like form inhabiting the adult environment until they have reached some arbitrary post-settlement time period defined by the researcher, and, thereafter, become recruits.

Research on these processes have focused on barnacles (Connell 1985, Raimondi 1990, Sutherland 1990, Menge 1991), reef fishes (Jones 1987*a*, *b*, Forrester 1990, 1995), and a handful of other sessile benthic invertebrates (Keough and Downes 1982, Keough 1986, Roegner 1991). In a majority of these studies, researchers have found that density-independent processes affect survival of recruits to adults. In general, researchers have found that recruit–adult relationships are density-independent, although in a single study of barnacles, workers found a settler–recruit relationship to be density-dependent (Raimondi 1990). While in studies of reef fish density-dependent relationships have been found, they are for recruit–juvenile–adult relationships (Jones 1987*a*, *b*, Forrester 1990, 1995). Connell (1985) most accurately points out that there are few available data that accurately distinguish between settlers and recruits and are relevant to their relationships.

The blue crab, *Callinectes sapidus*, is a marine and estuarine species with a complex life history characterized by ontogenetic habitat shifts. Within Chesapeake Bay, adult females migrate to the bay mouth where larvae are released from June to mid-September (Van Engel 1958, McConaugha et al. 1983, Provenzano et al. 1983). Larval development through seven or eight zoeal stages lasts ≈4 wk and occurs on the continental shelf (Costlow and Bookhout 1959, McConaugha et al. 1983, Epifanio et al. 1989) prior to re-invasion of the estuary by the megalopae (i.e., postlarvae) in summer and fall (van Montfrans et al. 1990). The initial settlement and nursery habitat for postlarvae and young juvenile blue crabs is seagrass in the Chesapeake Bay (Heck and Thoman 1984, Orth and van Montfrans 1987), while other complex habitats, such as marshes, are utilized in other regions of the crabs' extensive range (Orth and van Montfrans 1990, Fitz and Wiegert 1991). Newly recruited juveniles are found at highest densities in seagrass beds and are very rarely found in unvegetated habitats until about the third through fifth juvenile instars (Orth and van Montfrans 1987). In crustaceans such as the blue crab, the population is composed of various instars reflecting the discrete increases in organismal size due to periodic shedding of the exoskeleton. For this study, a settler is defined as the first instar crab, recruit at the third instar, and juvenile after the fifth instar until sexual maturity. Fifth-instar crabs are found in moderate densities in both vegetated and unvegetated habitats, whereas by the time the crabs have reached the ninth juvenile instar, between 18–20 mm spine-to-spine carapace width, they have dispersed widely and are most abundant in unvegetated habitats (Orth and van Montfrans 1987). Larger juvenile crabs generally inhabit shallow-water, lower salinity habitats devoid of vegetation, and are partitioned by sex, molt stage, and size (Hines et al. 1987), whereas adults utilize a range of habitats, both estuarine and marine (Milliken and Williams 1984).

In ecosystems with vegetation, newly settled postlarvae and young juveniles of the blue crab are found mainly in vegetated habitats, suggesting that they either select these habitats or do not survive in unvegetated habitats. Thus, in the seagrass beds of the lower Chesapeake Bay the abundance of larger crabs will be dependent on the abundance of the smaller instars. We therefore consider seagrass beds to be a black box, in which additions come from immigration due to settlement of larvae that metamorphose into first-instar crabs (settlers) or immigration by recruits and juveniles, with losses occurring due to mortality and emigration to other habitats.

Structurally complex habitats are generally characterized by diverse assemblages comprising an abundance of small individuals or species. In shallow marine environments, these abundance patterns often are a result of differential predation (Woodin 1978, Sih et al. 1985) or evolutionary selection due to predation pressure (Leber 1985, Main 1987), both for small organisms such as amphipods (Ryer 1988, Hacker and Steneck 1990) and the juveniles of larger benthic and demersal species (Heck and Thoman 1984, Kneib 1987, Wahle and Steneck 1992). Juveniles that utilize these nursery habitats often exhibit a shift in habitat due either to a relative refuge in size from predation (Paine 1966), or to a decline in effectiveness of predation refuge afforded by the structurally complex habitat as animal size increases (Eggleston et al. 1990). Concurrent with the increase in animal size, animals must either compete for a limited number of appropriately scaled refugia, emigrate to suitable habitat, or reduce growth until a suitable habitat is available (Caddy 1986). Distinguishing between density-dependent and density-independent relationships is further compounded if mortality is caused by a growth-related function such as space limitation (Bertness 1989). Typically these organisms inhabit a variety of habitats as part of a complex life history (Roughgarden et al. 1988, Lipcius and Cobb 1994).

In this study, we have determined the instar at which juveniles depart vegetated habitats by (1) determining the settler–recruit–juvenile relationships using a function-fitting approach based on 10 years of data on blue crab abundance in a nursery habitat in the Chesapeake Bay and (2) identifying potential density-dependent mechanisms governing loss of crabs in the nursery habitat by experimentally testing the effects of crab density, crab size, and habitat complexity on predation-induced mortality in field and laboratory experiments. Moreover, we demonstrate that tethering does not produce treatment-specific bias, and is useful in quantifying relative rates of predation-induced mortality in newly settled blue crabs. Finally, Tropical Storm Danielle traversed the mid-Atlantic coast during the field experiments, allowing for the serendipitous assessment of the storm's effect on predation-induced mortality and distribution of newly settled blue crabs.

Materials and Methods

Study sites

Benthic samples were collected from 1983 to 1992 in Brown's Bay, located north of the mouth of the York River, a tributary of lower Chesapeake Bay (Fig. 1). Field tethering experiments were performed at replicate locations within the York River: at the Goodwin Islands, located on the south shore of the York River; and near Guinea Marsh, located on the north shore (Fig. 1). Both sites are characterized by dense beds of eelgrass, *Zostera marina,* and widgeongrass, *Ruppia maritima,* with adjacent unvegetated areas of muddy sand. Tidal range is generally 0.8–1.0 m and underwater visibility 1–2 m. Water height was taken at the Ferry Pier of the Virginia Institute of Marine Science (VIMS), The College of William and Mary, Gloucester Point, Virginia. The pier is located ≈12 km upstream from the York River mouth (Fig. 1).

Field experiments were conducted 21–28 September 1992. During 23–26 September, Tropical Storm Danielle moved along the central Atlantic coast from southeast of Cape Hatteras, North Carolina, made landfall on the Delmarva Peninsula, and then moved inland towards Pennsylvania (Fig. 2), affecting both the Goodwin Islands and Guinea Marsh locations. This disturbance caused a storm surge of 0.81 m in Norfolk, Virginia, located south of the study site within Chesapeake Bay (National Hurricane Center Preliminary Report 1992), and 1.5–2.5 m waves at both York River locations. This period also coincided with astronomical high tides, increasing tidal range an additional 1.0 m. Underwater visibility decreased to 0 m at the field locations.

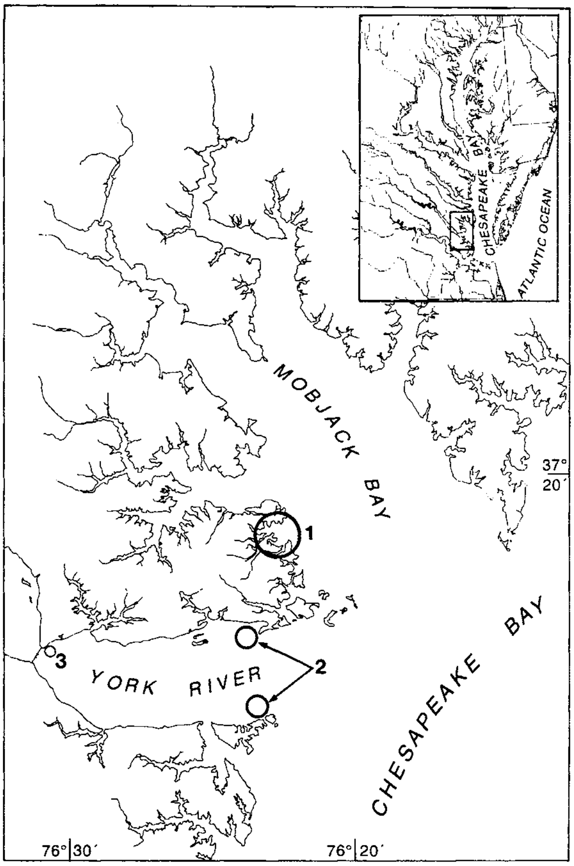

FIG. 1. Map of the field sites: 1 indicates Brown's Bay, the location of the long term benthic sampling; 2 indicates Goodwin Islands and Guinea Marsh, the locations of field tethering experiments; and 3 indicates Virginia Institute of Marine Science, the location of blue crab collection and water height measurements.

Benthic sampling

Macrobenthos were sampled in Brown's Bay from 1983 through 1992 using a suction dredge apparatus equipped with 500-μm mesh collection bags (Orth and van Montfrans 1987). During 1983 through 1989, six 3.0-m^2 (1.94 m diameter) cylindrical drop nets were haphazardly deployed at low tide in areas of 100% vegetation coverage, suctioned for 10 min, and dipnetted with a 1.2-mm mesh net for 5 min. Nets were deployed throughout the 98-ha grassbed. Efficiency studies modified the sampling protocol from 1990

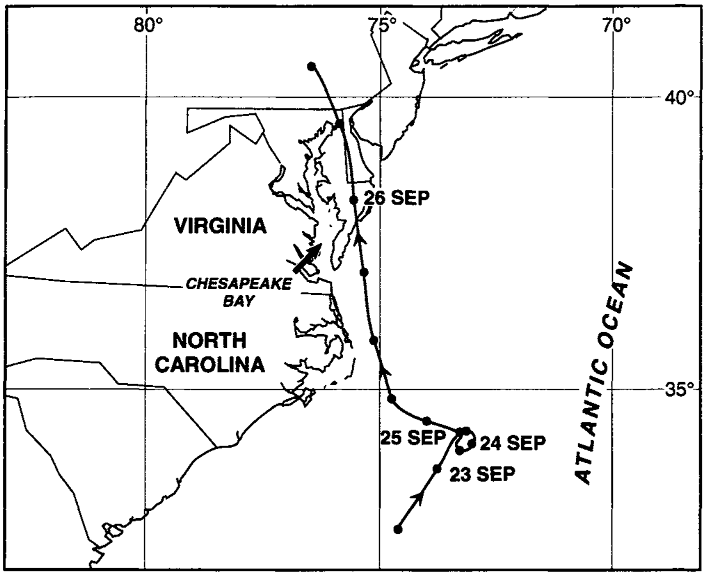

FIG. 2. Map of the path of Tropical Storm Danielle during 22–26 September 1992. Adapted from a National Oceanic and Atmospheric Administration preliminary report (National Hurricane Center 1992). For 22–25 September each dot represents the storm's location every 12 h, and for 25–26 September, each dot represents its location every 6 h.

through 1992 to deployment of 1.674-m^2 rings (1.46 m diameter), suctioning for 6 min, and dip-netting for 3 min. These modifications enhanced the collection efficiency, but did not statistically bias the samples such that data from the two time periods could be compared directly (R. Lipcius and M. Montane, *unpublished data*). Blue crabs were enumerated and measured at the spine-to-spine carapace width (CW), the width between the tips of the lateral spines. Crabs <15 mm CW were measured to the nearest 0.1 mm with a Wild M-5 dissecting microscope (Heerberg, Switzerland) and ocular micrometer. Crabs >15 mm CW were measured with calipers to the nearest 0.1 mm. Crabs were categorized by instars using CW measurements adapted from a variety of growth studies on laboratory-reared blue crabs (Newcombe et al. 1949; W. Van Engel and W. Van Heukelem, *unpublished data*; Table 1). The stage between molts (i.e., the shedding of the exoskeleton) is the instar; hence, the number of the instar represents the number of molts to attain a certain size. This is useful for categorizing small blue crabs since growth is relatively uniform until ≈10 mm CW (Newcombe et al. 1949).

Samples were collected during the primary settlement period, summer, fall, and winter of each year, either monthly or every other week. Sample dates from July through mid-November (N = 59) were used to determine the annual mean densities of each instar (Table 2). There was no sampling in mid-August of 1986 and the density for each instar was estimated using the mean of the 5 August and 2 September 1986 sampling dates, and the degrees of freedom reduced appropriately.

Regression analysis

Simple linear regression, a general functional response model, and the Ricker function were used to quantify within-year relationships between the coefficients of variation (CV) of the annual mean densities

TABLE 1. Parameters used for field tethering experiment: size of instar (spine-to-spine carapace width [CW]), number of crabs (of different sizes) per grid used to replicate low and medium densities, and number of crabs tethered in the field by habitat.

Instar	CW (mm)†	Crabs per grid (no.)‡ Low density	Medium density	Crabs per habitat (no.) Sand	Grass
First	2.2–3.0	6	18	278	284
Second	3.1–4.2	...	...	...	...
Third	4.3–5.9	3	7	117	120
Fourth	6.0–7.4	...	...	...	...
Fifth	7.5–9.1	2	5	58	60
Sixth	9.2–10.6	...	...	...	...
Seventh	10.7–12.6	1	2	34	36
Eighth	12.7–14.1	...	...	...	...
Ninth	14.2–16.1	1	2	34	36

† Adapted from Newcombe et al. 1949.

‡ Low density, 23 crabs/m^2; medium density, 46 crabs/m^2; see *Materials and methods*: *Field experiments*.

TABLE 2. Sample dates for the years 1983–1992 that were used to determine annual mean densities of blue crabs.

Year	Dates of samples	N
1983	19 JUL; 15, 29 AUG; 12, 26 SEP; 28 OCT	6
1984	31 JUL; 14, 29 AUG; 10, 24 SEP; 30 OCT	6
1985	5, 19 AUG; 3, 16, 30 SEP; 12 NOV	6
1986†	5 AUG; 2, 15, 29 SEP; 27 OCT	5
1987	3, 17 AUG; 1, 16 SEP; 1 OCT; 2 NOV	6
1988	3, 17, 31 AUG; 13 SEP; 3 OCT; 3 NOV	6
1989	1, 16, 29 AUG; 13, 28 SEP; 25 OCT	6
1990	1, 16, 29 AUG; 18, 27 SEP; 30 OCT	6
1991	1, 15, 29 AUG; 17 SEP; 2 OCT; 4 NOV	6
1992	3, 18, 31 AUG; 18 SEP; 1, 29 OCT	6
Total N		59

† No sample for mid-August.

of the first through ninth instars, as well as the relationships between annual mean densities of first, third, fifth, and seventh instars with larger instars. The combination of these analyses is an objective test for differentiating statistically between linear, hyperbolic, sigmoid, and parabolic functions (Ricker 1975, Real 1977, 1979, Lipcius and Hines 1986). First, a linear regression was performed on untransformed annual mean densities; if the fit was significant and met the statistical assumption of randomly distributed residuals, the relationship was determined to be linear. If the fit was not significant or if the residuals were not distributed randomly, then hyperbolic, sigmoid, and parabolic functions were distinguished using simple linear regression of log-transformed data, the general functional response model, and the Ricker function.

A power curve has the function:

$$Y = \alpha X^{\beta},$$

where

Y = annual mean density of the larger instar, and
X = annual mean density of the smaller instar.

The log transformation of Y and X linearizes the equation to:

$$\log Y = \log \alpha + \beta(\log X)$$

where

$\log \alpha$ = y intercept in the linearized function, and
β = the parameter associated with the form of the curve.

The curve is positively exponential when $\beta > 1$, hyperbolic when $0 < \beta < 1$, and linear when $\beta = 1$.

The general functional response model (Real 1977, 1979) was employed to distinguish between hyperbolic and sigmoid relationships. The model is:

$$Y = \frac{A \cdot X^{\beta}}{B + X^{\beta}}$$

where

A = asymptotic density of the dependent instar (the highest density recorded on an individual sample date for each instar from 1983 through 1992),
B = the value of X at which $Y = 0.5(A)$, and
β = the parameter associated with the form of the function.

The function is hyperbolic when $0 < \beta \leq 1$, sigmoid when $\beta > 1$, and approaches a horizontal line as β approaches 0. β is determined using the linearized form of the equation:

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

Linear regression was employed with both linearized forms, yielding an estimate of β that was tested against hypothetical values of 0 and 1 with standard t tests.

The Ricker function was used to fit a parabolic curve and is:

$$Y = A(X)e^{(-\beta X)},$$

where

Y = yearly mean density of the larger instar,
X = yearly mean density of the smaller instar.

The linearized form of the equation is:

$$\ln(Y/X) = \ln(A) - \beta X.$$

Mean annual densities were transformed and linear regression was employed to determine the fit of the Ricker function.

The best fitting function was first determined by assuming that the statistical assumption of randomly distributed residuals was met, as determined by visual inspection. When the fit of more than one function was significant and met all statistical assumptions, we selected that function with the highest r^2 values and the lowest P value.

Experimental animals

First, third, fifth, seventh, and ninth instar crabs were used in all experiments (Table 1). These instars are ecologically significant in that the first through third instars are predominantly resident in seagrass beds; emigration to unvegetated habitats begins at about the fifth instar (Orth and van Montfrans 1987). Postlarvae and juveniles were collected nightly from the plankton at the VIMS Ferry Pier in the York River, sorted by instars, and held in the laboratory until needed. Crabs were staged in the laboratory to identify day of molting, thereby reducing the number of crabs molting off tethers. First and third instar crabs were laboratory-reared and fed frozen adult *Artemia*; all others were fed frozen silver perch.

Tethering

Tethering is a technique commonly employed during field studies with decapod crustaceans (Heck and Thoman 1981, Herrnkind and Butler 1986, Wilson et al. 1987, 1990, Eggleston et al. 1990, 1992, Wahle and Steneck 1991, 1992, Marshall 1992, Fernandez et al. 1993, Mintz et al. 1994) to measure relative predator-induced mortality rates between experimental treatments. It is not intended to measure absolute rates of predation, but to assess the effects of experimental treatments on survival.

The type of tether line depended on the size of a crab. First and third instars were tethered with nylon thread, fifth and seventh instars with 17.8-N test monofilament line, and ninth instars with 26.7-N test monofilament line. Tethers were 5 cm long and tied to a Number 12 snap swivel (Berkeley Outdoor Technologies Group, Iowa). Tethering involved: (1) placing the free end of the tether in cyanoacrylate glue (Krazy Glue Extra Strength Gel, The Bordon Company), (2) affixing this end to the dry carapace of the crab and applying light pressure so that it extended between the fifth pair of walking legs, (3) allowing the glue to dry for 30–45 s, and (4) checking the tether before returning crabs to the water. Crabs were tethered and held in the laboratory 12–24 h prior to use. Tethered crabs were observed in the laboratory and with underwater video equipment in the field. Crabs appeared to behave naturally 2–3 min after acclimation to the tether and new environment; observed behaviors included foraging, feeding, burial into the substrate, climbing on seagrass, and attempted escapes from predators. The only means of escape from the tether was to molt, an act easily identified by the intact molt shell attached to the tether. This differed from situations where tethered crabs were consumed by predators, which typically either left a small portion of the carapace secured to the tether or severed the tether, leaving it noticeably shorter with the nylon pinched at the free end.

Laboratory experiment

A laboratory study conducted from October to December 1992 tested: (1) whether tethering provided unbiased estimates of predation in newly settled blue crabs and (2) the effects of crab size, predator presence, and habitat type upon crab survival. Although tethering has been used to assess relative predation rates in the field for crustaceans (Heck and Thoman 1981, Herrnkind and Butler 1986, Wilson et al. 1987, 1990, Barshaw and Able 1990, Eggleston et al. 1990, 1992, Wahle and Steneck 1991, 1992, Smith and Herrnkind 1992, Fernandez et al. 1993, Mintz et al. 1994), mollusks (Poole et al. 1991, Ambrose and Irlandi 1992, Marshall 1992) and fish (Shulman 1985, McIvor and Odum 1988), only four studies (Barshaw and Able 1990, Marshall 1992, Barbeau and Scheibling 1994, Zimmer-Faust et al. 1994) have quantitatively examined tethering artifacts.

Since tethering is assumed to measure relative rates of predation and not absolute predation rates, previous investigators have assumed that the test is an unbiased measure of predation. This implies that the relative effects of treatments for tethered individuals will be proportional to those for untethered organisms, thereby allowing use of the technique to quantify treatment-specific relative predation rates. However, treatment-specific bias (Peterson and Black 1994) may be introduced into the data if tethering effects are not proportional across all treatments (e.g., tangling of the tether in one type of habitat and not another). Such a treatment-specific bias does not decrease survival proportionally across all treatments, and thereby confounds treatment effects with those of the technique. Previous studies have addressed bias using qualitative observations of tethered organisms (Heck and Thoman 1981, Herrnkind and Butler 1986, Wilson et al. 1987, 1990, Eggleston et al. 1990, 1992, Wahle and Steneck 1991, 1992, Smith and Herrnkind 1992, Fernandez et al. 1993, Mintz et al. 1994, Zimmer-Faust et al. 1994) and only two investigations (Marshall 1992, Barbeau and Scheibling 1994) have experimentally tested for treatment-specific bias.

In the context of a full-factorial experimental design using tethered and untethered experimental animals, a statistically significant main effect of tethering indicates that relative rather than absolute rates of predation are measured. Treatment-specific bias is indicated by a statistically significant interaction effect between the main effect of tethering and any other main effect. If present, it precludes the interpretation of those main effects in affecting relative rates of predation within the experimental framework.

This study determined the effects of tethering upon bias in treatments involving predator presence or absence, habitat type, and crab size with tethered and untethered crabs. Trials were conducted in 12 aerated 38-L aquaria, an appropriate size for the small crabs used in this study, with the randomly assigned factors of habitat (vegetated or unvegetated), tethering (tethered or untethered), size (first, third, fifth, seventh, or ninth instars), and predator (presence or absence). Aquaria were filled with 2 cm of sand sieved through a 500-μm mesh, and 20 cm of filtered estuarine water. Vegetated aquaria were haphazardly planted with eelgrass trimmed to a shoot height of 20–24 cm and a density equivalent to 300 shoots/m^2 (Orth and Moore 1986). Grass was cleaned of epifauna and epiphytes by soaking in fresh water. Photoperiod was 12 h L/12 h D, water temperature was 23.6 ± 1.0°C (mean ± 1 SD), and salinity was 19.6 ± 0.5 (practical salinity scale).

Six prey crabs of a single instar were placed in aquaria 12 h prior to introduction of predators. In tethering treatments, two tethered crabs were secured with the snap swivel to opposite ends of each of three 10 × 3 cm vexar mats, buried 10 cm apart. The predator suite, which had been starved for 24 h prior to experiments, was represented by one naked goby, *Gobiosoma bosci*, 20–30 mm standard length (SL), one naked goby 30–40 mm SL, and one blue crab 20–30 mm CW. Both predators were observed in the field consuming tethered early-instar crabs using underwater video cameras, as well as during the laboratory study. Further, in this region of the Chesapeake Bay cannibalism is a major contributor to crab mortality (Mansour 1992, Moody 1994) while the pelagic and benthic feeding fishes *Micropogonias undulatus* (Atlantic croaker), *Leiostomus xanthurus* (spot), *Sphoeroides maculatus* (northern puffer), and *Centropristis striata* (black sea bass) have only recently been identified as consumers of crabs of these sizes within the study area (K. Metcalf, R. Lipcius, J. van Montfrans, and R. Orth, *unpublished data*). Predators were removed after 24 h, aquaria drained through a 500-μm sieve, and remaining crabs enumerated. Crabs that had been killed by predators were apparent from a small piece of carapace remaining on the tether, from obvious mortal wounds, or from complete absence in non-tethered treatments. Crabs that died during trials due to the fitness of the crab, handling, or the tethering procedure were distinguished by the presence of an intact dead crab on the tether or in the tank; these were not considered in the statistical analysis. Dead crabs accounted for 1% of all crabs and their percentage did not differ significantly between tethered and untethered crabs (ANOVA, $F_{1,206} = 2.00$, $P = 0.139$, $0.50 < \text{power} < 0.55$), or by trial (ANOVA, $F_{4,206} = 1.50$, $P = 0.204$, $\text{power} > 0.80$).

Number of surviving crabs were converted to proportion surviving per treatment and analyzed as dependent on habitat type, tether, and crab size using three-way fixed-factor analysis of variance models (ANOVA; Sokal and Rohlf 1981). Five trials of each treatment were performed and time was used as a blocking factor; where time was not significant separate trials were combined (Sokal and Rohlf 1981).

Field experiments

Field tethering trials were performed 21–28 September 1992 to test the effects of habitat type, crab density, and crab size on the survival of newly settled blue crabs. The unexpected arrival of Tropical Storm Danielle on 23–25 September allowed deployment of tethered crabs before (21–22 September), during (23–24 September), and after the storm (26–27 September), and assessment of the effects of the storm on crab survival. Rough weather prevented deployment of crabs on 25 September.

Tethering grids were used to mimic crab densities. Tethering grids were 1.1 × 1.1 m rebar frames with 222.4-N test monofilament line woven at 10-cm intervals. This created a 1-m^2 tethering arena capable of holding $\leq$100 crabs. Snap swivels were used to secure tethered crabs at intersecting lines. Each grid was marked with an orange buoy at a corner.

Tethering grids were tested prior to use to determine if individual crabs or grids should be considered independent for statistical analysis. Eight grids with 45 crabs/m^2, proportionally correct for the first, third, fifth, and seventh instars (Table 1) were deployed at the Guinea Marsh site in vegetated and unvegetated habitats for 24 h during a 3-d period. There was no apparent pattern in the proportional survival due to size or habitat, nor a significant correlation between proportional survival of each instar and grid. The absence of pattern in crab survival on the grids indicated that the statistical assumption of independence between individual crabs was reasonable.

A total of 1057 crabs was randomly allocated to the grids at densities of 23 crabs/m^2 (low) or 46 crabs/m^2 (medium). Size frequency analysis of the first through seventh instars at Brown's Bay from 1983 through 1988 (July through December) indicated the most common densities were 22, 41, and 89 juvenile crabs/m^2 with densities rarely as great as 89 crabs/m^2. The correct proportion of each experimental instar from total crab densities of 23 (low) and 46 (medium) crabs/m^2 (Table 1) was allocated to a grid 12–24 h prior to a trial (e.g., low density grid contained six first instars, three third instars, two fifth instars, one seventh instar, and one ninth instar), and held in flow-through tanks before field deployment.

One grid of each density was deployed for a 24-h trial at each location in vegetated and adjacent unvegetated sand habitats. Grids were: (1) wrapped in damp sheets and transported to the site, (2) checked for proper placement of crabs prior to deployment and any missing or dead crabs replaced, and (3) haphazardly deployed and secured with one 30-cm rebar stake in the buoy corner. At vegetated sites care was taken to prevent seagrass from being flattened by the grids.

Grids were examined every 4–6 h during daylight and crab survival recorded. About 2% of the tethered crabs either molted while on the tethers or were missing appendages and had hollow intact carcasses. Mottled dog whelks, *Nassarius trivittatus*, were observed consuming live crabs with missing appendages. The snail utilized its proboscis to extract the internal soft body tissues of the constrained tethered crab, leaving a hollow intact carcass. These crabs were considered tethering artifact and not used in analyses.

Mortality and survival for 24 h were converted to frequencies per treatment and did not differ significantly by location (G test, $\chi^2_1 = 0.51$, $P = 0.47$); hence, data from the separate locations were combined (Sokal and Rohlf 1981). These data were analyzed using a log-linear model (G test; Sokal and Rohlf 1981) as dependent on habitat (vegetated or unvegetated), crab density (low or medium), size (first, third, fifth, seventh, or ninth instars), and storm conditions (pre-storm, storm, or post-storm). Time was used as a blocking factor and data from separate trials were combined when time was not significant (Sokal and Rohlf 1981).

Physical data; blue crab abundance

Temperature and salinity were recorded during each visit to the field sites and analyzed with two-way fixed-factor ANOVA models (Sokal and Rohlf 1981) as functions of location and day. Hourly water height was measured at VIMS and compared to projected tidal height to determine storm surge.

Prior to retrieval, 4-cm sediment cores were taken from each grid and analyzed as described by Folk (1974) into three size categories: <1.0 phi (gravel), 1.0–4.0 phi (sand), and >4.0 phi (mud). Sediment type was characterized by the frequency of each category per treatment and analyzed as dependent on habitat and location using the G test (Sokal and Rohlf 1981). Grids in vegetated habitats had 10 randomly selected 10 × 10 cm plots within the tethering arena clipped of vegetation near the roots. Vegetation was identified to species, and shoot density and dry biomass determined for

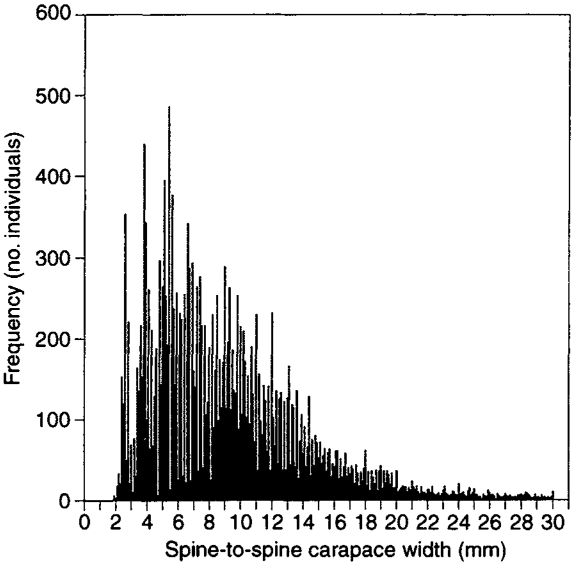

FIG. 3. Size frequency histogram of blue crabs for vegetated habitats in Brown's Bay during 1983 through 1992 from mid-July through mid-November.

each plot. Shoot density and dry mass were $\log(x + 1)$ transformed to maintain the assumption of homogeneity of variance, and analyzed as dependent on location with a one-way fixed-factor ANOVA model (Sokal and Rohlf 1981). Water turbidity prevented obtaining vegetation samples for trials on 22–24 September and sediments were not sampled on 24 September due to rough weather.

Benthic suction samples were taken on 21 and 28 September to quantify short-term changes in blue crab abundance at the study sites (Goodwin Islands and Guinea Marsh) during the tethering experiments. Densities of blue crabs were square-root transformed to maintain the assumption of homogeneity of variance, and analyzed with three-way fixed-factor ANOVA models (Sokal and Rohlf 1981) as dependent on location, habitat, and time. Frequencies of megalopae and first instars (newly recruited), second and third instars (newly settled), fourth and fifth instars (grass-bed residents), sixth instar through 23 mm CW (0^+ year class), and >23 mm CW (1^+ year class) were converted to frequency per treatment and analyzed as dependent on location, habitat, and time using the G test (Sokal and Rohlf 1981).

Statistical analysis

The assumption of homogeneity of variance was tested with Cochran's C test. In all cases, either the variances were homogeneous, or the hypotheses were rejected at alpha values lower than the P values of the test for homogeneity of variance (Underwood 1981). Power analysis was performed for all the tests where the null hypothesis was not rejected, and except where noted, power was >0.80 (Peterman 1990). Differences among means in parametric analyses were determined using Ryan's Q test (Day and Quinn 1989) unless there was a significant interaction effect; then lower level ANOVA models were utilized. In nonparametric analyses, differences within treatments were determined using lower level G tests and hypotheses rejected at an alpha level lower than the observed P values for the main effect (Underwood 1981).

RESULTS

Benthic sampling

Numerically, blue crabs <20 mm CW dominated in seagrass beds (Fig. 3). Annual mean densities of blue crab varied over nearly an order of magnitude from 1983 through 1992 (Fig. 4) with high densities in 1984, 1991, and 1992. Across years, densities of crabs smaller than the seventh instar were highly variable, whereas densities became more uniform at the seventh instar. Crab densities in 1984, 1991, and 1992 were high enough that there was a generally decreasing trend from the third instar to the seventh instar, indicative of a loss of newly settled blue crabs from the seagrass habitat. Within years there was a trend of increasing densities from the first to the third instar. Though sampling was designed to evaluate 0^+ year class crab densities, it did not always coincide with episodic recruitment events associated with the new and full moon (van Montfrans et al. 1990). Given the short intermolt periods for the first through the third instar (≈10 d; W. Van Engel and A. Pile, *unpublished data*), twice-monthly sampling that did not occur immediately following a recruitment event would miss most of the first and second instars and provide a low estimate for the annual mean density of first and second instars.

Coefficients of variation (CVS) for annual mean densities of each instar generally decreased from the first to the fifth (1988, 1990, 1992), sixth (1989), and, most commonly, the seventh instars (1983–1987, 1991). Upon reaching a minimum, CVS then increased through the ninth instar for all years except 1990 (Fig. 5). Simple linear regression of the within-year relationships of the CVS of the first through the ninth instars were either not significant or exhibited a poor fit associated with non-random residuals. CVS were transformed for the linearized equations of the hyperbolic and parabolic functions, and the relationships of the within-year CVS for the first through the ninth instar was a concave parabolic function for all years (Table 3).

Inter-instar relationships: linear, hyperbolic, sigmoid, or parabolic functions?

Most linear regressions of the densities of the large to smaller instars were either not significant or exhibited a poor fit associated with non-random residuals (Figs. 6–8, Table 4); these residuals were typically low at high and low densities and large at intermediate densities. Only the simple linear regression of ninth instar dependent on seventh instar was linear (Fig. 8, Table

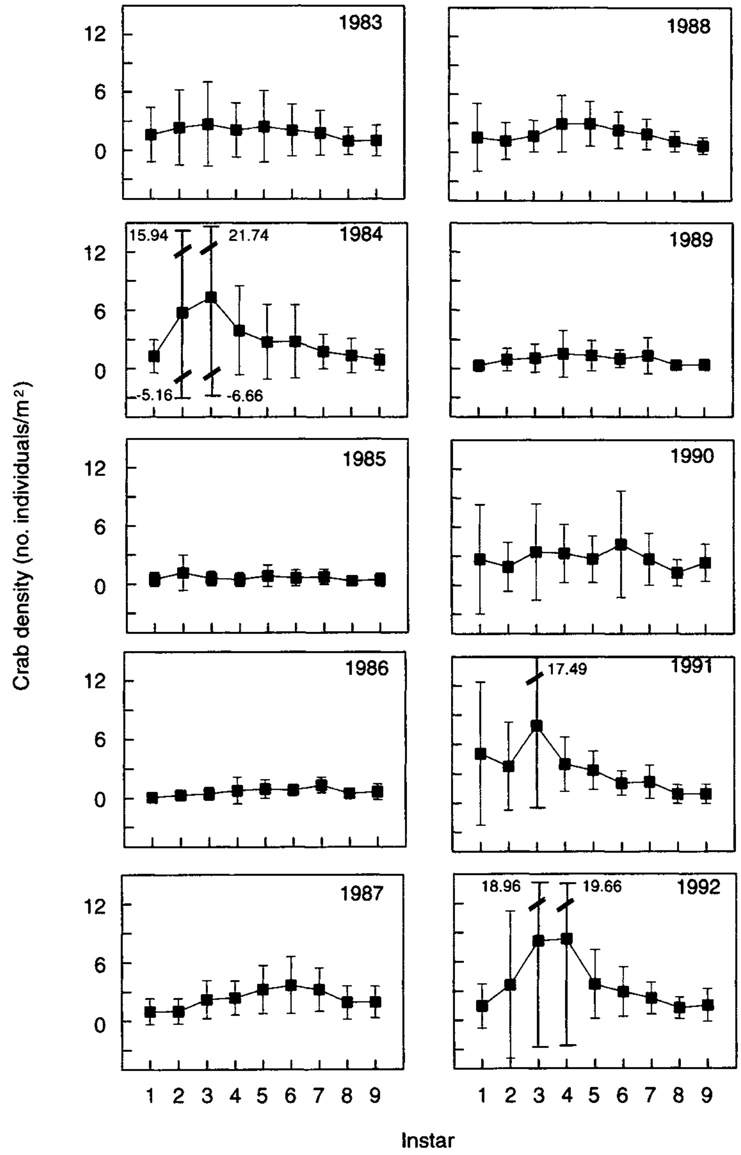

FIG. 4. Mean annual densities of the first through ninth instar blue crabs from 1983 through 1992 in seagrass beds in Brown's Bay. Yearly values are the mean of six suction samples taken on six dates (see Table 2). Error bars indicate ±1 SD.

4). Subsequent analysis with log-transformed densities and the functional response model distinguished between hyperbolic and sigmoid functions when the regression was significant, while the Ricker function distinguished parabolic functions (Tables 5–7). There was no statistical difference between the log-transformed data and the functional response model.

Relationships between the annual mean densities of first instars and successive instars were hyperbolic with third and fifth instars, and parabolic with seventh and ninth instars (Fig. 6, Tables 4–7). Annual mean densities of fifth instars were dependent on third instars and considered hyperbolic since the residuals of the parabolic function were non-random. Seventh and ninth instars were dependent on third instars as a parabolic function (Fig. 7, Tables 4–7). Annual mean densities of seventh and ninth instars were dependent on fifth instars and the relationships hyperbolic (Fig. 8, Tables 4–7). In general, as size of the dependent instar increased relative to the independent instar, the percentage of the fit described by the function (r^2) decreased (Table 8).

Laboratory experiment

Crab survival differed significantly for all main effects, whereas all interaction effects were not significant (Table 9A). Crab survival was higher: (1) in vegetated habitats, (2) when untethered, and (3) with increasing crab size (Fig. 9). Crab survival for seventh and ninth instars, while not significantly different, was

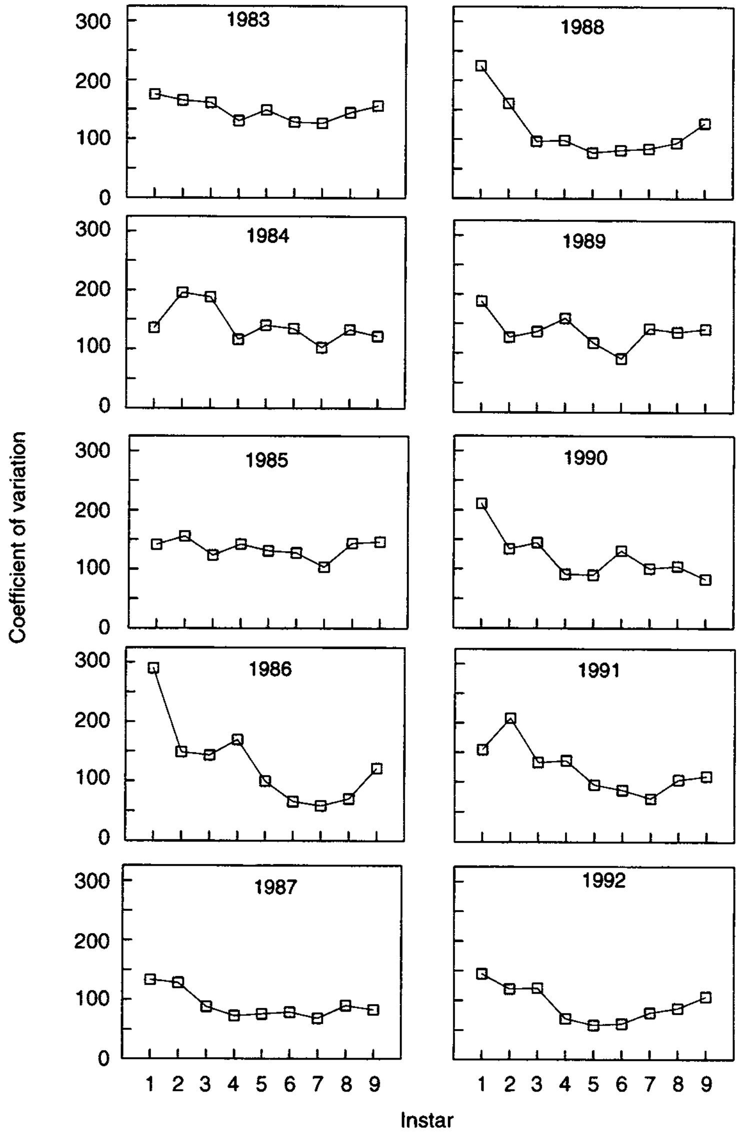

FIG. 5. Coefficients of variation of the mean annual densities of first through ninth instar blue crabs from 1983 through 1992.

significantly higher than survival for fifth, third, and first instars, which all differed significantly from each other (Table 9B). Predation occurred in only 8% of the control treatments due to prey crabs molting and subsequently cannibalizing conspecifics.

Field experiment

Mean water temperature at the field sites differed significantly by day (ANOVA, $F_{5,31}$ = 10.76, $P <$ 0.0001), but not by location (ANOVA, $F_{1,31}$ = 0.07, P = 0.7883). Mean water temperature was highest prior to the storm, decreased during the storm, and was lowest the day after the storm (Fig. 10B). Mean salinity did not differ by location (ANOVA, $F_{1,31}$ = 0.85, P = 0.3642), but was significantly higher during post-storm conditions (ANOVA, $F_{5,31}$ = 5.53, P = 0.0009; Fig. 10A).

Water height within the York River increased above expected tidal height from 23 September until reaching a maximum of 0.71 m above expected on 25 September (Fig. 10C). Water levels then decreased until returning to expected levels on 28 September.

Sediment composition did not differ significantly by location (G test, χ^2_1 = 0.49, P = 0.7838) or habitat (G test, χ^2_1 = 0.11, P = 0.9488) and the mean composition was 2% gravel, 90% sand, and 8% mud. Total shoot density (ANOVA, $F_{1,39}$ = 0.01, P = 0.93), dry weight (ANOVA, $F_{1,39}$ = 0.03, P = 0.875), and frequency of widgeongrass and eelgrass (ANOVA, $F_{1,39}$ = 0.37, P = 0.52) did not differ significantly by location. Back-

TABLE 3. Analyses of the coefficient of variation of the annual mean density of each instar using the Ricker Stock-Recruit function.

Year	Source of variation	SS	df	MS	F	r^2
1983	Regression	4.490	1	4.490	47.33***	0.87
	Error	0.664	7	0.095		
1984	Regression	5.244	1	5.244	75.37***	0.91
	Error	0.487	7	0.070		
1985	Regression	4.067	1	4.067	47.01***	0.87
	Error	0.606	7	0.087		
1986	Regression	9.251	1	9.251	32.28***	0.82
	Error	2.000	7	0.286		
1987	Regression	5.665	1	5.665	35.85***	0.84
	Error	1.106	7	0.158		
1988	Regression	6.260	1	6.260	21.99**	0.76
	Error	1.993	7	0.285		
1989	Regression	4.538	1	4.538	30.96***	0.82
	Error	1.026	7	0.147		
1990	Regression	6.600	1	6.600	41.84***	0.86
	Error	1.104	7	0.158		
1991	Regression	5.226	1	5.226	19.63**	0.73
	Error	1.864	7	0.266		
1992	Regression	7.154	1	7.154	55.13***	0.89
	Error	0.908	7	0.130		

** $P < 0.01$, *** $P < 0.001$.

transformed total shoot density was 192.94 ± 19.82 shoots/m^2 (mean ± 1 SD) with a dry mass of 8.35 ± 5.21 g/m^2.

Relative rates of predation

Crab survival was significantly higher (1) in vegetated habitats, (2) with increasing crab size (fifth, seventh, and ninth instars greater than first and third instars), and (3) during storm and post-storm conditions. Location (north shore vs. south shore) and density of tethered crabs (23 crabs/m^2 [low density] vs. 46 crabs/m^2 [medium density]) did not significantly affect survival of newly settled blue crabs and there were no significant interaction effects (Fig. 11, Table 10).

Blue crab abundance

Blue crab densities at the Goodwin Islands and Guinea Marsh during the field study were significantly lower in (1) sand habitats and (2) under pre-storm conditions. While location was not a significant main effect, the location × date and location × habitat interaction effects were significant (Table 11A, Fig. 12). Crab densities at Guinea Marsh were significantly higher after the storm (ANOVA, $F_{1,20} = 37.80$, $P < 0.0001$), whereas densities at the Goodwin Islands did not differ significantly by date (ANOVA, $F_{1,20} = 2.00$, $P = 0.1723$). Blue crab densities in vegetated habitats were not significantly different by location on the pre-storm date

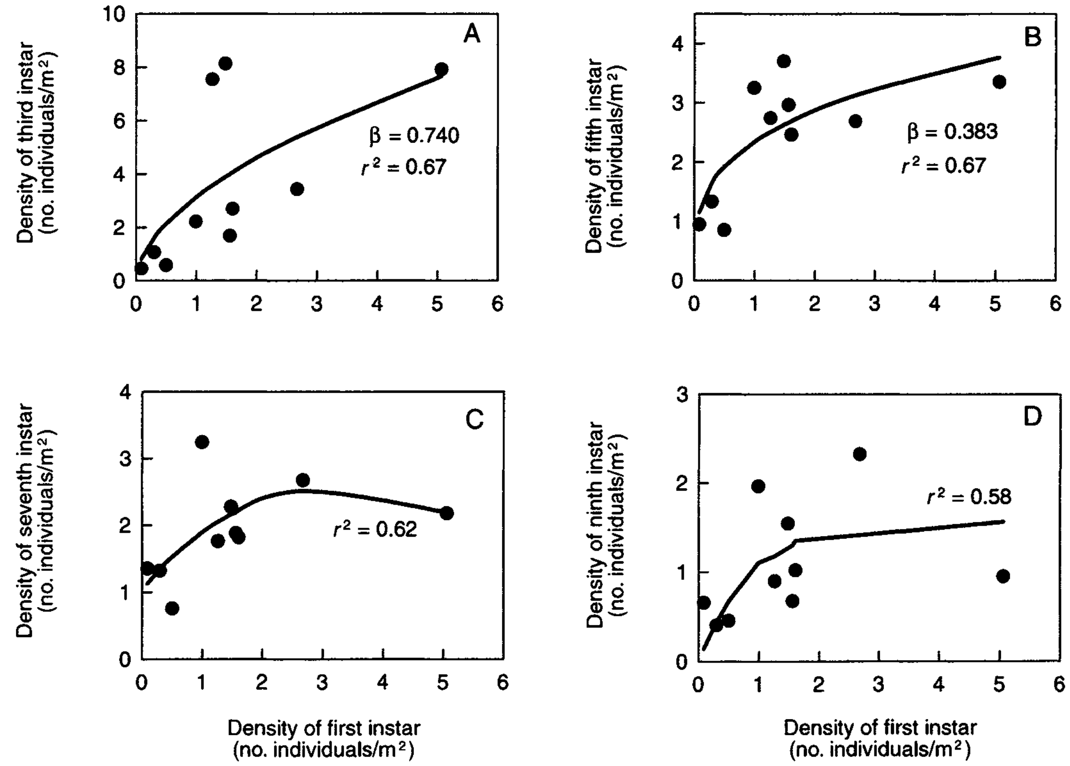

FIG. 6. Mean annual densities of (A) third, (B) fifth, (C) seventh, and (D) ninth instars against first instars from 1983 through 1992. Regression lines are the best-fitting functions (Table 8).

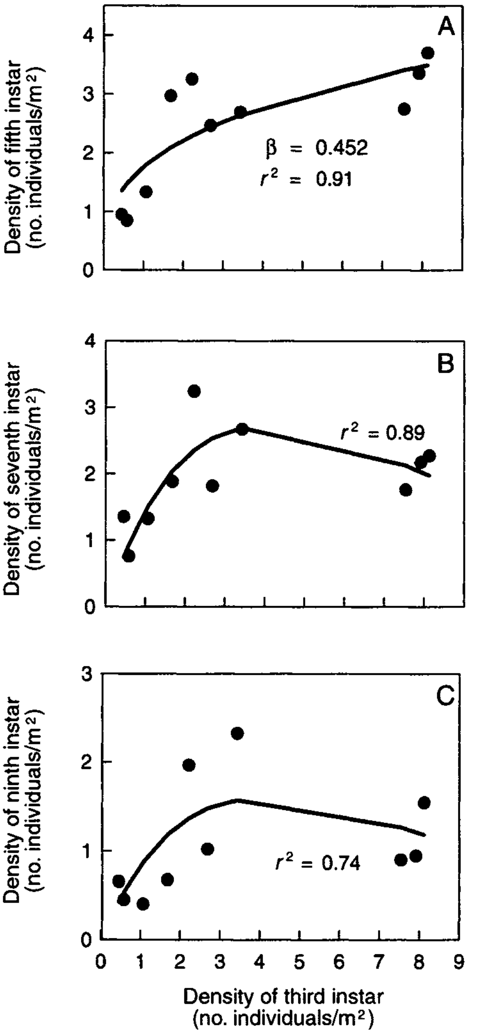

FIG. 7. Mean annual densities of (A) fifth, (B) seventh, and (C) ninth instars against third instars from 1983 through 1992. Regression lines are the best-fitting functions (Table 8).

(ANOVA, $F_{1,11}$ = 0.36, P = 0.5610), and significantly higher at the Guinea Marsh location on the post-storm date (ANOVA, $F_{1,11}$ = 34.51, $P < 0.0001$). Crab densities were significantly lower in unvegetated habitats at the Guinea Marsh location on the pre-storm date (ANOVA, $F_{1,11}$ = 27.48, P = 0.0004), but not significantly different by location on the post-storm date (ANOVA, $F_{1,11}$ = 0.003, P = 0.9553).

Instar frequencies differed significantly by date and there was a significant interaction between location and habitat (Table 12). The date effect was due to significantly higher frequencies of megalopae and first instars after the storm in both habitats and locations. Frequencies of 0^+ year class blue crabs larger than the first instars (Fig. 13) were not significantly different by date (G test, χ^2_2 = 2.13, P = 0.35), location (G test, χ^2_2 = 2.05, P = 0.36), or habitat (lower level G test, χ^2_2 = 4.05, P = 0.13). The location × habitat effect was due to significantly more 1^+ year class blue crabs in sand habitats than grass habitats at the Guinea Marsh location (χ^2_1 = 5.84, P = 0.0157) before and after the storm.

DISCUSSION

Density-dependent settler–recruit–juvenile relationships

The relationships between the mean annual densities of larger and smaller instars through the first seven instars were either a hyperbolic or parabolic function, indicating that settler–recruit–juvenile relationships are

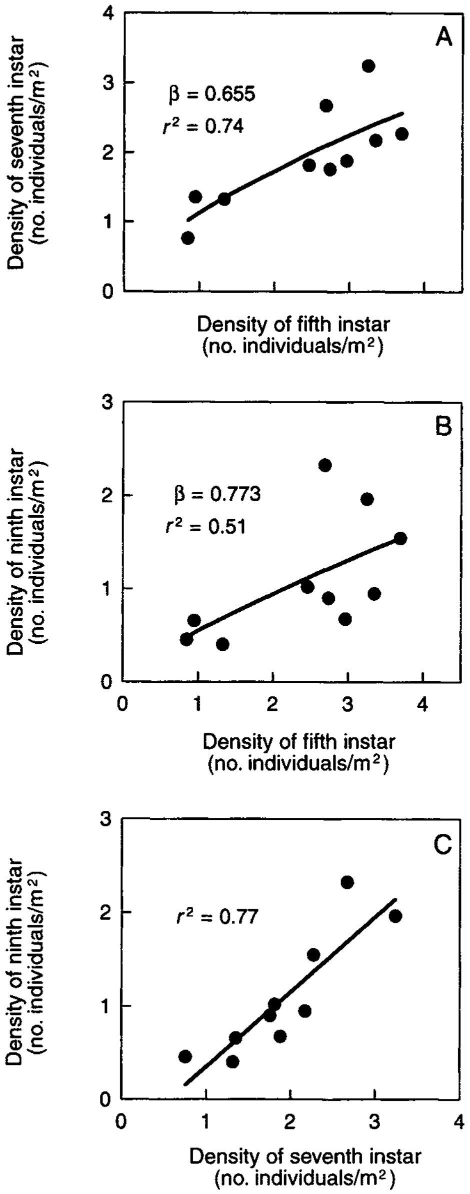

FIG. 8. Mean annual densities of the (A) seventh and (B) ninth instars against fifth instars and (C) ninth instars against seventh instars from 1983 through 1992. Regression lines are the best-fitting functions (Table 8).

TABLE 4. Linear regression with the annual mean density for each inter-instar relationship.

Instar	Source of variation	SS	df	MS	F	r^2	Residuals
A) First instar							
Third	Regression	33.663	1	33.663	5.09^{NS}	0.39	
	Error	52.867	8	6.608			
Fifth	Regression	3.478	1	3.478	4.64^{NS}	0.37	
	Error	5.993	8	0.749			
Seventh	Regression	0.774	1	0.774	1.63^{NS}	0.17	
	Error	3.795	8	0.474			
Ninth	Regression	0.351	1	0.351	0.82^{NS}	0.09	
	Error	3.436	8	0.430			
B) Third instar							
Fifth	Regression	5.066	1	5.066	9.20*	0.54	non-random
	Error	4.405	8	0.551			
Seventh	Regression	0.583	1	0.583	1.17^{NS}	0.13	
	Error	3.986	8	0.498			
Ninth	Regression	0.306	1	0.306	0.70^{NS}	0.08	
	Error	3.481	8	0.435			
C) Fifth instar							
Seventh	Regression	2.873	1	2.873	13.56**	0.63	non-random
	Error	1.695	8	0.212			
Ninth	Regression	1.363	1	1.363	4.50^{NS}	0.36	
	Error	2.424	8	0.303			
D) Seventh instar							
Ninth	Regression	2.926	1	2.926	27.17***	0.77	random
	Error	0.861	8	0.108			

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, $^{NS}P > 0.05$.

TABLE 5. Density curve analyses with the annual mean density log-transformed to assess the linear, hyperbolic, or sigmoidal characteristics of the curve.

Instar	Source of variation	SS	df	MS	F	r^2	β	$\beta > 0$	$\beta > 1$
A) First instar									
Third	Regression	1.246	1	1.246	15.96**	0.67	0.740	*	NS
	Error	0.827	8	0.103					
Fifth	Regression	0.334	1	0.334	16.12**	0.67	0.383	*	NS
	Error	0.166	8	0.021					
Seventh	Regression	0.095	1	0.095	3.98^{NS}	0.33	0.204		
	Error	0.191	8	0.024					
Ninth	Regression	0.177	1	0.177	3.48^{NS}	0.30	0.279		
	Error	0.408	8	0.051					
B) Third instar									
Fifth	Regression	0.382	1	0.382	26.13***	0.76	0.452	*	NS
	Error	0.117	8	0.015					
Seventh	Regression	0.120	1	0.120	5.79*	0.42	0.253	*	NS
	Error	0.166	8	0.021					
Ninth	Regression	0.203	1	0.203	4.24^{NS}	0.34	0.329		
	Error	0.382	8	0.048					
C) Fifth instar									
Seventh	Regression	0.214	1	0.214	23.71***	0.75	0.655	*	NS
	Error	0.072	8	0.009					
Ninth	Regression	0.298	1	0.298	8.32*	0.51	0.773	*	NS
	Error	0.287	8	0.036					
D) Seventh instar									
Ninth	Regression	0.443	1	0.443	24.98***	0.76	1.240	*	*
	Error	0.142	8	0.018					

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, $^{NS}P > 0.05$.

TABLE 6. Density curve analyses with the linearized functional response model to assess the linear, hyperbolic, or sigmoid characteristics of the curve.

Instar	Source of variation	SS	df	MS	F	r^2	β	$\beta > 0$	$\beta > 1$
A) First instar									
Third	Regression	1.370	1	1.370	15.18**	0.66	0.776	*	NS
	Error	0.722	8	0.090					
Fifth	Regression	0.411	1	0.411	16.03**	0.67	0.425	*	NS
	Error	0.205	8	0.026					
Seventh	Regression	0.134	1	0.134	3.98^{NS}	0.33	0.243		
	Error	0.276	8	0.035					
Ninth	Regression	0.246	1	0.246	3.26^{NS}	0.29	0.329		
	Error	0.605	8	0.076					
B) Third instar									
Fifth	Regression	0.472	1	0.472	26.30***	0.77	0.502	*	NS
	Error	0.144	8	0.018					
Seventh	Regression	0.164	1	0.164	5.34**	0.40	0.296	*	NS
	Error	0.246	8	0.031					
Ninth	Regression	0.272	1	0.272	3.76^{NS}	0.32	0.381		
	Error	0.579	8	0.072					
C) Fifth instar									
Seventh	Regression	0.300	1	0.300	21.69***	0.73	0.775	*	NS
	Error	0.111	8	0.014					
Ninth	Regression	0.409	1	0.409	7.41*	0.48	0.906	*	NS
	Error	0.441	8	0.055					
D) Seventh instar									
Ninth	Regression	0.633	1	0.633	23.29***	0.74	1.49	*	*
	Error	0.218	8	0.027					

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, $^{NS}P > 0.05$.

TABLE 7. Density curve analyses with the annual mean density of each instar using the Ricker Stock-Recruit function.

Instar	Source of variation	SS	df	MS	F	r^2
A) First instar						
	Regression	0.606	1	0.606		
Third	Error	3.52	8	0.440	1.38^{NS}	0.15
	Regression	3.652	1	3.652		
Fifth	Error	1.822	8	0.228	16.04**	0.67
	Regression	5.371	1	5.371		
Seventh	Error	3.280	8	0.410	13.10**	0.62
	Regression	4.874	1	4.874		
Ninth	Error	3.556	8	0.445	10.97**	0.58
B) Third instar						
Fifth	Regression	3.261	1	3.261	76.71***	0.91
	Error	0.340	8	0.043		
	Regression	5.727	1	5.727		
Seventh	Error	0.683	8	0.683	67.14***	0.89
	Regression	4.814	1	4.814		
Ninth	Error	1.678	8	0.210	22.94***	0.74
C) Fifth instar						
	Regression	0.322	1	0.322		
Seventh	Error	0.375	8	0.047	6.83*	0.46
	Regression	0.116	1	0.116		
Ninth	Error	1.541	8	0.193	0.60^{NS}	0.70
D) Seventh instar						
	Regression	0.156	1	0.156		
Ninth	Error	0.684	8	0.086	1.81^{NS}	0.19

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, $^{NS}P > 0.05$.

TABLE 8. Final functions used to describe inter-instar relationships. All relationships were statistically significant at the 0.05 level or less (see Tables 4–7).

Independent variable	Dependent variable	Function	r^2
First instar	third instar	hyperbolic	0.67
	fifth instar	hyperbolic	0.67
	seventh instar	parabolic	0.62
	ninth instar	parabolic	0.58
Third instar	fifth instar	hyperbolic	0.91
	seventh instar	parabolic	0.89
	ninth instar	parabolic	0.74
Fifth instar	seventh instar	hyperbolic	0.74
	ninth instar	hyperbolic	0.51
Seventh instar	ninth instar	linear	0.77

TABLE 9. (A) Three-way fixed-factor ANOVA table and (B) multiple comparisons (Ryan's Q-test of Multiple Comparisons, $\alpha = 0.05$) for proportional survival in laboratory study.

A)

Source	df	SS	F	Power
Habitat (H)	1	0.751115	16.00***	
Tether (T)	1	0.360001	7.67**	
Size (S)	4	11.473850	61.10***	
$H \times T$	1	0.004444	0.09^{NS}	
$H \times S$	4	0.301672	1.61^{NS}	>0.99
$T \times S$	4	0.409441	2.18^{NS}	>0.80
$H \times T \times S$	4	0.137221	0.73^{NS}	
Error	180	8.458866		

B)

	Instar				
	1	3	5	7	9
Mean survival	0.07	0.34	0.71	0.89	0.95

** $P < 0.01$; *** $P < 0.001$; ^{NS} $P > 0.05$.

Note: Power analyses performed when $P < 0.20$. Means sharing an underline are not significantly different.

density-dependent. Density-dependent losses occurred between all instars that utilized seagrass beds as their primary habitat. While both of these functions are indicative of regulation by density-dependent processes, they have differing end results on a population. The hyperbolic function indicates a constant maximum population level that is not affected by high values of the independent variable. The opposite is true of the parabolic function in that once the maximum sustainable population is reached further increases in the independent variable result in decreases in the dependent variable. These density-dependent losses may result from increased agonism, predation, parasitism, disease, or competition for resources resulting in increased natural mortality or emigration to other habitats (Menge and Sutherland 1987).

We examined the effect of density on predation-induced mortality and found that the densities of tethered crabs did not significantly affect the predation induced mortality of newly settled blue crabs in the field (Table 10A). This may have been due to selecting experimental densities that were not extreme enough to detect density-dependent survival. Moreover, the effect of tethered crab density on crab survival may have been confounded by the profound effect that Tropical Storm Danielle had on relative rates of predation. Further studies on the effects of newly settled crab densities on survival are warranted before predation can be eliminated as a factor in density-dependent loss within nursery habitats. More likely, the data suggest that density-

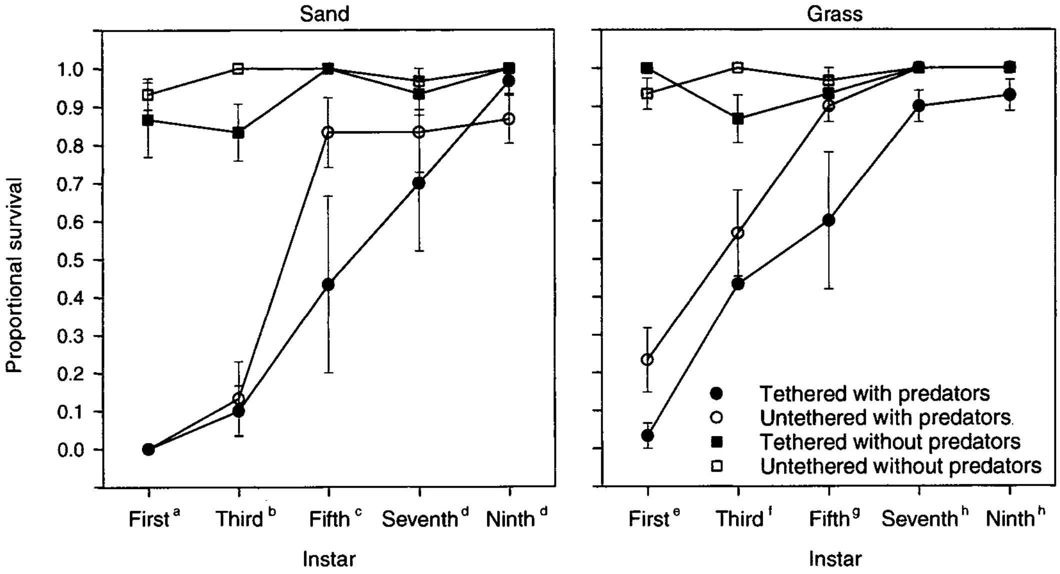

FIG. 9. Mean proportional survival after 24 h for each instar in sand or grass habitat, tethered and untethered, in the presence or absence of predators during the laboratory study ($n = 5$). Instars with the same superscripted letter are not significantly different. Predation in the absence of predators was due to cannibalism by crabs that molted during the trial. Error bars indicate ±1 SD.

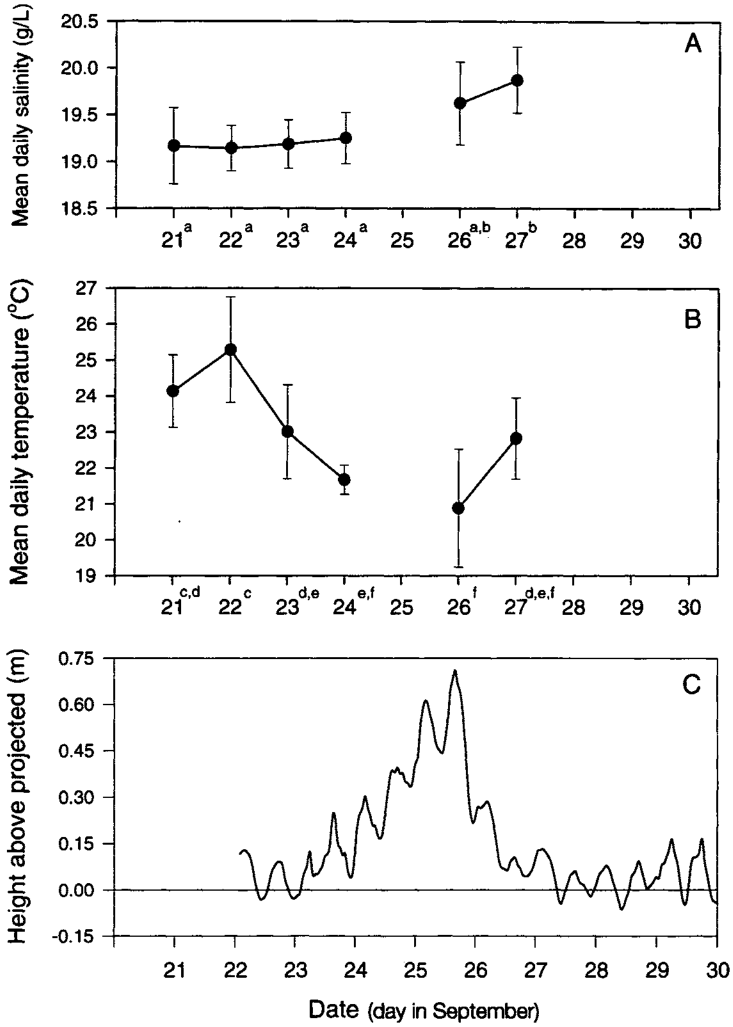

FIG. 10. Mean daily (A) salinity (g/L = practical salinity units [psu]) and (B) water temperature during the field tethering experiment. Water temperature was not significantly different between locations (two-way fixed-factor ANOVA with date and location as independent variables; salinity: $F_{1,31} = 0.85$, $P = 0.3642$; water temperature: $F_{1,31} = 0.07$, $P = 0.7883$); data have been combined for graphical representation. Dates with the same superscripted letter were not significantly different. Error bars indicate ±1 SD. (C) Water height deviation from the projected height for 21 September to 1 October 1992 at VIMS.

dependent emigration is the source of the density-dependent losses found in the settler–recruit–juvenile relationships.

The lack of effect of density on predation-induced mortality is similar to the well-documented recruit–juvenile relationships in sessile invertebrates (Keough and Downes 1982, Connell 1985, Keough 1986, Davis 1987, Sutherland 1990, Roegner 1991) where all losses were considered due to mortality. Yet, reef fishes have demonstrated density-dependent mortality in newly settled organisms and adults (Jones 1987*a*, *b*, Forrester 1990, 1995). More strikingly, Raimondi (1990) found density-dependent losses in settler–recruit relationships in barnacles. His sampling regime may have been critical in finding this relationship: he censused his sites every 12 h. Roegner (1991) also examined settler–recruit relationships in oysters and found density-independent losses and further concluded that weekly censuses may not have been rigorous enough. Censusing on time scales appropriate for the organism to detect the underlying patterns in settler–recruit–juvenile relationships is essential, since in this study and all others (Connell 1985, Raimondi 1990, Roegner 1991) initial mortality was extremely high and Connell (1985) notes that there are few data available that adequately examine the settler–recruit–juvenile relationships.

Tethering artifact

Tethering was demonstrated to be suitable for assessing relative predator-induced mortality on newly settled blue crabs. The lack of statistically significant interaction effects between habitat, crab size, and teth-

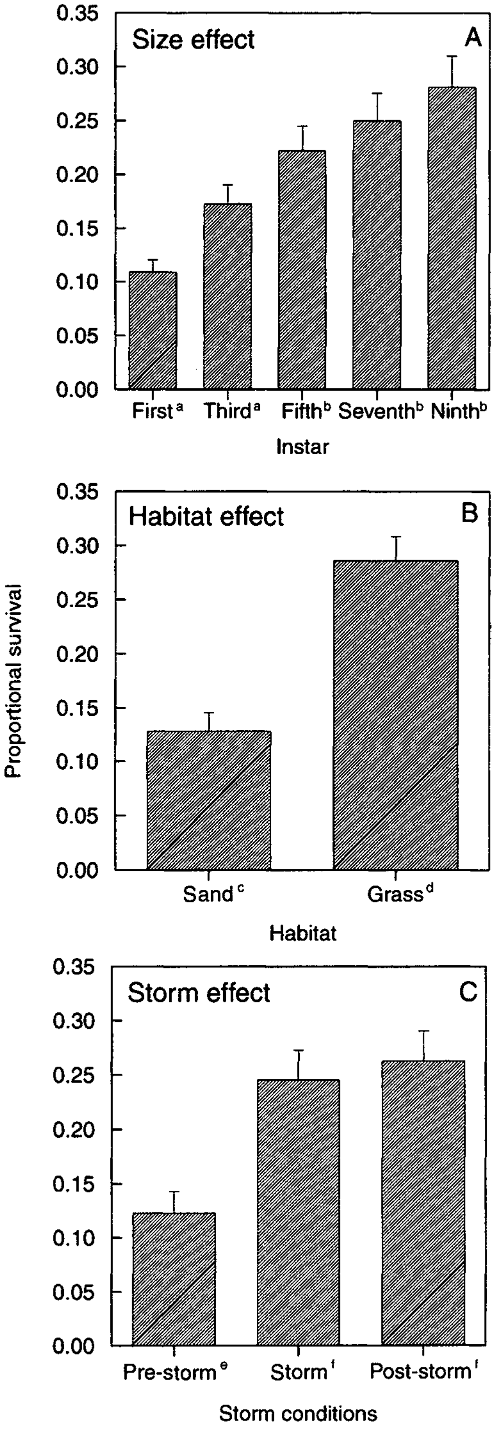

FIG. 11. Mean proportional survival by (A) instar, (B) habitat, and (C) storm conditions. Crab survival increased significantly with crab size, in seagrass, and during storm and post-storm conditions. Treatments with the same superscripted letter did not have significantly different survival. Crab survival did not differ by location or density. Data have been combined for graphical representation. Error bars indicate ±1 SD.

TABLE 10. (A) G test analysis of variance for the field tethering experiment and (B) lower level G test for multiple comparisons.

A)

Source	df	X^2	Power†
Size (S)	4	18.07**	
Density (D)	1	0.24^{NS}	
Habitat (H)	1	15.75***	
Storm (St)	2	8.38*	
$S \times D$	4	1.32^{NS}	
$S \times$ St	8	3.87^{NS}	
$S \times H$	4	4.41^{NS}	
$D \times H$	1	1.83^{NS}	>0.80
$H \times$ St	2	2.75^{NS}	
$D \times$ St	2	0.48^{NS}	
$S \times D \times H$	4	1.09^{NS}	
$S \times D \times$ St	8	2.35^{NS}	
$S \times H \times$ St	8	10.48^{NS}	
$D \times H \times$ St	2	4.17^{NS}	>0.80
$S \times D \times H \times$ St	8	5.78^{NS}	

B)

Main effect	Source	df	X^2
Size	First vs. fifth instar	1	8.57^{NS}
	First vs. third instar	1	3.07^{NS}
	First vs. ninth instar	1	15.40‡
	Fifth vs. ninth instar	1	0.81^{NS}
	First, third vs. fifth, seventh, ninth instars	1	22.33‡
Storm	Pre vs. storm	1	7.92‡
	Pre vs. post	1	11.47‡
	Storm vs. post	1	0.30^{NS}
	Pre, post vs. storm	1	1.30^{NS}

Part A: † Power analysis performed when $P < 0.20$.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ^{NS} $P > 0.05$.
Part B: ‡ $P < P$ (main effect), ^{NS} $P > P$ (main effect).

ering indicated that the technique did not result in treatment-specific bias (Peterson and Black 1994). Crab survival was also significantly lower for tethered crabs, indicating that tethering yields relative, not absolute, estimates of predation.

Previous field studies utilizing tethering to examine relative rates of predation for the blue crab (Heck and Thoman 1981, Wilson et al. 1987, 1990), Caribbean spiny lobster (Herrnkind and Butler 1986, Eggleston et al. 1990, 1992, Smith and Herrnkind 1992, Mintz et al. 1994), American clawed lobster (Wahle and Steneck 1991, 1992), and Dungeness crab (Fernandez et al. 1993) have not quantitatively tested for the presence of bias when measuring relative rates of predation. Such a quantitative test for the presence of bias, emphasizing statistical interactions between treatments (Marshall 1992, Peterson and Black 1994), is a simple and powerful method to determine bias and should be addressed in tethering experiments.

Effects of Tropical Storm Danielle

The close passage of Tropical Storm Danielle had profound effects on the relative rates of predation and habitat utilization of the 0^{+} year class juveniles. Survival of these juveniles was significantly higher during

TABLE 11. (A) Three-way ANOVA table for the abundance of blue crabs during the field tethering experiment. (B, C) Lower-level ANOVA results for (B) the $D \times L$ interaction effect by habitat and (C) the $L \times H$ interaction effect by date. Treatments are arranged in increasing order of abundance and are not significantly different if sharing an underline.

A)

Source	df	SS	F
Date (D)	1	7.24	7.26*
Location (L)	1	1.04	1.04^{NS}
Habitat (H)	1	202.73	203.37***
$D \times L$	1	24.10	24.18***
$L \times H$	1	31.16	31.26***
$D \times H$	1	1.34	1.34^{NS}
$D \times L \times H$		0.05	0.05^{NS}
Error	40	39.89	

B)

	Habitat			
	Sand		Grass	
Date				
21 Sep	GM†	GI†	GI	GM
28 Sep	GI	GM	GI	GM
Location				
Goodwin Islands	28 Sep	21 Sep	28 Sep	21 Sep
Guinea Marsh	21 Sep	28 Sep	21 Sep	28 Sep

C)

	21 September		28 September	
Location				
Goodwin Islands	Sand	Grass	Sand	Grass
Guinea Marsh	Sand	Grass	Sand	Grass
Habitat				
Sand	GM	GI	GI	GM
Grass	GI	GM	GI	GM

* $P < 0.05$; *** $P < 0.001$; $^{NS}P > 0.05$.
† GM, Guinea Marsh; GI, Goodwin Islands.

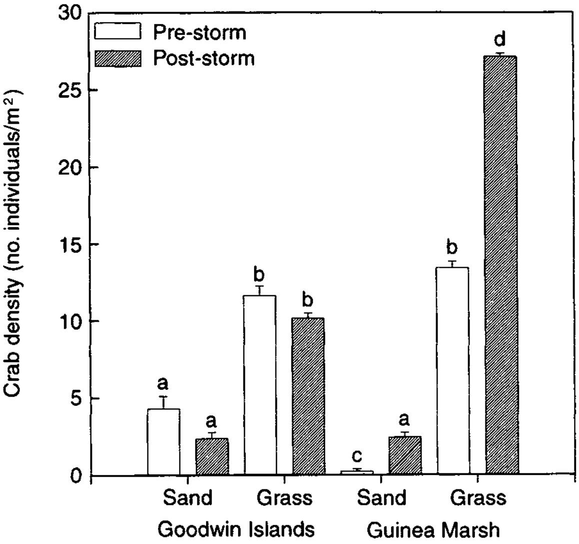

FIG. 12. Mean density of crabs at the Guinea Marsh and Goodwin Islands on 21 September (pre-storm) and 28 September (post-storm) in grass and sand habitats. Bars with the same superscripted letter are not significantly different; error bars indicate ±1 SD.

and immediately following the storm, with relative rates of predation at 0 for a 17-h period during the storm. This finding contrasts that of Aronson (1992) who found no effect of hurricanes on arm loss of tethered star fish, *Ophiothrix oerstedi,* in the Caribbean. Similar to our findings, suspension-feeding tropical sponges ceased filtering water during storm events (Reiswig 1971) as did zooplankton grazing on phytoplankton in the southern Kattegat (Nielsen and Kioerboe 1991).

Decreased predation during the storm may have been due to changing physical factors, which subsequently modified the behavior of predator and prey. There was a 5°C drop in mean water temperature associated with the storm. Sharp decreases in temperature are associated with decreased activity in crustacean predators (Eggleston 1990; R. Lipcius, *unpublished data*). Predators utilizing visual (e.g., Atlantic croaker [*Micropogonias undulatus*] and the naked gobi) and chemotactile (blue crabs) search modes might have been hampered during the storm due to increased turbidity (Gilmurray and Duborn 1981, Minello et al. 1985, 1987) and turbulent flow (Moore et al. 1991, Weissburg and Zimmer-Faust 1993).

The continued high survival after the storm's passing may have been linked to the residual effect of the storm on the physical environment. Water levels did not recede until 28 September, temperature did not rise until 27 September, and salinity increased after the storm. Such time lags in environmental response to storm events are typical in Chesapeake Bay. Time series analysis of actual water height to projected water height

TABLE 12. (A) G test analysis of variance for the size frequency of blue crabs during the field tethering experiment. (B) Lower level G test for the $L \times H$ interaction effect. Treatment levels that are not significantly different share an underline.

A)

Source	df	X^2
Date (D)	4	9.98*
Location (L)	4	9.03^{NS}
Habitat (H)	4	6.73^{NS}
$D \times L$	4	3.86^{NS}
$D \times H$	4	6.77^{NS}
$L \times H$	4	11.74**
$D \times L \times H$	4	7.16^{NS}

B)

Location	Habitat	
Goodwin Islands	Sand	Grass
Guinea Marsh	Sand	Grass

Habitat	Location	
Grass	Goodwin Islands	Guinea Marsh
Sand	Guinea Marsh	Goodwin Islands

* $P < 0.05$, ** $P < 0.01$, $^{NS}P > 0.05$.

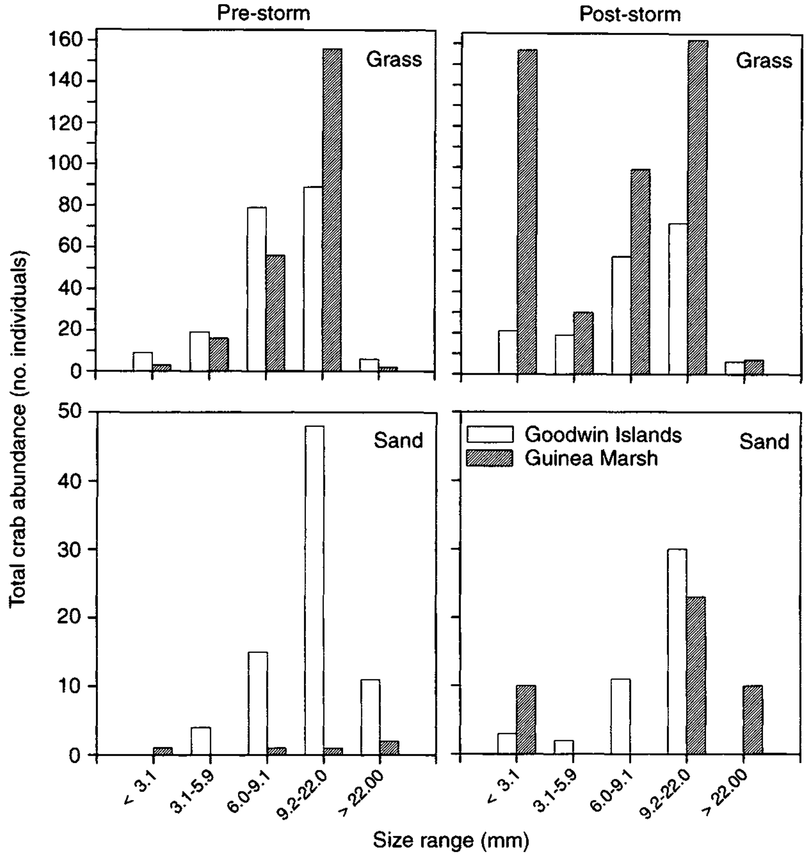

FIG. 13. Size frequencies of crabs during the field tethering study at the Guinea Marsh and Goodwin Islands. Frequencies of crabs >22 mm CW were significantly higher at the Guinea Marsh location, while frequencies of crabs <3.1 mm CW were significantly higher on the post-storm date at both locations, and at Guinea Marsh on both dates.

indicated that it typically takes 3 d for water heights to return to normal levels after a storm surge (D. Evans, *personal communication*). Such delays in the response of the physical environment to pre-storm levels apparently prolong the effect of the storm and contribute to the increased survival of newly settled blue crabs during post-storm conditions.

Blue crab density increased at the Guinea Marsh location after the storm. Crab densities were significantly higher on the northern shore, which was in the lee side of the storm, suggesting that crabs found refuge at the low-energy northern shore and were not moved with the storm surge to the southern shore. While a portion of the increase in crab density was due to a post-storm settlement event near the new moon, there was also a proportional increase in the frequencies of crabs larger than the first instar. The early benthic stages of blue crabs apparently are either transported to or select a low-energy habitat during storm events.

While storms of the magnitude of Tropical Storm Danielle are not frequent in Chesapeake Bay, storms of smaller magnitude are common and probably also influence the distribution, survival, and abundance of blue crabs.

Conceptual model of survival of newly settled blue crabs in vegetated and unvegetated habitats

Not surprisingly, we found higher survival from predation-induced mortality increased with increased habitat complexity and crab size. Higher survival in vegetated habitats has previously been observed in juvenile 0^+ and 1^+ year class blue crabs (Heck and Thoman 1981, Wilson et al. 1987, 1990). However, none of these studies examined survival in the first few instars, which may have a disproportionally high influence on population dynamics. Survival increased with increasing size through the fifth instar and was not significantly different for crabs from the fifth through the ninth instar, indicating that a relative refuge in size from predation for 0^+ year class blue crabs is reached around the fifth instar. Similarly, increased habitat complexity and individual size provide a relative refuge from predation for juveniles of the Caribbean spiny lobster (Herrnkind and Butler 1986, Smith and Herrnkind 1992), American clawed lobster (Wahle and Steneck 1991, 1992), Dungeness crab (Fernandez et al. 1993), and assorted marine invertebrates (e.g., Paine 1966, Ugaccioni and Posey, 1992, Sousa 1993) and vertebrates (e.g., Connell and Jones 1991, Cowan and Houde 1992).

Increasing size within a complex habitat hypothetically creates a situation in which the number of appropriate crevices becomes limiting, resulting in increased predation or emigration to a more suitable habitat (Caddy 1986, Bertness 1989). In this system, seagrass and algal habitats provide structure that creates suitable niches for hiding in both the leaf structure (Robinson and Wellborn 1987, Wellborn and Robinson 1987, Ryer 1988, Hacker and Steneck 1990) and rhizome mat (Orth et al. 1984). The number of niches formed by seagrasses are unlikely to be limiting as a refuge. Rather, as the crabs grow, foraging efficiency may be reduced, competition for food increased, or density of the rhizome mat prohibit burrowing ability, causing emigration to less complex habitats.

Given the results of this study, survival of newly settled blue crabs may be modeled schematically (Fig. 14) as a function of habitat type and crab size. Survival increases rapidly with increasing crab size through the ninth instar and may be described by a hyperbolic function (Fig. 14); however, habitat type alters the function critically in several ways. First, survival from predation-induced mortality of newly settled blue crabs is higher in vegetated habitat, with a subsequent reduction in the difference between survival by habitat as size increases (Fig. 14). Second, crabs smaller than the third instar are not found in unvegetated habitats, suggesting that they (1) do not settle in these habitats, (2) do not survive if they settle in unvegetated habitats, or (3) are so sparsely distributed that sampling efficiency is inadequate. This indicates that, while the shape of the survival curves may be the same, the size where survival increases significantly is dependent on habitat complexity (Fig. 14). Subsequently, survival of newly settled blue crabs is likely dependent on the availability of complex habitat.

Conclusions

The controlling factors of populations and the proportional influence of each factor vary during different life history stages (Paulik 1973, Fogarty and Idoine 1986, Lipcius and Cobb 1994). The results of this study present evidence that density-dependent processes influence the settler–recruit–juvenile relationships within the initial nursery habitat and subsequently detail the effects of habitat complexity, crab density, and size as refuges from predation.

This study is unique in demonstrating a density-dependent loss within the 0^+ year class of a large mobile crustacean within the initial nursery habitat. Settler–recruit relationships in marine ecosystems have been difficult to document because of high initial mortality of settlers (Keough and Downes 1982, Connell 1985, Keough 1986, Davis 1987, Forrester 1990, Raimondi 1990, Sutherland 1990, Roegner 1991) and the difficulty of censusing populations at time scales relevant to the mortality (Connell 1985, Roegner 1991). Crustaceans lend themselves to these types of studies because growth is associated with shedding of the exoskeleton and has little variation between instars. Some intermolt periods last only a couple of days and losses between successive instars are easily enumerated in censuses of closed systems, such as nursery habitats. These factors, as well as 10 consecutive years of data, have allowed us, for the first time, to examine settler–recruit–juvenile relationships for any mobile marine organism.

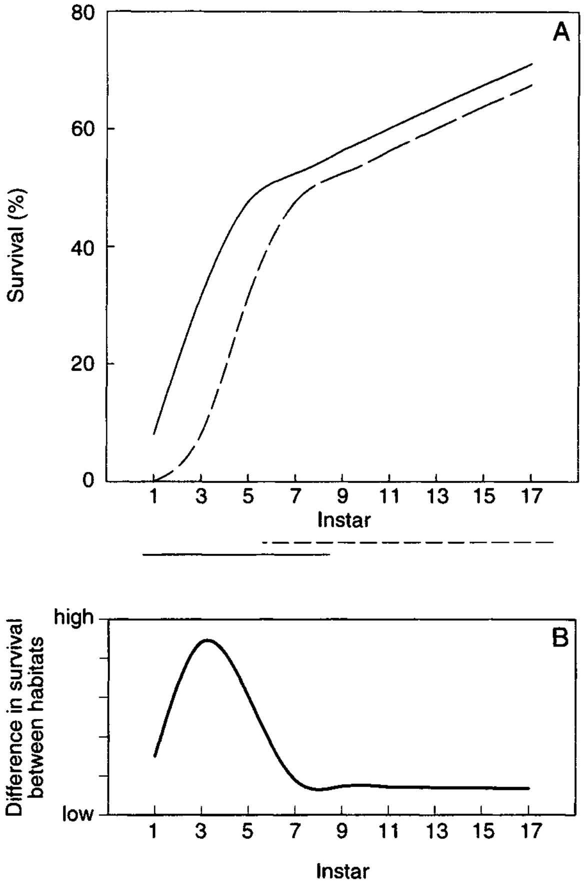

FIG. 14. Model of hypothesized relationship of blue crab survival (A) by size in vegetated and unvegetated habitats and (B) as the difference in proportional relative survival between habitats. The lines underlining instar sizes of the x axis of (A) indicate the primary habitat for that instar (solid lines indicates vegetated habitats; broken lines, unvegetated habitats). Survival curves are significantly different by habitat through the first nine instars with the relative difference decreasing as size increases. Survival increases linearly in both habitats after the ninth instar and may be asymptotic for adult crabs. Survival in vegetated habitats through the first nine instars is described by a hyperbolic function; it is described by a sigmoid function in unvegetated habitats.

Researchers have focused their attention on recruit–juvenile–adult relationships of sessile invertebrates (Keough and Downes 1982, Connell 1985, Keough 1986, Davis 1987, Sutherland 1990, Roegner 1991) and found the relationships to be density-independent.

These studies had long periods between censuses that may mask changes in relative mortality between successive life history stages.

In only one other study, that by Raimondi (1990) in which barnacles were studied, has the settler–recruit–juvenile relationships at the time scales relative to the life of the organism been examined (Connell 1985). Patterns in settler–recruit–juvenile relationships in both barnacles and blue crabs change from density-dependent to density-independent from recruit to the juvenile phase. Considering that barnacles are sessile and crabs are mobile invertebrates, it would seem that the underlying mechanisms are different. Density-dependent mortality is the most likely underlying mechanism in barnacles, while emigration is the most likely mitigating factor in this study.

Further, in studies using reef fishes, researchers have found density-dependent recruit–juvenile–adult relationships where censusing occurred at time scales relevant to the life history of the organism (Jones 1987*a*, *b*, Forrester 1990, 1995). As well, these data are congruent with suggested settler–recruit–juvenile relationships for other large decapod crustaceans. By examining larval abundance and subsequent harvests (stock–recruit relationships), Fogarty and Idoine (1986) concluded that the early benthic stages of the American clawed lobster may be subject to density-dependent controls. However, a density-dependent relationship within the 0^+ year class of the American clawed lobster has yet to be demonstrated. Phillips (1990) re-evaluated the claim that, for juvenile western rock lobster (*Panulirus cygnus*), density-dependent processes at nursery reefs determined year class strength. Instead, it was suggested that density-dependent processes only affect the population at the extreme highs and lows of population density.

Ontogenetic shifts in habitat utilization are common for other decapod crustaceans such as the Caribbean spiny lobster (Herrnkind et al. 1975, Marx and Herrnind 1985, Herrnkind and Butler 1986) and American clawed lobster (Cobb et al. 1983, Botero and Atema 1982, Wahle and Steneck 1991), but were unknown for earliest benthic juveniles of the blue crab. Ideally, the shift in habitat occurs when the risk of predation is higher than the energetic value gained by remaining in the habitat (Werner and Gilliam 1984). Frequently, ontogenetic shifts in habitat are associated with behavioral adaptations that additionally reduce predation risk (Connell and Jones 1991, Eggleston and Lipcius 1992, Smith and Herrnkind 1992).

Juvenile and adult blue crabs partition themselves by habitat type within Chesapeake Bay (Van Engel 1958, Milliken and Williams 1984, Hines et al. 1987). In this system, seagrass beds of the lower Chesapeake Bay serve as the initial nursery habitat (Heck and Thoman 1984, Orth and van Montfrans 1987, Orth and van Montfrans 1990). Blue crabs in the 0^+ year class are rarely found outside of vegetated habitats until the third instar, and not at significant densities until the fifth instar (Orth and van Montfrans 1987). In this study, the frequency of 0^+ year class crabs was significantly higher in vegetated habitats, while the frequency of 1^+ year class crabs was significantly higher in unvegetated habitats. The appearance of fifth instar crabs in unvegetated habitats was associated with a decrease in crab densities in seagrass habitats and the low variability in annual mean density associated with crabs larger than the seventh instar, indicating an ontogenetic shift in habitat utilization.

Further evidence for an ontogenetic shift in habitat use is provided by the inter-instar relationships. The densities of first through seventh instars were dependent on each other and described by non-linear functions, indicating that these instars are regulated by density-dependent processes such as predation and emigration. However, the inter-instar relationship between seventh and ninth instars was linear, indicating that density-independent processes are controlling these instars. Further, the size refuge associated with vegetated habitats is maximal between the fifth and ninth instar, resulting in a predation risk that may be similar in vegetated and unvegetated habitats by the ninth instar. If predation pressure is equal between habitats, then other factors (e.g., food availability) may be controlling emigration, the most likely source of the density-dependent losses in the nursery habitat, to unvegetated habitats.

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