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Effects of the Habitat and Size-Specific Predation on the Ontogenetic Shift in Habitat use by Newly Settled Blue Crabs, Callinectes sapidus

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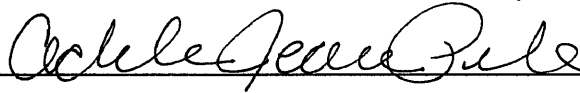
A thesis presented to the faculty of the

School of Marine Science
The College of William and Mary

in partial fulfillment
of the requirements for the degree of
Master of Arts

Adele Jean Pile
August 1993

Approval Sheet

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

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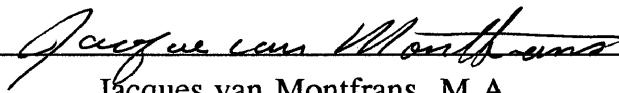
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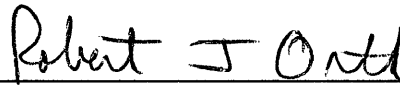
Romuald N. Lipcius, Ph.D.
Committee Co-Chairman/Advisor

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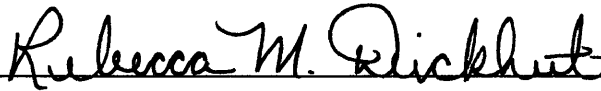
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This thesis is dedicated to my brother, Chris, and sister, Ronni, and the little engine that could.

Acknowledgements

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Abstract

Newly settled blue crabs, *Callinectes sapidus*, are found in highest densities in seagrass beds within the Chesapeake Bay. Densities of newly settled blue crabs in seagrass beds were highly variable from 1983-1992 and are regulated by density-dependent processes. The mean annual densities 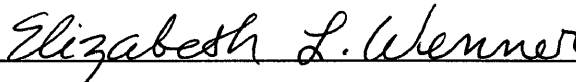of larger instars were dependent on smaller instars. These inter-instar relationships between the mean annual densities first seven instars were determined to be either hyperbolic or parabolic functions. The inter-instar relationship began to decay at the fifth instar, the size when crabs begin to emigrate to unvegetated habitats. Subsequent laboratory and field tethering experiments were performed to assess the effects of habitat, crab size, and crab density on the relative rates of predator-induced mortality on first, third, fifth, seventh and ninth instar crabs. A full-factorial experimental design laboratory experiment with tethered and untethered prey was conducted and determined that tethering was an unbiased technique for assessing predation -induced mortality on newly settled blue crabs. Crab survival was significantly higher in vegetated habitats (ANOVA, $F_{1,199}=16.00$, $p < .001$), with increasing crab size (ANOVA, $F_{4,199}=61.10$, $p < .001$), and in the absence of a tether (ANOVA, $F_{1,199}=7.677, p < .01$). Similarly, the field tethering experiments performed at replicate locations near the mouth of the York River, Virginia indicated that crabs survival was significantly higher in vegetated habitats (G-Test, $X^2_1=15.75$, $p < .0001$) and with increasing crab size (G-Test, $X^2_4=18.07, p < .001$); densities of tethered crabs had no effect on survival (G-Test, $X^2_1=.24$, $p > .05$). Additionally, the close passage of Tropical Storm Danielle to the field location allowed for the assessment of the effects on relative rates of predation and on habitat utilization by newly settled blue crabs. Crabs had significantly higher survival during and after the tropical storm (G-Test, $X^2_2=8.38$, $p < .01$) and significantly higher densities at locations of lower energy regime (ANOVA, $F_{1,40}=202.73$, $p < .0001$).

Introduction

Structurally complex habitats are common in nature and have been generally characterized by diverse assemblages of high density, small-sized individuals. However, the ecological processes that contributes to this pattern are poorly understood. In shallow marine environments the association of small mobile organisms with structurally complex habitats has been demonstrated to be in response to differential predation (Woodin 1978, Sih et al. 1985) as well as selection due to predation pressure (Leber 1985, Main 1987). This is true for small organisms (Ryer 1988, Hacker and Steneck 1990) as well as juvenile forms of larger benthic (Wahle and Steneck 1992) and demersal (Heck and Thoman 1984, Kneib 1987) species that utilize structurally complex habitats as initial nursery habitats. Organisms that utilize structurally complex habitats as nursery habitats exhibit a shift in habitat due to the decline in effectiveness of predation refuge afforded by the structurally complex habitat declines as size increases. As animal size increases, animals must compete for a limited number of appropriately sized niches, emigrate to appropriate habitat, or halt growth until the appropriate habitat is available (Caddy 1986). Typically these organisms inhabit a variety of habitats during complex life histories.

In recent years a more comprehensive approach to understanding the population dynamics of organisms with complex life-history patterns has occurred. Many researchers hypothesize that stochastic forces and density-dependent processes regulate populations during various phases of the life-history (Paulik 1973, Fogarty and Idoine 1986, Lipcius and Cobb 1993). Within these models, densities of the larval life-history stage is deemed to be controlled by stochastic variation (e. g. meteorological or

oceanographic processes) resulting in density-independent survival and dispersal. Populations of early juvenile stages, sub-adults, and adults are regulated by density-dependent processes such as predation and emigration.

Further, Menge and Sutherland (1986) suggest that there are three major ecological processes that regulate communities and ultimately individual species abundances; physical factors, predation, and competition. The Menge-Sutherland model define predation and competition as density-dependent processes and physical factors as density-independent processes. Mathematically, density-independent processes are represented by linear functions and density-dependent processes by nonlinear functions.

Ontogenetic shifts in habitat utilization are common for early benthic forms of large decapod crustaceans (Smith and Herrnkind 1992, Wahle and Steneck 1992). Predation on juveniles is inversely related to habitat complexity (Leber 1985, Wilson et al. 1987, Eggleston et al. 1990, Connell and Jones 1991) and increasing size (e. g., Paine 1966, Wilson 1975, Robinson and Wellborn 1987). Ideally, the shift in habitat occurs when the risk of predation is higher than the energetic value gained by remaining in the habitat. Frequently, ontogenetic shifts in habitat are associated with behavioral adaptations that additionally reduce predation risk (Connell and Jones 1991, Smith and Herrnkind 1992, Eggleston and Lipcius 1993).

The blue crab, *Callinectes sapidus*, is an estuarine species and typifies all of these processes. Within the Chesapeake Bay, female blue crabs migrate to the mouth where larvae are released in early summer through late fall (Van Engel 1958, Provenzano et al. 1983). Larval development through 7 or 8 zoeal stages occurs on the continental shelf

(Costlow and Bookhout 1959, McConaugha et al. 1983, Epifanio et al. 1989) and is followed by a reinvasion of the estuary by the megalopal stage from July to November (van Montfrans et al. 1990). The initial nursery habitat for young juvenile blue crabs is seagrass (Heck and Thoman 1984, Orth and van Montfrans, 1987, Lipcius 1993). Newly recruited juveniles are found in the highest densities in seagrass beds and are not found in unvegetated habitats until the third instar and are at very low densities. Fifth instar crabs are found in moderate densities in both vegetated and unvegetated habitats, whereas by the time the crabs have reached between 18-20 mm spine to spine carapace width they are found in highest abundance in unvegetated habitats (Orth and van Montfrans 1987). Juvenile crabs are found in shallow-water lower salinity regions typified by unvegetated habitats and are partitioned by sex, molt stage and size (Miliken and Williams 1984, Hines et al. 1986). Mature crabs utilize higher salinity deep-water habitats.

Primarily, recruitment to the benthic form occurs in the seagrass beds of the lower Chesapeake Bay and tributaries. Newly settled blue crabs are found only in vegetated habitats which suggests that they are either selecting these habitats or not surviving in unvegetated habitats. Therefor, the abundance of larger newly settled crabs is dependent on the abundances of the smaller instars during the period of residence within the seagrass beds. The function that describes the relationship of larger to smaller instars indicates what ecological processes may be regulating the abundances of newly settled blue crabs. This study was undertaken to address (1) the relationships between successive instars within the initial nursery habitat, (2) the effects of habitat complexity, crab size, and crab density on predation-induced mortality with field and laboratory experiments.

Additionally, Tropical Storm Danielle moved along the mid-Atlantic coast during the field experiments allowing for the assessment of the storms effect on the habitat utilization and predation-induced mortality of newly settled blue crabs.

Materials and methods

<u>Study sites</u>

Benthic suction samples were collected from 1983 to 1992 in Brown's Bay, which is located north of the mouth of the York River, a tributary of lower Chesapeake Bay (Figure 1). Field tethering experiments were performed at replicate locations within the York River: Goodwin Islands, located on the south shore of the York River, and near Guinea Marsh, located on the north shore (Figure 1). Both sites are characterized by dense beds of eelgrass, *Zostera marina*, and widgeongrass, *Ruppia maritima*, and adjacent unvegetated areas of muddy sand. Tidal range is generally 0.8-1.0 m and underwater visibility 1-2 m. Samples from the plankton and artificial settlement substrates, and measurements of wind speed, wind direction and water height were 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 approximately 12 km upstream from the mouth of the York River (Figure 1) .

Field experiments were conducted 21-28 September 1992. Tropical Storm Danielle moved along the central Atlantic coast from southeast of Cape Hatteras to Pennsylvania on 23-26 September 1992, impacting both the Goodwin Islands and Guinea Marsh locations (Figure 2). Tropical Storm Danielle 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 1.0 m. Underwater visibility decreased to 0 m at the field locations.

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Figure 1. Map of the field sites. 1=Brown's Bay the location of the long term benthic sampling, 2=Goodwin Islands and Guinea Marsh the location of field tethering experiments, 3=Virginia Institute of Marine Science location of the plankton sampling and artificial substrate deployment.
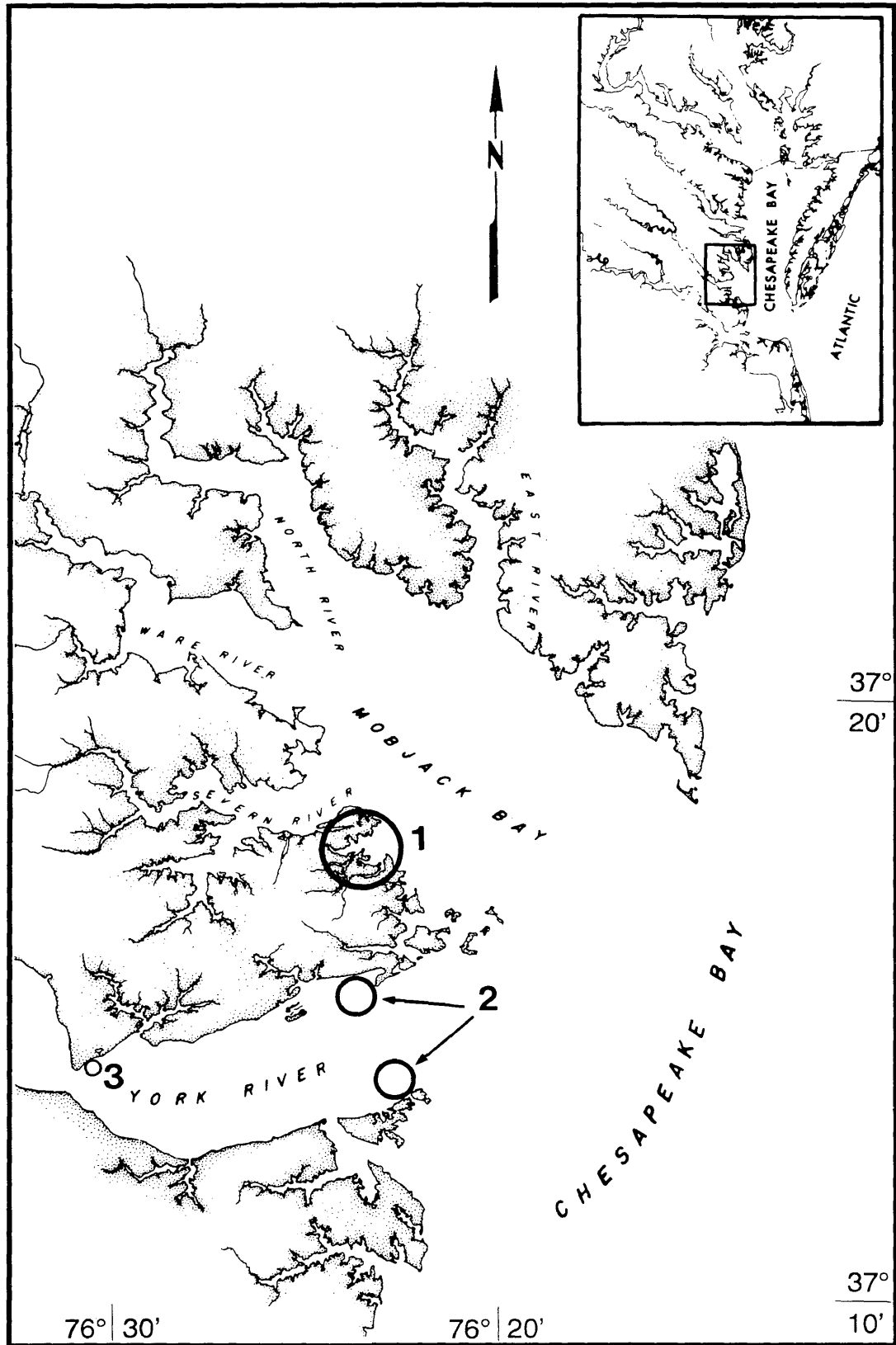
Figure 2. Map of the path of Tropical Storm Danielle from 22-26 September 1992.

Adapted from NOAA preliminary report. From 22-25 September each dot represents the

storms location every 12 h and every 6 h from the 25th -26th.

80°　　　　　　　　75°　　　　　　　70°

40°

VIRGINIA

9/26

CHESAPEAKE
BAY

**NORTH
CAROLINA**

ATLANTIC OCEAN

35°

9/25　　9/24

9/23
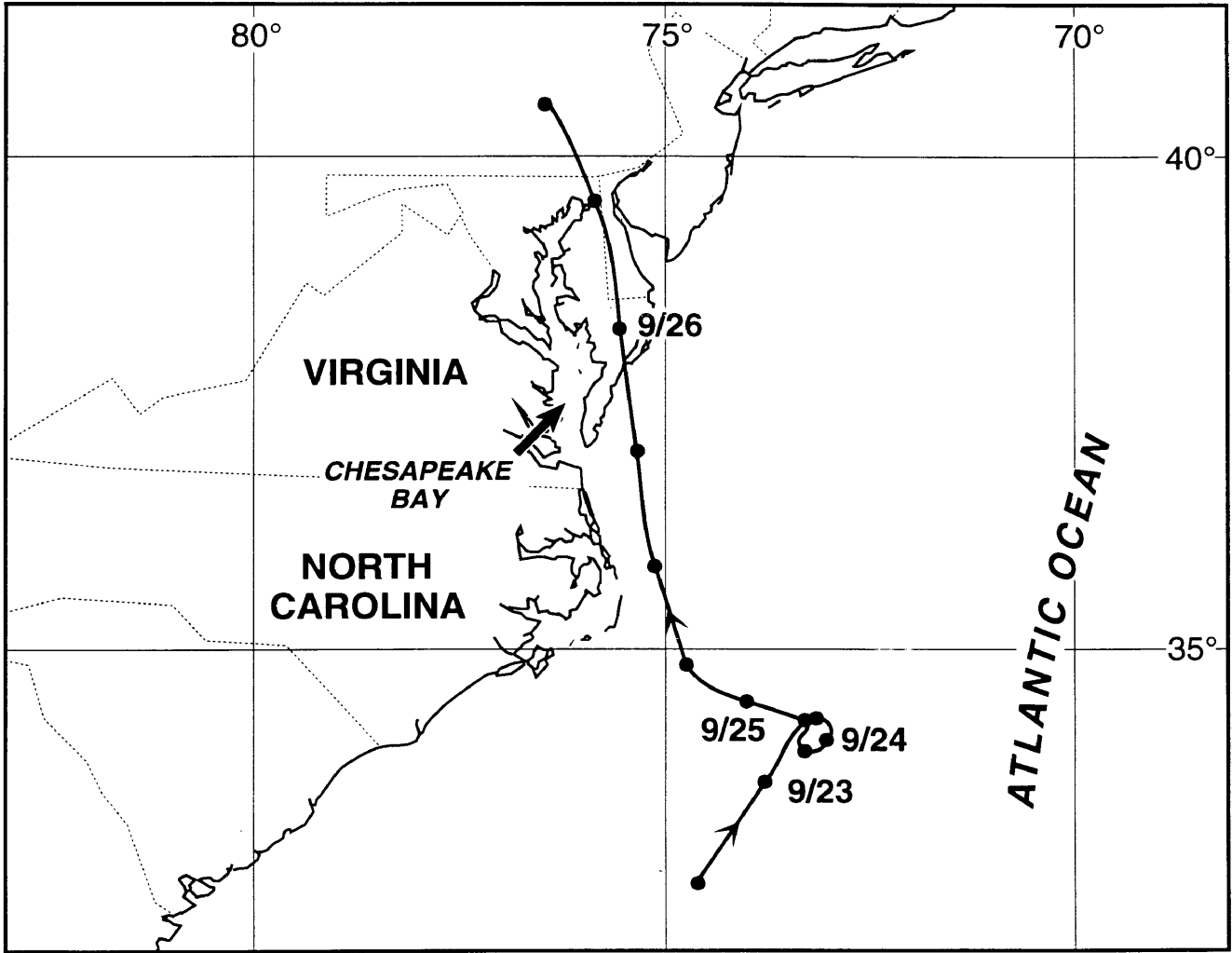
Benthic sampling

Macrobenthos were sampled in Brown's Bay from 1983-1992 using a suction dredge apparatus (Orth and van Montfrans 1987). From 1983-1989 six 3 m² cylindrical drop nets were haphazardly deployed in areas of 100% vegetation coverage during low tide, suctioned for 10 min, and dip netted with a 1.2 mm mesh net for 5 min. Efficiency studies by Lipcius (1993) modified the sampling protocol from 1990-1992 to deployment of 1.674 m² rings, suctioning for 6 min, and dip netting for 3 min. Samples from 1983-1987 were live-sorted, whereas samples from 1988-1992 were frozen for processing at a later date. Blue crabs were enumerated and spine to spine carapace width (cw) measured as 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 and ocular micrometer. Crabs > 15 mm cw were measured with calipers to the nearest 0.1 mm.

Samples were collected during the summer, fall, and winter of each year either monthly or biweekly, resulting in 90 sample dates. Sample dates from July through December were used in this analysis (Table 1).

Size classification

Crabs were categorized by instars using two systems of size classification (Table 2). The stage between molts is the instar, hence, the number of the instar represents the number of molts to obtain a certain size. This is useful for categorizing small blue crabs since growth is relatively uniform until approximately 10 mm (Newcombe et al. 1949). Size ranges for each instar were adapted from laboratory growth studies performed from

Table 1. Sample dates for the years 1983-1992 that were used to determine the annual mean densities.

Year	Dates of Samples	N
1983	7/19, 8/15, 8/29, 9/12, 9/26, 10/13, 10/28, 11/7, 12/7	9
1984	7/31, 8/14, 8/29, 9/10, 9/24, 10/30, 12/10	7
1985	7/8, 8/5, 8/19, 9/3, 9/16, 9/30, 11/12	7
1986	7/8, 8/5, 9/2, 9/15, 9/29, 10/27, 12/12	7
1987	7/15, 8/3, 8/17, 9/1, 9/16, 10/1, 11/2, 12/1	8
1988	7/12, 8/3, 8/17, 8/31, 9/13, 10/3, 11/3, 12/1	8
1989	7/11, 8/1, 8/16, 8/29, 9/13, 9/28, 10/25	7
1990	7/12, 8/1, 8/16, 8/29, 9/18, 9/27, 10/30, 12/11	8
1991	7/11, 8/1, 8/15, 8/29, 9/17, 10/2, 11/4, 12/9	8
1992	7/13, 8/3, 8/18, 8/31, 9/18, 10/1, 10/29, 12/9	8

Total N   77

Table 2. Size of instar, number used to replicate each density on a tethering grid, and total crabs tethered in the field by habitat.

Instar	Spine to Spine Carapace Width (mm)		Total per Grid[4]		Total per Habitat	
	Newcombe[1]	Newcombe-Van-Engel[3]	23 crabs/m²	46 crabs/m²	Sand	Grass
First	2.2- 3.0	2.2- 3.0	6	18	278	284
Second	3.1- 4.2	3.1- 4.2				
Third	4.3- 5.9	4.3- 5.9	3	7	117	120
Fourth	6.0- 7.4	6.0- 7.6				
Fifth	7.5- 9.1	7.7- 9.7	2	5	58	60
Sixth	9.2-10.6	9.8-11.8				
Seventh	10.7-12.6	11.9-13.3	1	2	34	36
Eighth	12.7-14.1	13.4-16.5				
Ninth	14.2-16.1	16.6-18.4	1	2	34	36

[1] Adapted from Newcombe et al. 1949.
[3] Adapted from a combined means from Newcombe et al. (1949) and Van Engel (unpublished data).
[4] See materials and methods for field study. Newcombe size ranges used.1943-1946 by Newcombe et al. (1949) and

Van Engel in 1951 (personal communication) at VIMS. Size ranges for each instar were determined from the mean and standard deviations reported in the two studies. The first system of size ranges was modified from Newcombe et al. (1949), and the second from a combination of Newcombe et al. (1949) and Van Engel (unpublished data). All analyses were done using both systems.

Annual mean densities of each instar were determined from sampling dates when an instar was present in at least 50% of the replicate rings. 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 (approximately 10 days; Van Engel, Pile unpublished data), bimonthly sampling that did not occur immediately following a recruitment event would miss most of the first and second instars.

The size ranges for the first through fourth instars are not different using the Newcombe and Newcombe-Van Engel size classification systems. However, the size ranges for the Newcombe-Van Engel instars are larger than the Newcombe size ranges, which results in different annual density estimates using the two systems. Differences between the annual density estimates for the fifth, seventh, and ninth instars using the two classification systems were evaluated with (1) 95% confidence limits of annual density, a, calculated as $a \pm d$, where $d=t(a(1-a)/n)^{0.5}$, t being the normal deviate (1.96 at the 95% level, and n the sample size (Sokal and Rohlf 1981) and (2) correlation of the annual density determined with Newcombe size ranges to the annual density determined

using the Newcombe-Van Engel size ranges.

Instar-specific abundance and relationships

Relationships between annual mean densities of first, third, fifth and seventh instars with larger instars were determined using simple linear regression, a general functional response model, and the Ricker function. 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, Lipcius et al. 1993 in review). First, a linear regression was performed on untransformed annual mean densities and 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 = yearly mean density of the larger instar,

X = yearly 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,

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 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 1983-1992),

$B =$ the value of X at which $Y = 0.5(A)$, and

$\beta =$ 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:

$$Y = A(X)\exp(-BX)$$

where $Y =$ yearly mean density of the larger instar,

$X =$ yearly mean density of the smaller instar.

The linearized form of the equation is:

$$\ln(Y/X) = \ln(A) - BX$$

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

The best fitting function was determined by meeting the statistical assumption of linear regression of randomly distributed residuals as determined by visual inspection. Additionally, r^2 values and the significance of the regression were considered to determine the best fitting function when more than one was significant.

Experimental animals

First, third, fifth, seventh, and ninth instar crabs were used in all experiments (Table 2). These instars appear to be ecologically significant in that through the third instar crabs are residents in the seagrass beds; emigration to unvegetated habitats begins at the fifth instar and completed by the ninth instar (Orth and van Montfrans 1987). Juveniles and megalopae of the blue crab were collected nightly from the plankton at the VIMS Ferry Pier, sorted by instars using the Newcombe size ranges, and held in the laboratory until needed. Crabs were staged in the laboratory so that the day of molting was known; only crabs that had molted within 24 h were used, to reduce the occurrence of crabs molting off their tethers. First and third instar crabs were laboratory reared and maintained on a diet of frozen adult *Artemia*(sp); 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, Mintz 1992, Fernandez et al. 1993, Lipcius et al. 1993 in review) 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 treatments on survival.

Tethering material depended on the size of the crab. First and third instars were tethered with nylon thread, fifth and seventh instars with 4-pound-test monofilament line, and ninth instars with 6-pound-test monofilament line. Tethers were 5 cm long and tied to a #12 snap swivel. Tethering involved: (1) placing the free end of the tether in cyanoacrylate glue (Krazy Glue Extra Strength Gel, The Bordon Company), (2) placing 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 sec, and (4) checking the tether before returning crabs to the water. Crabs were tethered and held in the laboratory 12 to 24 h prior to use.

Tethered crabs were observed in the laboratory and with underwater video equipment in the field. These crabs exhibited natural behaviors after becoming accustomed to the tether; observed behaviors included foraging, feeding, burial into the substrate, climbing on seagrass, and attempted escapes from predators. The only means of escapement by a crab from the tether was to molt, a process which was 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.

<u>Laboratory Experiment</u>

A laboratory study conducted from October to December 1992 tested: (1) whether tethering provides accurate and 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 (e.g. Heck and Thoman 1981, Herrnkind and Butler 1986, Wilson et al. 1987, 1990, Barshaw and Able 1990, Eggleston et al. 1990, Wahle and Steneck 1991,1992, Mintz 1992, Smith and Herrnkind 1992, Fernandez et al. 1993), mollusks (Poole et al. 1991, Ambrose and Irlandi 1992, Marshall 1992) and fish (Shulman 1985, McIvor and Odum 1988), only two studies (Barshaw and Able 1990, Marshall 1992) have quantitatively partitioned tethering artifacts.

Tethering artifact may be partitioned into two types, accuracy and bias. Accuracy is defined as the closeness to the absolute value. Since tethering is assumed to measure relative rates of predation and not absolute predation rates, previous investigators have assumed that the test is not an accurate measure of predation. This implies that the relative effects of treatments will be proportional in untethered organisms, thereby allowing use of the technique to quantify relative predation rates. However, bias may be introduced into the data if tethering effects are specific to the treatments (e.g. tangling of the tether in one type of habitat and not another). Such biases do not decrease survival proportionally across all treatments, and thereby confound 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, Mintz 1992, Smith and Herrnkind 1992, Fernandez et al. 1993, Lipcius et al. 1993 in review) but none have conducted experimental tests of bias.

Accuracy is addressed as a main effect of tethering in the context of a full-factorial experimental design using tethered and untethered experimental animals. If the effect is statistically significant tethering would decrease survival and relative rates of predation are measured. Bias is indicated by statistically significant interaction effects and if present precludes utilization of tethering to measure relative rates of predation within the experimental framework.

This study was designed to determine the accuracy of the tethering if there was any bias between the treatments of predator presence or absence, habitat, and crab size with tethered and untethered crabs. Tethering artifact trials were conducted in 12 aerated 10-gallon aquaria with the randomly assigned factors of habitat (vegetated and unvegetated), tethering (tethered and untethered), size (first, third, fifth, seventh and ninth instars), and predators (presence or absence). Aquaria were filled with 2 cm of 500 um sieved sand and 20 cm of filtered estuarine water. Vegetated aquaria were haphazardly planted with eelgrass trimmed to a shoot height of 20-24 cm and planted equivalent to 300 shoots/m^2 (Orth and Moore 1986). Grass was cleaned of epifauna and epiphytes by soaking in fresh water. Photoperiod was on a 12/12 cycle; water temperature and salinity were measured at the beginning and end of each trial. The mean water temperature was 23.6° C (1.0° C sd) and mean salinity was 19.6 ppt (0.5 ppt sd).

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 0.1 x 0.03 m vexar mats, which were buried 0.1 m apart in the sand. The predator suite 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. These predators have been observed in the field consuming early instar crabs. Predators were starved for 24 h prior to experiments. Predators were removed after 24 h, aquaria drained through a 500 um sieve, and remaining crabs enumerated. Missing claws or walking legs were noted for survivors and considered as sublethal predation. Crabs that were killed by predators were indicated by a small piece of carapace remaining on the tether, by obvious mortal wounds, or by complete absence. Crabs that died during trials due to the fitness of the crab 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 composed 1% of all crabs and their percentage did not differ significantly between tethered and untethered crabs (ANOVA, $F_{1,206}=2.00$, $P=0.139$, $0.50 <$ power < 0.55) or trial (ANOVA $F_{4,206}=1.50$, $P=0.204$, power > 0.80).

Numbers of surviving crabs were converted to proportion of survival per treatment and analyzed as dependent on habitat, tether, and crab size using three-way fixed-factor analysis of variance models (ANOVA, Sokal and Rohlf 1981). Numbers of surviving crabs with sublethal predation were converted to proportion per treatment and analyzed as dependent on habitat, tether, crab size, and predator presence or absence using four-

way fixed-factor ANOVA models (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 complexity, 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 (September 21-22), during (September 23-24), and after the storm (September 26-27) and assessment of the effects of the storm on the survival of newly settled blue crabs. Rough weather prevented deployment of crabs on September 25th.

Tethering grids were used to facilitate the replication of crab densities and the retrieval of tethered crabs in the turbid conditions at the field sites. Tethering grids were 1.1 x 1.1 m rebar frames with 50-pound test monofilament line woven at 0.1 m intervals (Figure 3). This created a 1 m^2 tethering arena capable of holding 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 utilization to determine if individual crabs or grids could be considered independent for statistical analysis. Eight grids with 45 crabs/m^2, proportionally correct for the first, third, fifth, and seventh instar, were deployed at the Guinea Marsh site in vegetated and unvegetated habitats for 24 h during

Figure 3. Schematic diagram of a tethering grid.

1.1 m

1.1 m

0.1 m

3/8" Rebar

50 pound-test
monofilament line
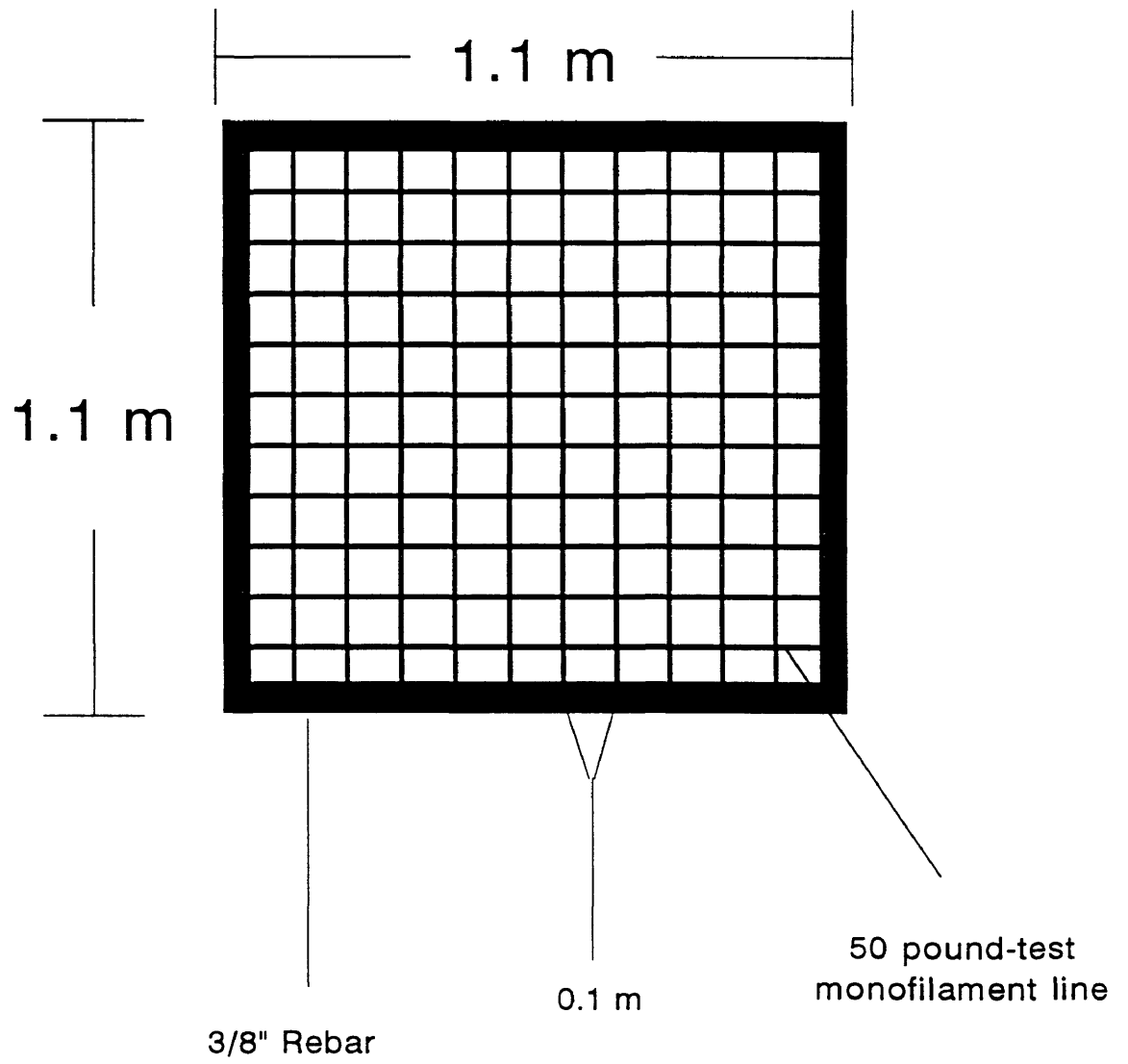
a three day period. There was no apparent pattern in the proportional survival due to size or habitat nor a significant correlation between proportional survival of each instar and grid. The absence of pattern in crab survival on the grids indicated that the assumption of independence between individual crabs for statistical analysis was reasonable.

A total of 1,057 crabs were randomly allocated to the grids at densities of 23 crabs/m² (low) or 46 crabs/m² (medium). Size-frequency analysis of the first through seventh instars at Brown's Bay from 1983-1988 (July through December) indicated the most common densities were 22, 41, and 89 total juvenile crabs/m² with densities rarely reaching 89 crabs/m². The correct proportion of each instar (Table 2) was allocated to a grid 12 to 24 h prior to a trial, 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 (Figure 4). 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 down 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

Figure 4. Schematic diagram of tethering grid placement during the field tethering experiment. L=low density grid M=medium density grid.

Guinea Marsh

L

M

L

M

Grassbed

Adjacent sandy area

York River

M

L

Grassbed

Adjacent sandy area

Goodwin Islands

M

L
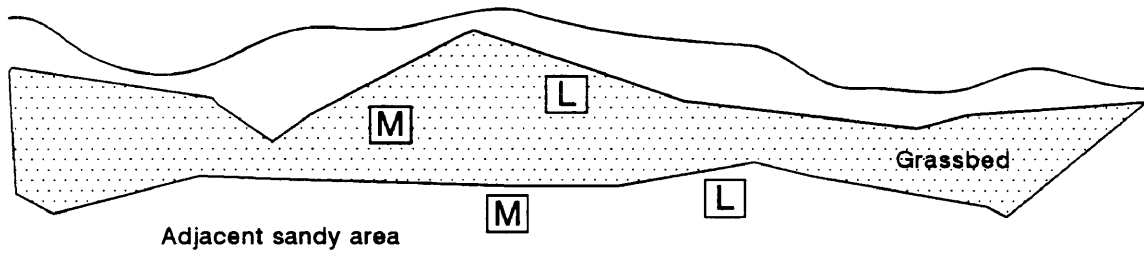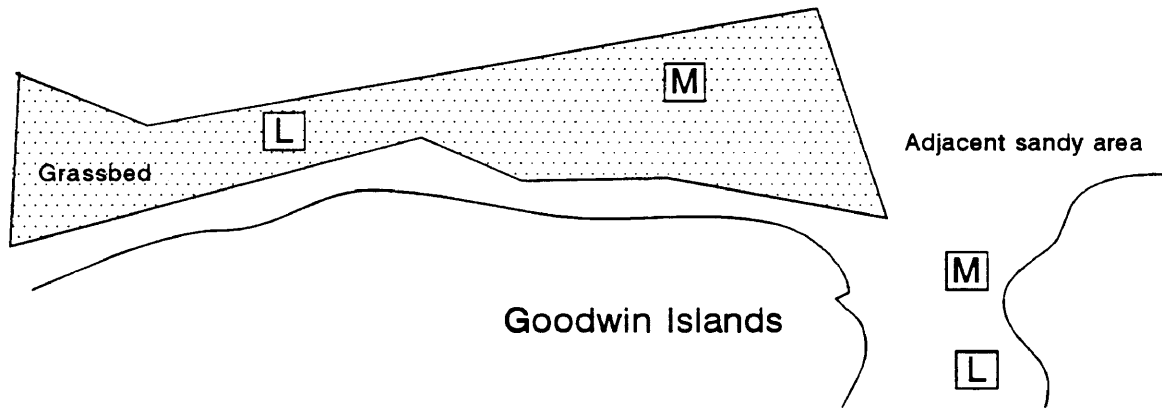
proboscis to extract the internal soft body tissues of the constrained tethered crab, leaving a hollow intact carcass. These crabs were considered tethering artifact and not used in analyses.

Mortality and survival for 24 h were converted to frequencies per treatment and did not differ significantly by location ($X^2_1=0.51$, $P=0.4735$); 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 and unvegetated), crab density (low and medium), size (first, third, fifth, seventh, and ninth instars), and storm (pre-storm, storm, and 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, and video identification of predators

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. Wind speed and direction were taken every six min at the VIMS Ferry Pier and daily mean direction and speed calculated. Hourly water height was measured at VIMS and compared to projected height to determine storm surge.

Prior to retrieval, 4-cm sediment cores were taken from all grids and analyzed as described by Folk (1974) into 3 size categories: less then ⁻1.0 phi (gravel), 4.0-⁻1.0 phi (sand), and greater than 4.0 phi (mud). Sediment type was converted to frequency 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 0.1 x 0.1 m plots within the tethering arena clipped of vegetation near the roots. Vegetation was identified to species, and shoot density and biomass by dry weight determined for each plot. Shoot density and dry weight 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; sediments were not sampled on September 24 due to rough weather.

Benthic suction samples were taken on September 21st and 28th 1992 to quantify short-term changes in crab abundance at the study sites (Goodwin Islands and Guinea Marsh) during the tethering experiments. Densities of 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 instar (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 greater than 23 mm cw (1^+-year class) using the Newcombe and Newcombe-Van Engel size ranges were converted to frequency per treatment and analyzed as dependent on location, habitat and time using the G-Test (Sokal and Rohlf 1981).

Predation events at the Goodwin Islands site were recorded with underwater video equipment (Fieldcam, Fuhrman Diversified, Inc., Laporte, Texas, USA) using fifth instars. Crabs were tethered within the focal range of the camera in vegetated and

unvegetated habitats for 2-h trials. Trials were run twice a day on September 22nd and 27th near dawn and dusk.

Planktonic abundance and settlement of blue crab megalopae

Blue crab megalopae recruit and settle during nocturnal flood tides (Meredith 1982, Olmi unpublished data) from July through November. Paired plankton nets were fished during this period at the VIMS Ferry Pier for 20 min during maximum nocturnal flood tides. 750 μm mesh nets were 1 m apart and filtered an area 50 cm wide and 80 cm deep from the surface. Megalopae were enumerated, standardized to water flow by attached current meters (General Oceanics Model 2030), and mean nightly abundance determined.

Four artificial settlement substrates were retrieved and deployed daily between 0700-0900 h. Artificial settlement substrates were 37.5 cm PVC pipe, outside diameter 16.3 cm, fitted with a synthetic fiber air conditioning filter (hog's hair) sleeve, weighted at the bottom with a float attached at the top, and deployed so that they were 10 cm from the bottom. Megalopae were enumerated and daily mean settlement calculated.

Mean annual planktonic abundance and settlement were determined from daily samples taken from July through November. A peak in planktonic abundance or settlement was twice the respective annual mean (van Montfrans et al. 1990). Planktonic abundance and settlement of blue crab megalopae are reported for August 15 through October 15, 1992.

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 greater than 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 ANOVAs were utilized. In non-parametric analyses, differences with in treatments were determined using lower level G-tests and hypotheses rejected at probabilities lower than the p-values for the main effect (Underwood 1981).

Instar classification systems

The 95% confidence intervals for annual mean densities of the Newcombe and Newcombe-Van Engel size ranges for the fifth instars were significantly different for 1987 and 1990 and highly correlated (R^2=0.927, Figure 5). For the seventh instar, the Newcombe annual mean densities were significantly higher in 1983, 1985, 1987, 1988, 1990, 1991, and 1992, yet the two classification systems were not significantly different and highly correlated (R^2=0.936, Figure 6). The Newcombe annual mean densities were significantly higher for all years except 1988 and 1991 for ninth instars. Similarly, the size ranges were highly correlated (R^2=0.840, Figure 7).

Benthic sampling

Numerically, blue crabs smaller than 20 mm cw dominated crabs found in seagrass beds. Mean annual blue crab densities varied over nearly an order of magnitude from 1983-1992 (Figure 8) with high densities in 1984, 1991, and 1992. Across years, densities of crabs smaller than the seventh instar were highly variable, yet 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.

Figure 5. (a) 95% confidence intervals for the mean annual density determined using the

Newcombe and Newcombe-Van Engel size ranges for the fifth instar. (b) Correlation of

the mean annual densities determined using the Newcombe-Van Engel size ranges with

the Newcombe size range.

Mean density (crabs/m^2)

● Newcombe–Van Engel size range
○ Newcombe size range

$R^2 = 0.927$
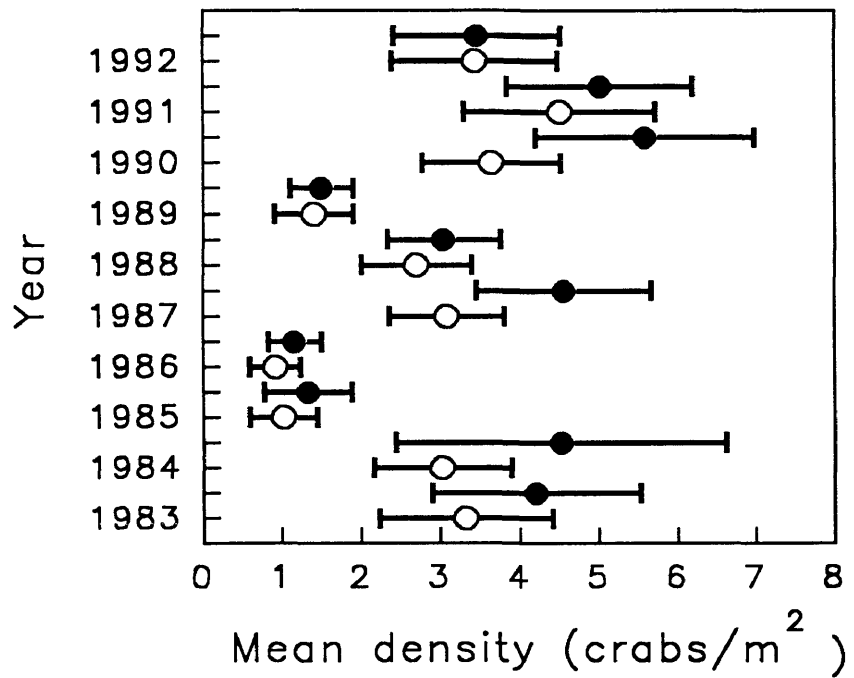
Newcombe size range
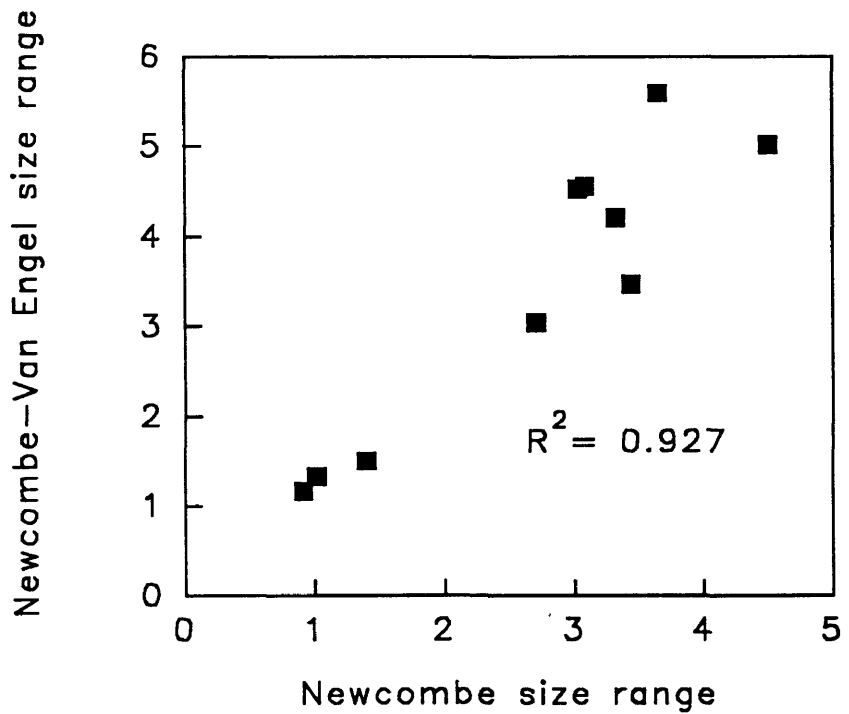
Figure 6. (a) 95% confidence intervals for the mean annual density determined using the

Newcombe and Newcombe-Van Engel size ranges for the seventh instar. (b) Correlation

of the mean annual densities determined using the Newcombe-Van Engel size ranges with

the Newcombe size range.

● Newcombe–Van Engel size range
○ Newcombe size range

$R^2 = 0.936$
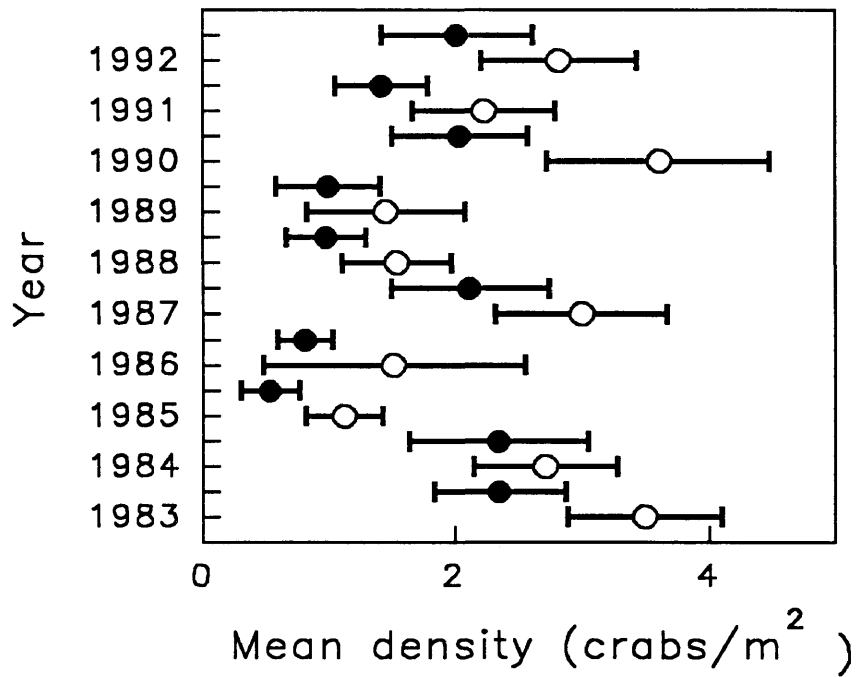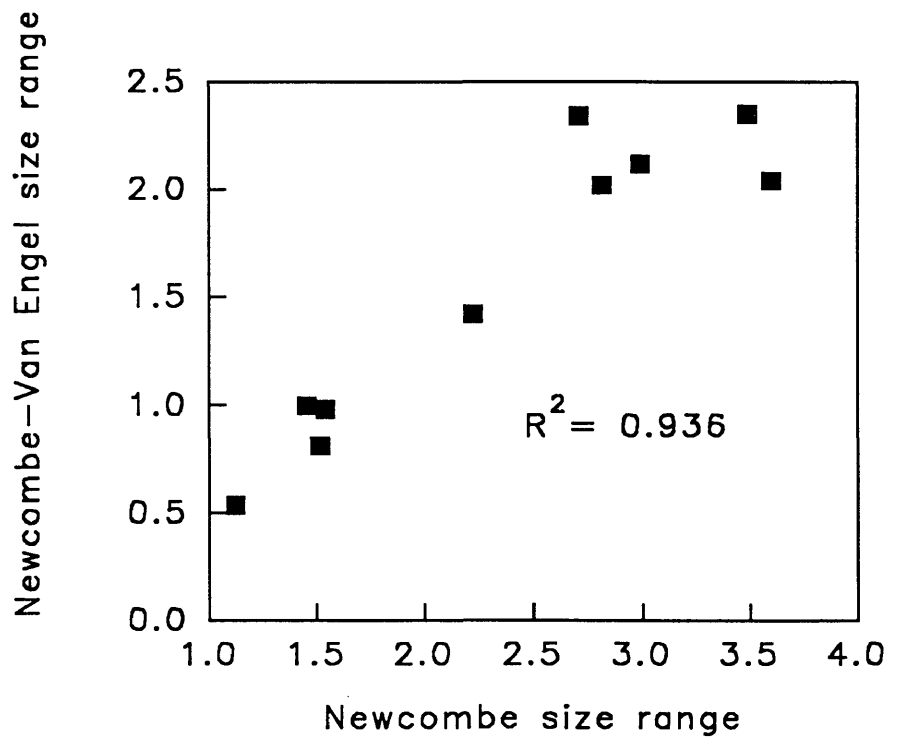
Figure 7. (a) 95% confidence intervals for the mean annual density determined using the

Newcombe and Newcombe-Van Engel size ranges for the ninth instar. (b) Correlation

of the mean annual densities determined using the Newcombe-Van Engel size ranges with

the Newcombe size range.
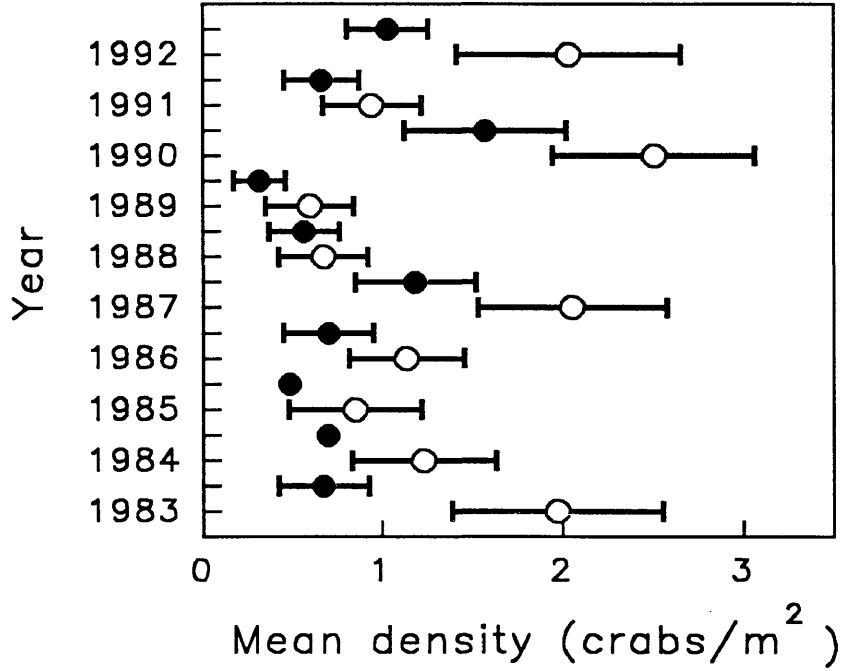
● Newcombe–Van Engel size range
○ Newcombe size range
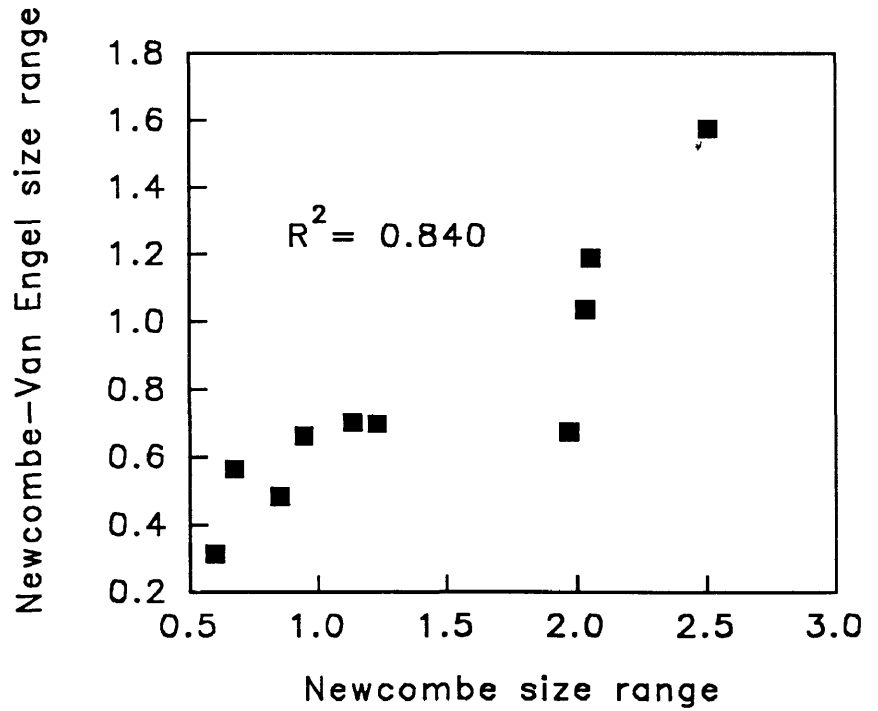
Figure 8. Mean annual densities (± 1 sd) of the first through ninth instar crabs from 1983 to 1992 in seagrass beds in Brown's Bay (a) determined using the Newcombe size ranges (b) determined using the Newcombe-Van Engel size ranges.
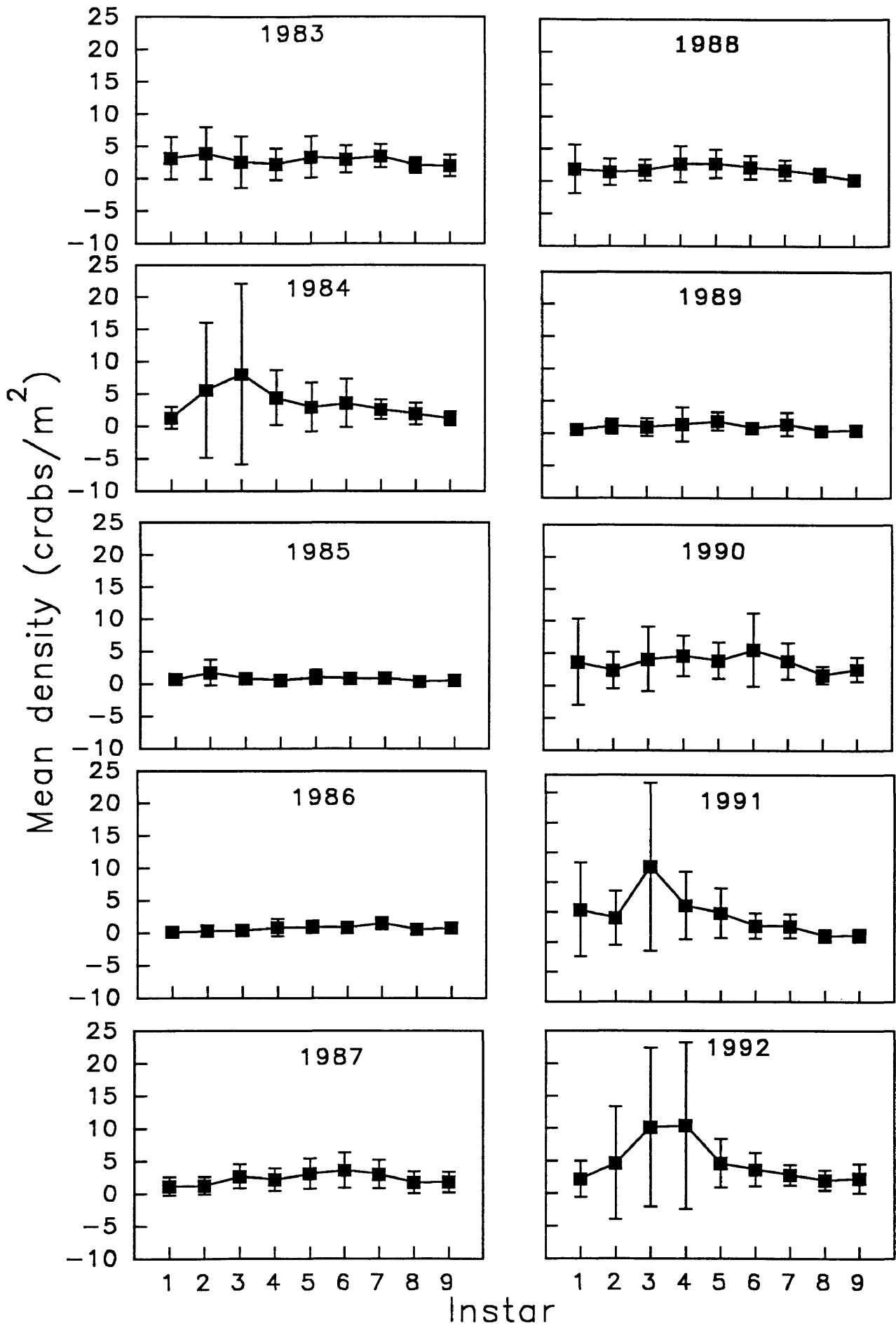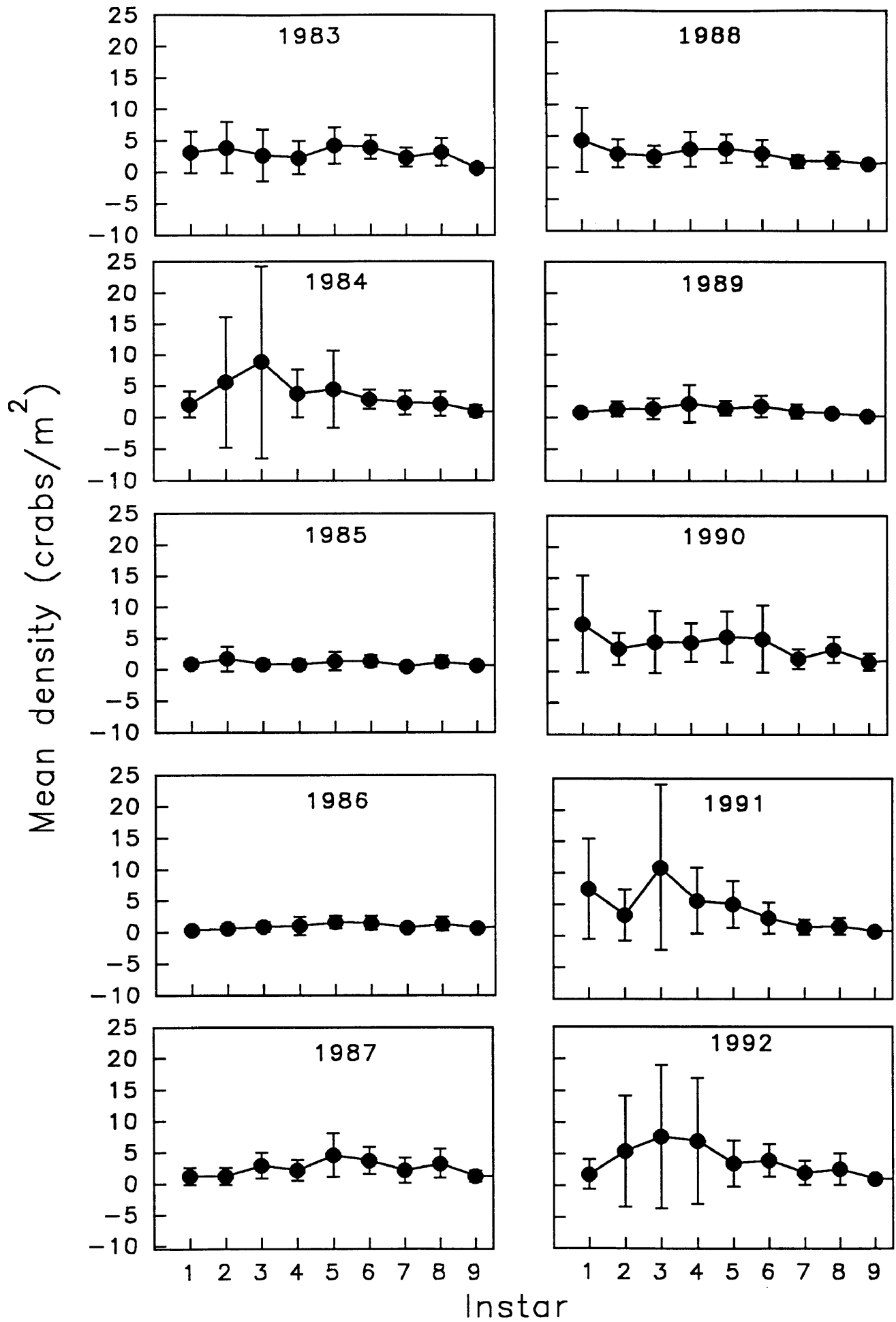
Density decreases: linear, hyperbolic, sigmoid or parabolic functions?

Except for the relationship between ninth and seventh instars, the regressions, r^2, and β between the Newcombe and Newcombe-Van Engel size ranges did not differ. Only the simple linear regression of ninth instar dependent on seventh instar using the Newcombe size ranges was linear (Figure 9, Regression; $F_{1,9}=33.22$, $P < 0.001$, $r^2=80.6$). All other regressions of large to smaller instars were either not significant or exhibited a poor fit associated with non-random residuals with lower than average residuals at the high and low densities and larger than average residuals at intermediate densities. Subsequent analysis with the 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 3-5). There was no difference between the log-transformed data and the functional response model.

Mean annual densities of third and fifth instars were dependent on first instars and the relationship hyperbolic, while seventh instars had a parabolic function with third instars and ninth instars were not dependent on third instars (Figure 10, Table 3-5). The r^2 and β decreased from the third through the ninth instars. Annual mean densities of fifth, seventh, and ninth instars were all dependent on third instars. The relationship to third instars was a parabolic function for all larger instars (Figure 11, Table 3-5). Mean annual densities of seventh instars were dependent on fifth instars and the relationship

Figure 9. Plot of the annual mean densities of the ninth instars against the seventh instars

(a) using the Newcombe and (b) Newcombe-Van Engel size classification systems.
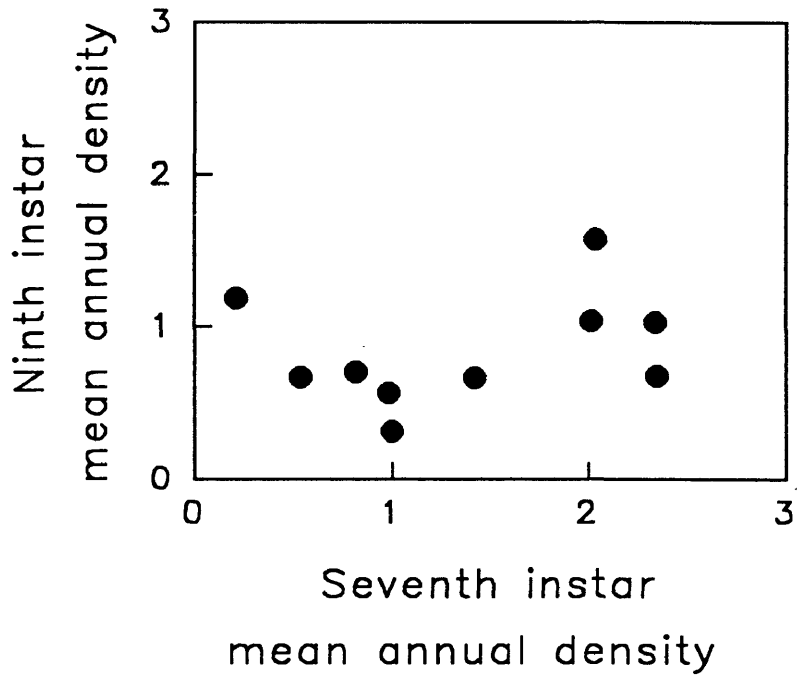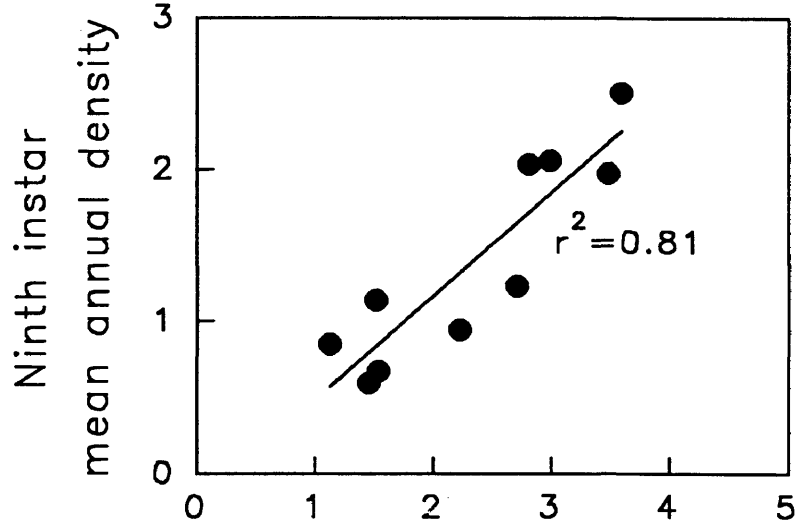
Table 3a. Density curve analyses with the annual mean density log transformed to assess the linear, hyperbolic or sigmoid characteristics of the curve for the Newcombe size ranges.

Instar	Source of variation	SS	df	ms	F	r^2	β	$\beta > 0$?	$\beta > 1$?
First Instar									
Third	Regression	0.615	1	0.615	5.95*	42.7	0.615	*	ns
	Error	0.827	8	0.103					
Fifth	Regression	0.376	1	0.376	17.94**	69.2	0.481	*	ns
	Error	0.167	8	0.021					
Seventh	Regression	0.078	1	0.078	2.95ns	27.0	0.220		
	Error	0.219	8	0.219					
Ninth	Regression	0.023	1	0.023	0.45ns	5.3	0.120		
	Error	0.417	8	0.052					
Third Instar									
Fifth	Regression	0.410	1	0.410	24.53****	75.4	0.533	*	ns
	Error	0.136	8	0.136					
Seventh	Regression	0.141	1	0.141	7.52*	48.5	0.312	*	ns
	Error	0.150	8	0.019					
Ninth	Regression	0.077	1	0.077	1.70ns	17.5	0.231		
	Error	0.363	8	0.045					
Fifth Instar									
Seventh	Regression	0.186	1	0.186	14.34**	64.2	0.586	*	ns
	Error	0.104	8	0.013					
Ninth	Regression	0.110	1	0.110	2.68ns	25.1	0.451		
	Error	0.330	8	0.041					
Seventh Instar									
Ninth	Regression	0.328	1	0.328	23.29****	74.4	1.063	*	ns
	Error	0.113	8	0.014					

* $P < 0.05$, ** $P < 0.01$, **** $P < 0.001$, ns $P > 0.05$.

Table 3b. Density curve analyses with the annual mean density log transformed to assess the linear, hyperbolic or sigmoid characteristics of the curve for the Newcombe-Van Engel size ranges.

Instar	Source of variation	SS	df	ms	F	r^2	β	$\beta > 0$?	$\beta > 1$?
				First Instar					
Third	Regression	0.615	1	0.615	5.95^*	42.7	0.615	*	ns
	Error	0.827	8	0.103					
Fifth	Regression	0.384	1	0.384	17.34^{**}	68.4	0.486	*	ns
	Error	0.177	8	0.022					
Seventh	Regression	0.100	1	0.100	2.24^{ns}	21.9	0.249		
	Error	0.358	8	0.045					
Ninth	Regression	0.028	1	0.028	0.23^{ns}	2.8	0.132		
	Error	0.969	8	0.121					
				Third Instar					
Fifth	Regression	0.323	1	0.323	10.84^{**}	57.5	0.473	*	ns
	Error	0.238	8	0.030					
Seventh	Regression	0.265	1	0.265	$10.92.^{**}$	57.7	0.429	*	ns
	Error	0.194	8	0.024					
Ninth	Regression	0.012	1	0.012	0.09^{ns}	1.2	0.090		
	Error	0.985	8	0.123					
				Fifth Instar					
Seventh	Regression	0.292	1	0.292	14.03^{**}	63.7	0.722	*	ns
	Error	0.167	8	0.021					
Ninth	Regression	0.112	1	0.112	1.01^{ns}	11.2	0.447		
	Error	0.885	8	0.111					
				Seventh Instar					
Ninth	Regression	0.000	1	0.000	0.00^{ns}	0.0	0.021		
	Error	0.999	8	0.125					

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

Table 4a. Density curve analyses with the linearized functional response model to assess the linear, hyperbolic or sigmoid characteristics of the curve for the Newcombe size ranges.

Instar	Source of variation	SS	df	ms	F	r^2	β	$\beta > 0$?	$\beta > 1$?
First Instar									
Third	Regression	0.744	1	0.744	5.78^*	41.9	0.659	*	ns
	Error	0.975	8	0.123					
Fifth	Regression	0.481	1	0.481	18.45^{**}	69.8	0.544	*	ns
	Error	0.209	8	0.026					
Seventh	Regression	0.128	1	0.128	2.96^{ns}	27.0	0.281		
	Error	0.346	8	0.043					
Ninth	Regression	0.035	1	0.035	0.49^{ns}	5.8	0.147		
	Error	0.575	8	0.071					
Third Instar									
Fifth	Regression	0.410	1	0.410	25.55^{****}	76.2	0.604	*	ns
	Error	0.134	8	0.017					
Seventh	Regression	0.217	1	0.217	6.76^*	45.8	0.388	*	ns
	Error	0.257	8	0.032					
Ninth	Regression	0.104	1	0.104	1.65^{ns}	17.1	0.269		
	Error	0.505	8	0.063					
Fifth Instar									
Seventh	Regression	0.295	1	0.295	13.26^{**}	62.4	0.738	*	ns
	Error	0.178	8	0.022					
Ninth	Regression	0.155	1	0.155	2.73^{ns}	25.4	0.534		
	Error	0.455	8	0.057					
Seventh Instar									
Ninth	Regression	0.457	1	0.457	23.64^{****}	74.7	1.253	*	*
	Error	0.154	8	0.019					

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

Table 4b. Density curve analyses with the linearized functional response model to assess the linear, hyperbolic or sigmoid characteristics of the curve for the Newcombe-Van Engel size ranges.

Instar	Source of variation	SS	df	ms	F	r^2	β	$\beta > 0$?	$\beta > 1$?
First Instar									
Third	Regression	0.704	1	0.704	5.78*	41.9	0.659	*	ns
	Error	0.975	8	0.122					
Fifth	Regression	0.467	1	0.467	17.40**	68.5	0.533	*	ns
	Error	0.215	8	0.027					
Seventh	Regression	0.131	1	0.131	2.15ns	21.2	0.284		
	Error	0.488	8	0.061					
Ninth	Regression	0.047	1	0.047	0.30ns	3.6	0.171		
	Error	1.272	8	0.159					
Third Instar									
Fifth	Regression	0.388	1	0.388	10.56**	56.9	0.519	*	ns
	Error	0.294	8	0.037					
Seventh	Regression	0.351	1	0.351	10.50**	56.8	0.494	*	ns
	Error	0.268	8	0.033					
Ninth	Regression	0.007	1	0.007	0.04ns	0.5	0.071		
	Error	1.312	8	0.164					
Fifth Instar									
Seventh	Regression	0.389	1	0.389	13.49**	62.8	0.832	*	ns
	Error	0.231	8	0.030					
Ninth	Regression	0.177	1	0.177	1.24ns	13.4	0.562		
	Error	1.142	8	0.143					
Seventh Instar									
Ninth	Regression	0.004	1	0.004	0.03ns	0.3	0.095		
	Error	1.315	8	0.164					

* $P < 0.05$, ** $P < 0.01$, ns $P > 0.05$.

Table 5a. Density curve analyses with the annual mean density of each instar using the Ricker Stock Recruit Function for the Newcombe size ranges.

Instar	Source of variation	SS	df	ms	F	r^2
		First Instar				
Third	Regression	0.274	1	0.274	2.76	25.6
	Error	0.793	8	0.099		
Fifth	Regression	0.468	1	0.468	27.26****	77.3
	Error	0.137	8	0.017		
Seventh	Regression	0.929	1	0.929	27.39****	77.4
	Error	0.271	8	0.034		
Ninth	Regression	1.125	1	1.125	16.40**	67.2
	Error	0.417	8	0.052		
		Third Instar				
Fifth	Regression	0.381	1	0.067	45.30****	85.0
	Error	0.067	8	0.008		
Seventh	Regression	0.777	1	0.777	114.33****	93.5
	Error	0.054	8	0.007		
Ninth	Regression	0.973	1	0.973	32.08****	80.0
	Error	0.243	8	0.030		
		Fifth Instar				
Seventh	Regression	0.094	1	0.094	7.33*	47.8
	Error	0.102	8	0.013		
Ninth	Regression	0.155	1	0.155	3.65^{ns}	31.3
	Error	0.339	8	0.042		
		Seventh Instar				
Ninth	Regression	0.003	1	0.003	0.24^{ns}	2.9
	Error	0.111	8	0.014		

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

Table 5b. Density curve analyses with the annual mean density of each instar using the Ricker Stock Recruit Function for the Newcombe-Van Engel size ranges.

Instar	Source of variation	SS	df	ms	F	r^2
		First Instar				
Third	Regression	0.274	1	0.274	2.76	25.6
	Error	0.793	8	0.099		
Fifth	Regression	0.517	1	0.517	17.72^{**}	68.9
	Error	0.233	8	0.029		
Seventh	Regression	0.956	1	0.956	23.98^{****}	75.0
	Error	0.319	8	0.040		
Ninth	Regression	0.918	1	0.918	14.12^{**}	63.8
	Error	0.520	8	0.065		
		Third Instar				
Fifth	Regression	0.461	1	0.461	42.72^{****}	84.2
	Error	0.086	8	0.011		
Seventh	Regression	0.587	1	0.587	60.30^{****}	88.3
	Error	0.078	8	0.010		
Ninth	Regression	0.912	1	0.912	33.99^{****}	80.9
	Error	0.215	8	0.027		
		Fifth Instar				
Seventh	Regression	0.016	1	0.016	1.16^{ns}	12.6
	Error	0.111	8	0.014		
Ninth	Regression	0.067	1	0.067	2.87^{ns}	26.4
	Error	0.188	8	0.023		
		Seventh Instar				
Ninth	Regression	0.085	1	0.085	2.98^{ns}	27.2
	Error	0.228	8	0.029		

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

Figure 10. Plot of the annual mean densities of third, fifth, seventh and ninth instars

against first instars using the Newcombe size classification system.

Fifth instar mean annual density vs First Instar mean annual density: $\beta=0.544$, $r^2=0.69$

Ninth instar mean annual density vs First Instar mean annual density

Third instar mean annual density: $\beta=0.659$, $r^2=0.42$
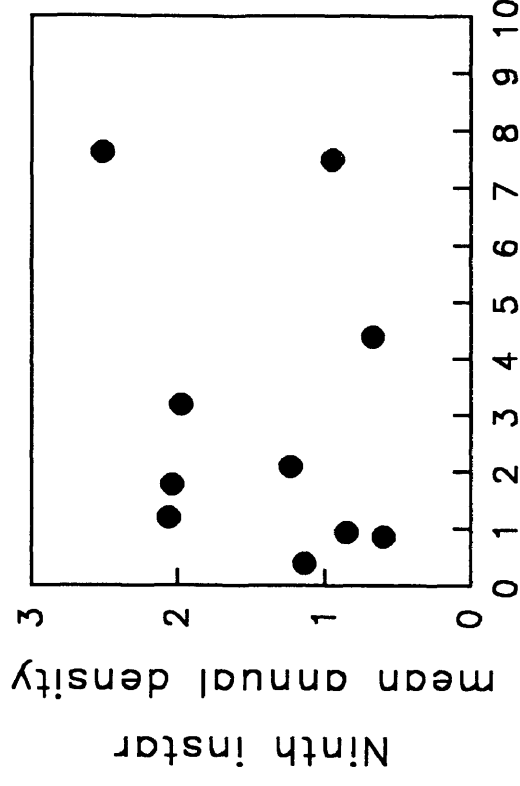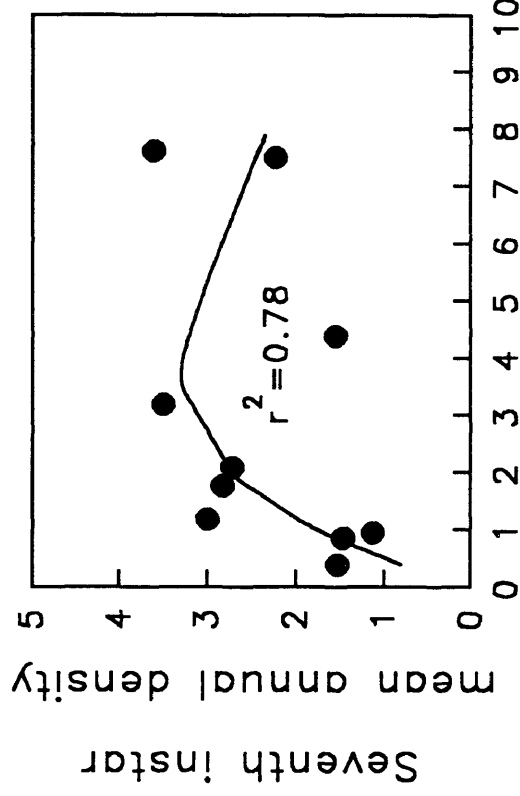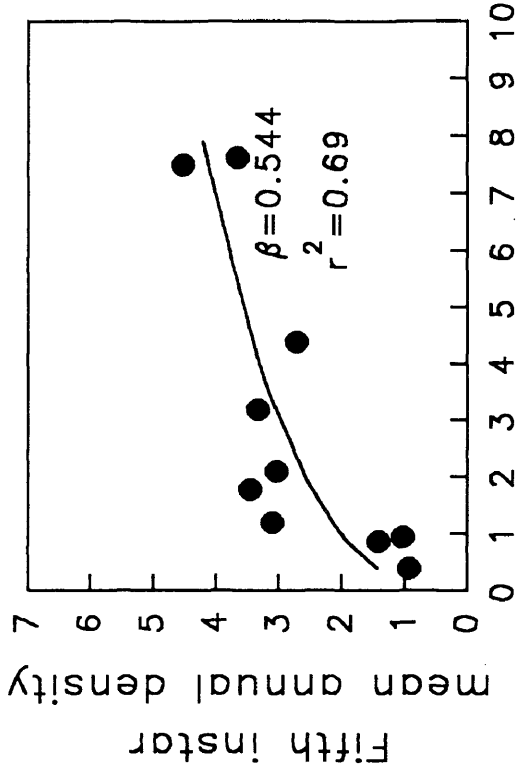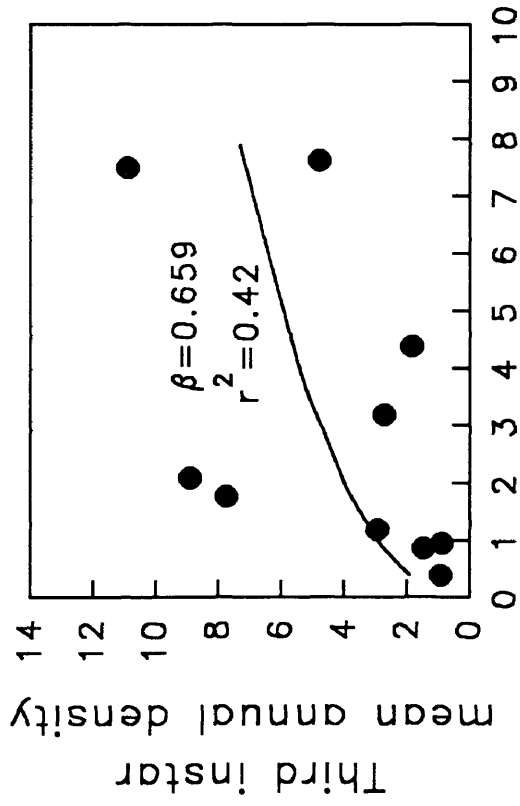
Seventh instar mean annual density vs First Instar mean annual density: $r^2=0.78$

Figure 11. Plot of the annual mean densities of fifth, seventh and ninth instars against

third instars using the Newcombe size classification system.

Fifth instar mean annual density vs Third instar mean annual density. $r^2=0.85$

Seventh instar mean annual density vs Third instar mean annual density. $r^2=0.94$

Ninth instar mean annual density vs Third instar mean annual density. $r^2=0.80$
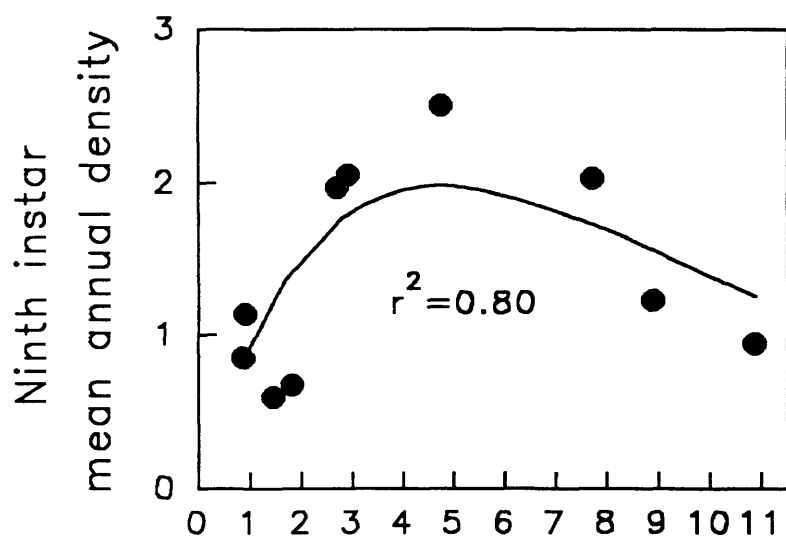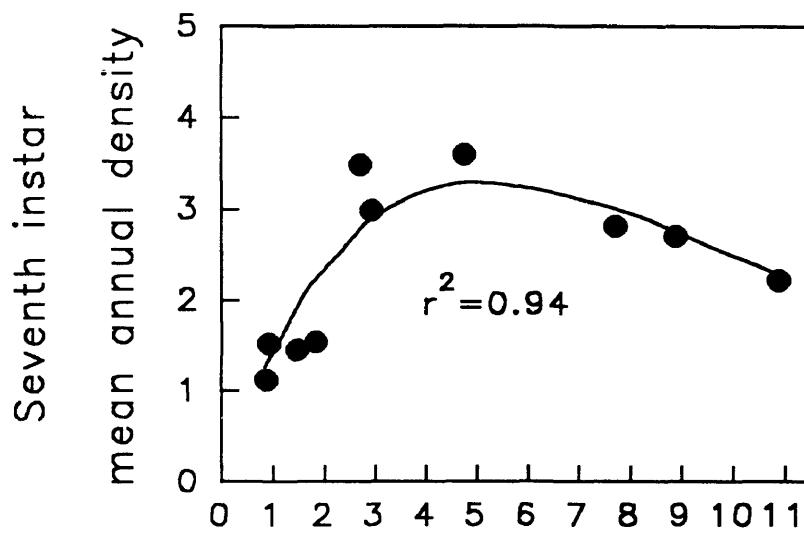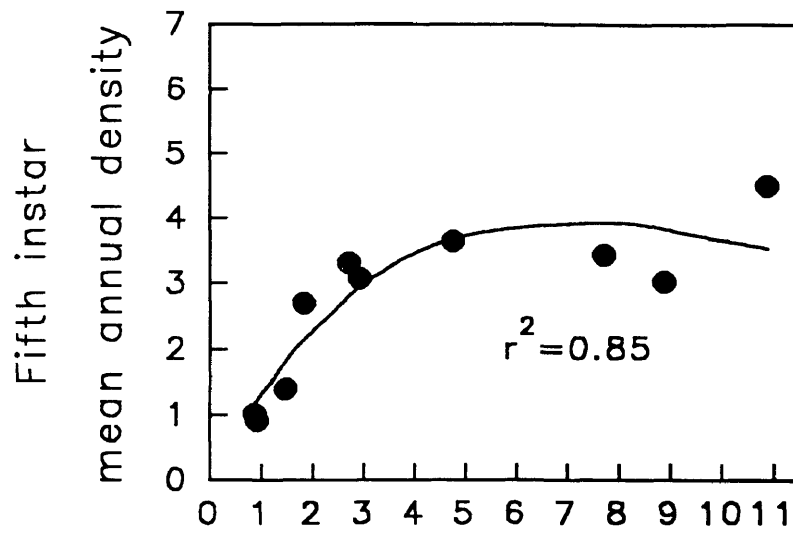
Third instar

mean annual density

hyperbolic while ninth instars were not dependent (Figure 12, Table 3-5). Ninth instars

determined using the Newcombe-Van Engel size ranges were not dependent on seventh

instars (Figure 9, Table 3-5).

Laboratory experiment

There were significant differences in crab survival for all main effects and no

statistically significant interactions of effects (Table 6). Crab survival was higher (1) in

vegetated habitats, (2) when untethered, and (3) with increasing crab size (Figure 13).

Crab survival for seventh and ninth instars, while not being significantly different from

each other, was significantly higher than survival for fifth, third, and first instars, which

were all significantly different from each other (Ryan's Q, $\alpha = .05$, Table 6). Predation

occurred in only 8% of the control treatments due to prey crabs molting and cannibalizing

cohorts.

Sub-lethal predation

Sub-lethal predation was significantly higher in the presence of predators and when

crabs were untethered for the fifth, seventh, and ninth instars (Figure 14). No sub-lethal

predation occurred in crabs from the first and third instars and in treatments of control

tethered crabs. Sub-lethal predation was not effected by habitat or size and there were

no significant interactions of effects (Table 7). Percent of total missing appendages for

all instars was 20% for claws, 68% for legs and 12% for swimming legs (Figure 14) and

did not deviate from expected of 20% for claws, 60% for legs and 20% for swimming

Figure 12. Plot of the annual mean densities of the seventh and ninth instars against fifth instars using the Newcombe size classification system.
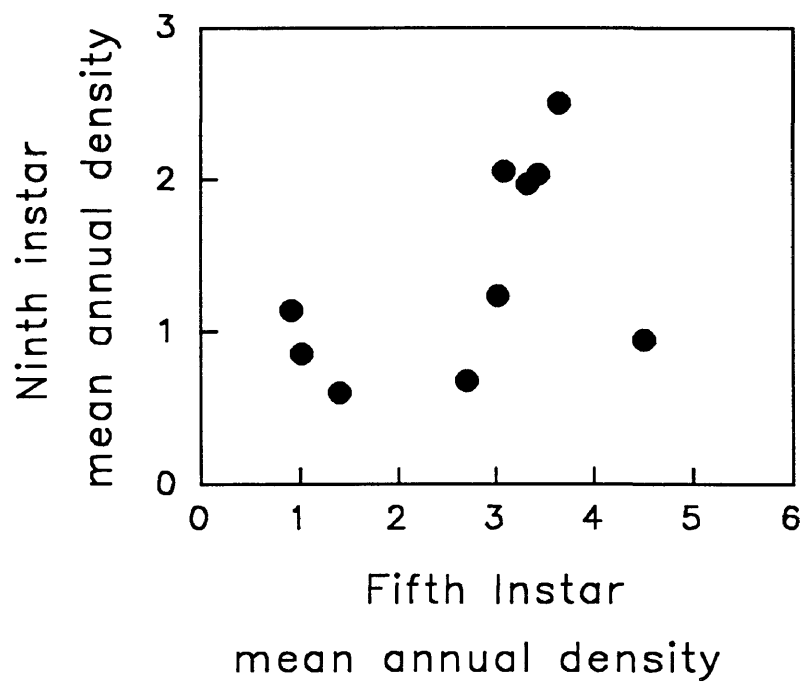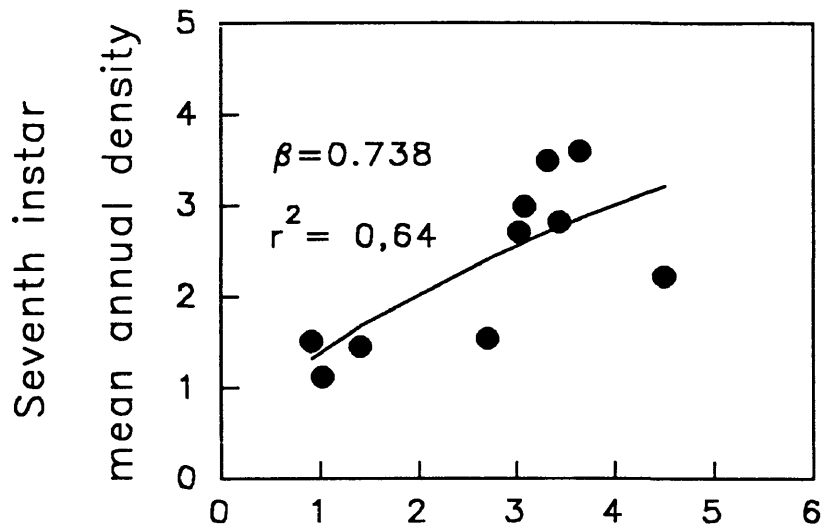
Table 6. 3-way fixed factor ANOVA table and multiple comparisons for proportional survival in laboratory study.

Source	df	SS	F	Power
Habitat (H)	1	0.75111516	16.00^{****}	
Tether (T)	1	0.36000120	7.67^{**}	
Size (S)	4	11.47385028	61.10^{****}	
H*T	1	0.00444422	0.09^{ns}	
H*S	4	0.30167257	1.61^{ns}	$>.99$
T*S	4	0.40944186	2.18^{ns}	$>.80$
H*T*S	4	0.13722161	0.73^{ns}	
ERROR	180	8.458866		
TOTAL	199	21.8877932		

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

Ryan's Q Test of Multiple Comparisons ($\alpha=0.05$). Means with the same letter are not significantly different.

Instar	Mean survival	Grouping
1	0.93333	A
3	0.67500	B
5	0.29167	C
7	0.11667	D
9	0.05000	D

Figure 13. Proportional survival (X±1 se) after 24 h for each instar, tethered and untethered, in the presence or absence of predators. Underlined instars are not significantly different. Predation in the absence of predators was due to cannibalism by crabs that molted during the trial.
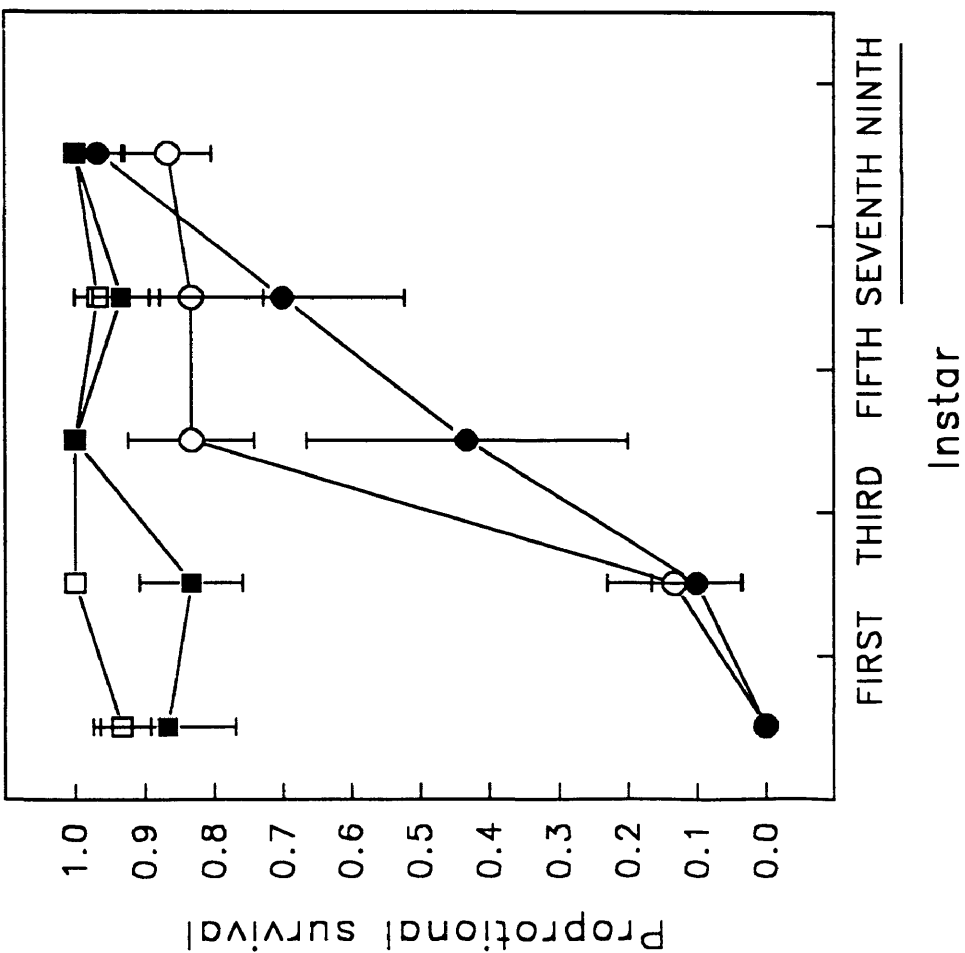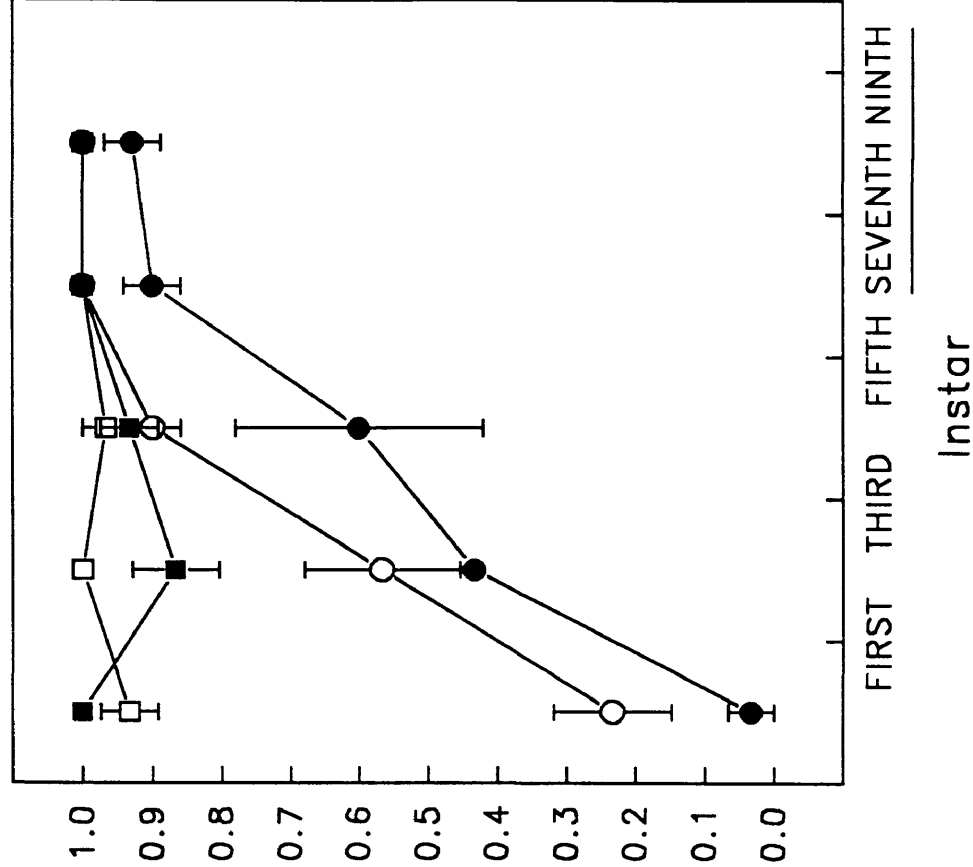
Table 7. 4-way fixed factor ANOVA table for proportion of sub-lethal predation in laboratory study.

Source	df	SS	F	POWER
SIZE (S)	2	0.08224035	1.42^{ns}	
HABITAT (H)	1	0.02845920	0.98^{ns}	
TETHER (T)	1	0.13912830	4.79^{*}	
PREDATOR (P)	1	0.41043603	14.13^{**}	
S*H	2	0.05173035	0.89^{ns}	
S*T	2	0.12167855	2.09^{ns}	.74 < P < .76
S*P	2	0.11835732	2.04^{ns}	.72 < P < .74
H*T	1	0.00389880	0.13^{ns}	
H*P	1	0.00221880	0.08^{ns}	
T*P	1	0.01302083	0.45^{ns}	
S*H*T	2	0.01916295	0.33^{ns}	
S*H*P	2	0.03615845	0.62^{ns}	
S*T*P	2	0.02407032	0.41^{ns}	
H*T*P	1	0.03386880	1.17^{ns}	
S*H*T*P	2	0.03279185	0.56^{ns}	
ERROR	96	2.78933		
TOTAL	119	3.90655		

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

Figure 14. Proportional sub-lethal predation (X ± 1 se) tethered and untethered crabs in the presence or absence of predators. There was no sub-lethal predation for first and third instars and tethered controls. For graphical representation data has been combined along the nonsignificant main effects of instar and habitat. Pie charts represent proportion of limbs missing for each treatment.
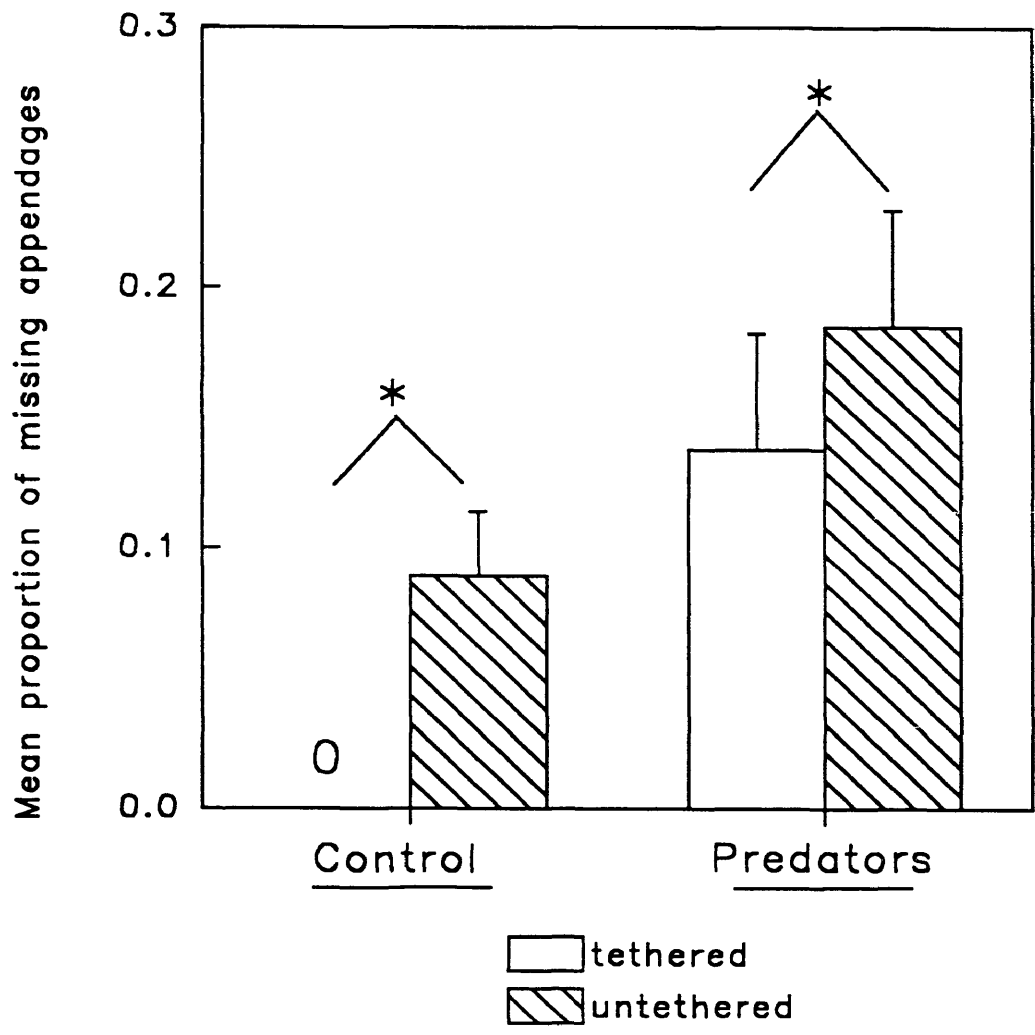
Missing Appendages
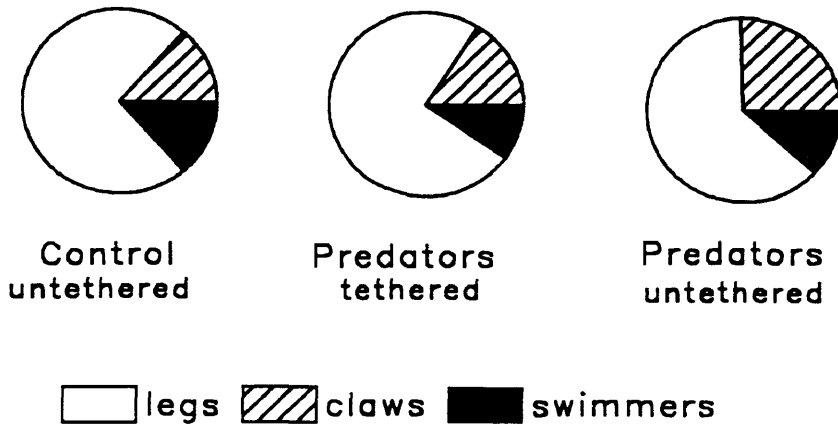
legs (X^2_2=4.721, 0.05 < P < 0.1). Composition of missing appendages for the fifth instars was 13% claws, 73% legs, and 14% swimming legs, for the seventh instars was 33% claws, 63% legs, and 4% swimming legs, and for the ninth instars 22% claws, 66% legs, and 12% swimming legs.

<u>Field Experiment</u>

The mean water temperature at the field sites differed significantly by day (ANOVA, $F_{5,31}$=10.76, P < 0.0001) and 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, (Figure 15). The 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) (Figure 15).

Water height within the York River increased above expected height from 23 September until reaching a maximum of 2.34 ft above expected on 25 September (Figure 16). Water levels then decreased until returning to expected levels on 28 September.

Sediment composition did not differ significantly by location (G-Test, X^2_1=0.49, P=0.7838) or habitat (G-Test, X^2_1=0.11, P=0.9488) and the mean composition was 2% gravel, 90% sand, and 8% mud. Mean proportion of eelgrass of total shoot density of eelgrass did not differ by location (ANOVA, $F_{1,39}$=0.01, P=0.93). Total shoot density (ANOVA, $F_{1,39}$=0.01, P=0.93) and dry weight (ANOVA, $F_{1,39}$=0.03, P=0.875) did not differ significantly by location. Back transformed mean total shoot density was 19.294 (1.982 sd) shoots/0.1 m^2 with a mean dry weight of 0.835 (0.521 sd) g/0.1 m^2.

Figure 15. Mean daily salinity and water temperature (X $\pm$ 1 sd) during tethering experiment. Water temperature was not significantly different between location (two-way fixed factor ANOVA with date and location as independent variables, $F_{1,31}$ salinity=5.53, p=.0009; $F_{1,31}$water temperature=0.07, p=.7883) and data combined. Dates with the same letter were not significantly different.
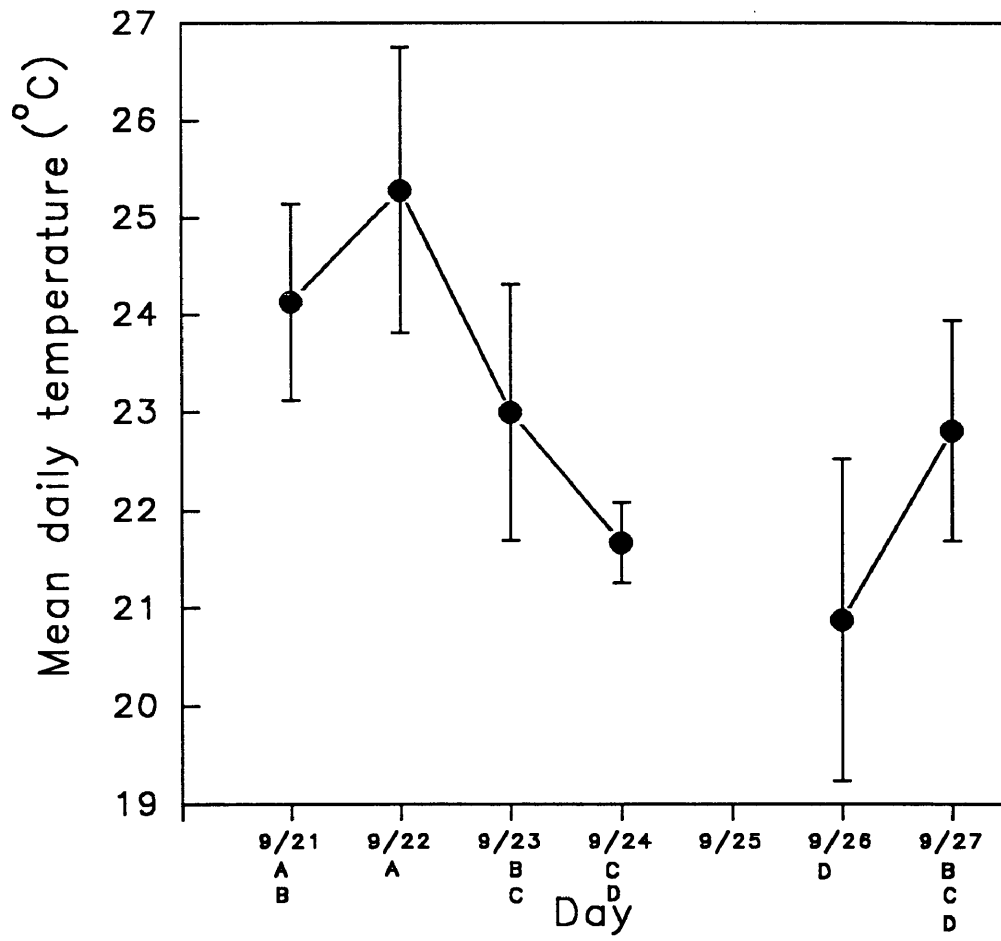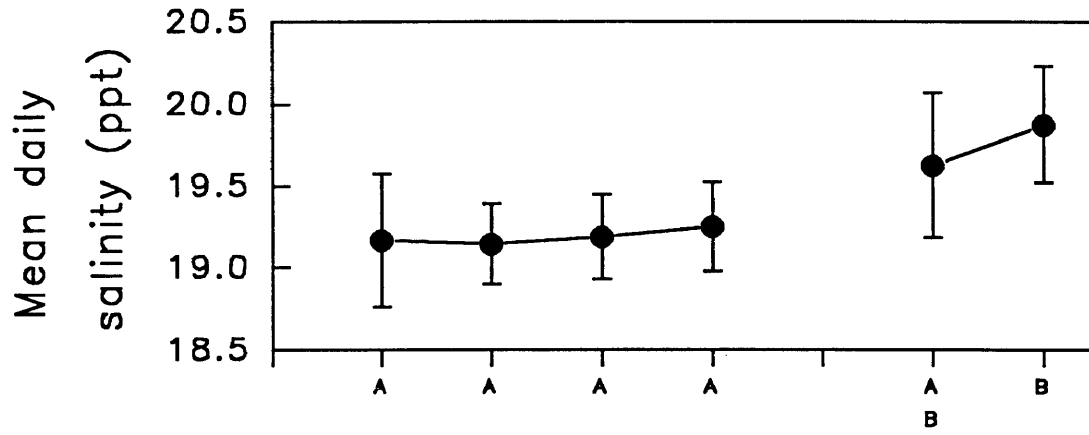
Figure 16. Water height deviation from projected from 21 September to 1 October 1992

at VIMS.
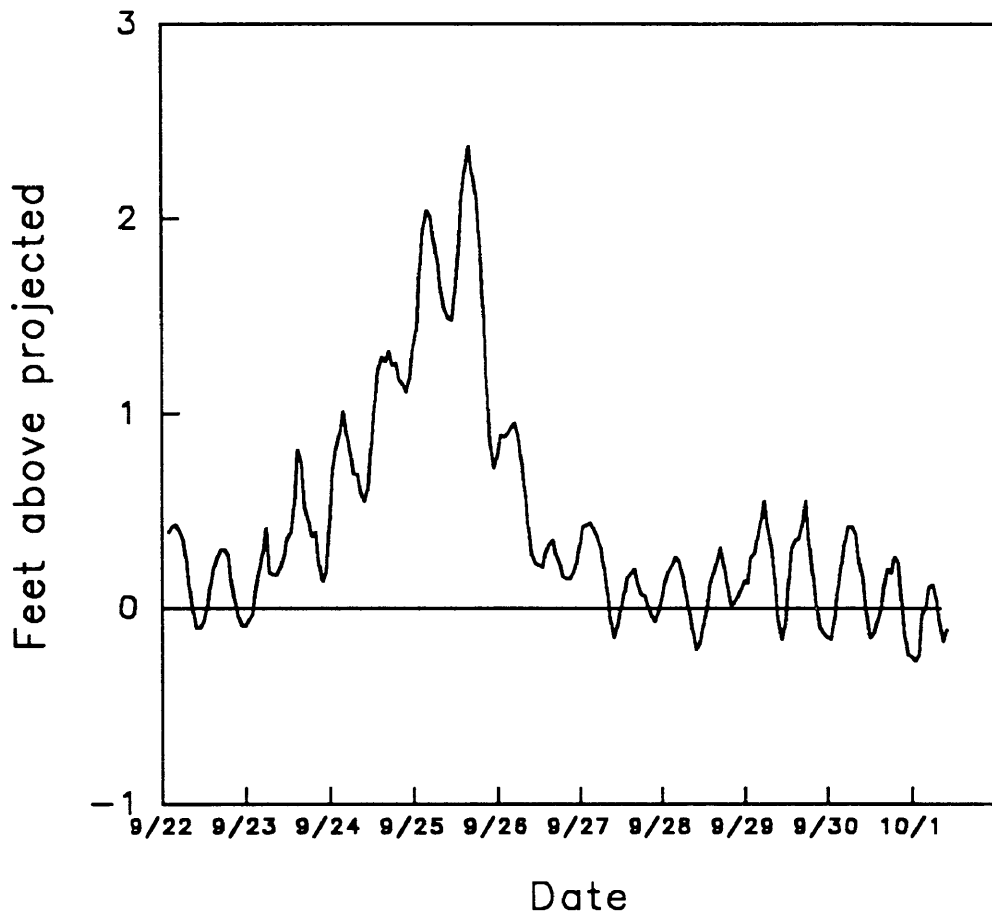
Relative rates of predation

Crab survival was significantly higher (1) in vegetated habitats, (2) with increasing crab size (fifth, seventh, and ninth instars survival > first and third instars survival), and (3) during storm and post-storm conditions. Location (north shore vs south shore) and density of tethered crabs (23 crabs/m^2 vs 46 crabs/m^2) did not significantly effect survival of newly settled blue crabs and there were no significant interaction effects (Table 8).

During pre-storm conditions crab survival was higher in vegetated habitats for first and third instars while for the fifth, seventh and ninth instars not significantly different than survival in unvegetated habitats. Survival was higher for fifth, seventh, and ninth instars. Under storm conditions, survival was significantly higher for all instars in both habitats with survival in vegetated habitats significantly higher than unvegetated habitats, and retaining the increased survival with size. Losses at low density crab treatments in both habitats was zero from September 24th at 1400 to 0700 on September 25th, indicating that crabs were not "ripped off" their tethers by increased tidal and wave action during the storm. Survival during post-storm conditions decreased from storm conditions for both habitats for first, third, and ninth instar crabs while remaining elevated for fifth and seventh instars and was significantly higher than pre-storm survival (Figure 17, Table 8).

Qualification of predators

One lethal predation event by a larger blue crab and 4 sub-lethal attacks by *Gobisoma (sp)* in groups of two or three were recorded in the grass habitat. No lethal or sub-lethal predation events were recorded in the sand habitat. Four larger than fifth

Table 8. G-test analysis of variance table for the field tethering experiment.

Source	df	X^2	P	Power
Intercept	1	154.06	0.0001	
Size (S)	4	18.07	0.0012	
Density (D)	1	0.24	0.6276	
Habitat (H)	1	15.75	0.0001	
Storm (ST)	2	8.38	0.0152	
S*D	4	1.32	0.8585	
S*ST	8	3.87	0.8686	
S*H	4	4.41	0.3531	
D*H	1	1.83	0.1764	>.80
H*ST	2	2.75	0.2532	
D*ST	2	0.48	0.7857	
S*D*H	4	1.09	0.8960	
S*D*ST	8	2.35	0.9684	
S*H*ST	8	10.48	0.2327	
D*H*ST	2	4.17	0.1244	>.80
S*D*H*ST	8	5.78	0.6717	

$^{**} P < 0.01,$ $^{****} P < 0.0001,$ $^{ns} P > 0.05.$

(b) Lower level G-Test for multiple comparisons

Main Effect	Source	df	X^2
Size	1st vs 5th	1	8.57^{ns}
	1st vs 3rd	1	3.07^{ns}
	1st vs 9th	1	15.40^{*}
	5th vs 9th	1	0.81^{ns}
	1st,3rd vs 5th,7th,9th	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}

$^{*} P < P$ main effect $^{ns} P > P$ main effect

Figure 17. Proportional survival for each instar in vegetated and unvegetated habitats during pre-storm, storm, and post-storm conditions. Crab survival significantly increased in vegetated habitats (G-Test, $X^2_1 = 15.75$, p=.0001) with crab size (G-Test, $X^2_4 = 18.07$, p=.0012), and during storm and post-storm conditions (G-Test, $X^2_2 = 8.38$, p=0.0152). Instars sharing an underline did not have significantly different survival. Crab survival did not differ by location (G-Test, $X^2_1 = 0.51$, p=.4735) or density (G-Test, $X^2_1 = 0.24$, p=.6276) and data combined.
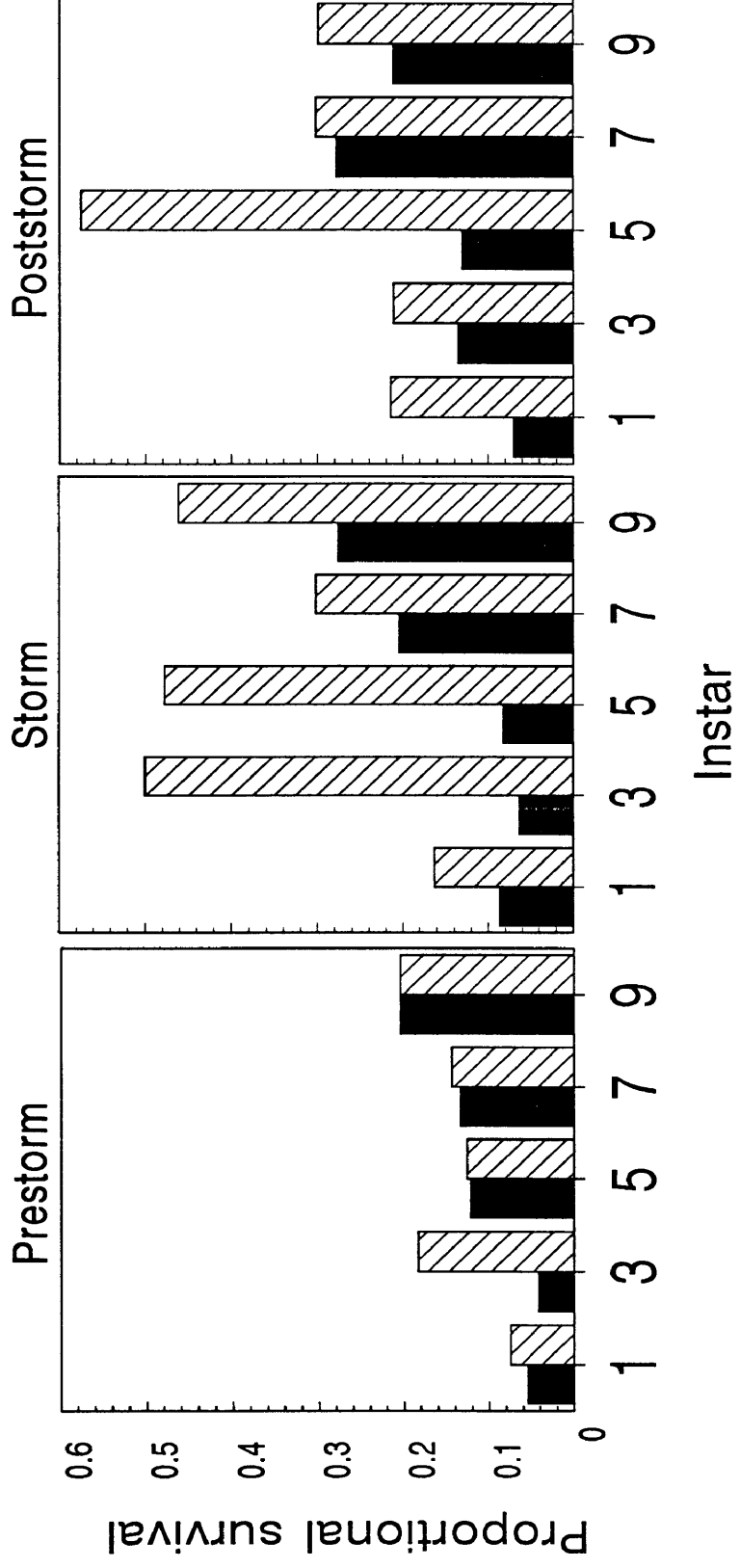
instar blue crabs were observed in foraging behavior; however they did not successfully find the tethered prey crab.

Lethal attacks by larger blue crabs on smaller blue crabs (video analysis, personal observation) are characterized by ambushing of the prey crab with swift forward sweeping motions of the claws of the larger blue crab. The predator crab then holds the smaller crab by the body and systematically fractured the claws of the prey crab with an outward snapping motion. The crab then manipulated the prey so that the dactyl of one claw is placed in the mouth of the prey crab and the other held the carapace of the crab along the anterior margin. The predator crab then pried the crab apart and consumed the internal soft portions.

In contrast, *Gobisoma (sp)* consumed first and third instar crabs whole (personal observation) and attacks on larger instar were sublethal, resulting in missing appendages (video analysis, personal observation). While attacking, *Gobisoma (sp)* in groups of two or three swam quickly towards the lateral or posterior aspects of the prey crabs from various angles, conspicuously avoiding the anteriorly located claws. The fish would then bite at a leg of the crab as the crab attempted to escape by swimming upward (video analysis, personal observations) Tethered and untethered crabs exhibited the same escape response with equal success. The attacking *Gobisoma (sp)* (a benthic fish) would not swim after the crab once it was 5 cm above the bottom.

<u>Blue crab abundance</u>

Blue crabs 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, there was a significant interaction effect between location and date and location and habitat (Table 9, Figure 18). Crab densities at the Guinea Marsh were significantly higher after the storm (lower level ANOVA $F_{1,20}=37.80$, $P < 0.0001$) while the densities at the Goodwin Islands were not significantly different by date (lower level 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 (lower level ANOVA $F_{1,11}=0.36$, $P=0.5610$) and significantly higher at the Guinea Marsh location on the post-storm date (lower level 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 (lower level ANOVA $F_{1,11}=27.48$, $P=0.0004$) and not significantly different by location on the post-storm date (lower level ANOVA $F_{1,11}=0.003$, $P=0.9553$).

There was no difference between the analysis of size frequencies using the two size ranges. Hence, the results using the Newcombe size range are reported to be consistent with the tethering experiments. Size frequencies were significantly different by date and there was a significant interaction between location and habitat (Table 10). The date effect is 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 first instars were not significantly different by date (lower level G-test,

Table 9. Three-way ANOVA table for the abundance of blue crabs during the field tethering experiment.

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*L	1	24.10	24.18[****]
L*H	1	31.16	31.26[****]
D*H	1	1.34	1.34[ns]
D*L*H	1	0.05	0.05[ns]

[*] $P < 0.05$, [****] $P < 0.001$, [ns] $P > 0.05$.

(b) Lower level ANOVA's for the date x location interaction effect by habitat. Treatments are arranged in increasing order of abundance and are not significantly different if sharing an underline. GI=Goodwin Islands, GM=Guinea Marsh.

Date	Interaction Sand		Grass	
September 21	GM	GI	GI	GM
September 28	GI	GM	GI	GM

Location				
Goodwin Islands	9/28	9/21	9/28	9/21
Guinea Marsh	9/21	9/28	9/21	9/28

(c) Lower level ANOVA's for the location x habitat interaction effect by date. Treatments are arranged in increasing order of abundance and are not significantly different if sharing an underline. GI=Goodwin Islands, GM=Guinea Marsh.

Location	Interaction September 21		September 28	
Goodwin Islands	Sand	Grass	Sand	Grass
Guinea Marsh	Sand	Grass	Sand	Grass

Habitat				
Sand	GM	GI	GI	GM
Grass	GI	GM	GI	GM

Figure 18. Density of crabs/m^2 at the Guinea Marsh and Goodwin Islands on 21 (pre-storm) and 28 (post-storm) September 1992 in grass and sand habitats. Bars with the same symbol are not significantly different.
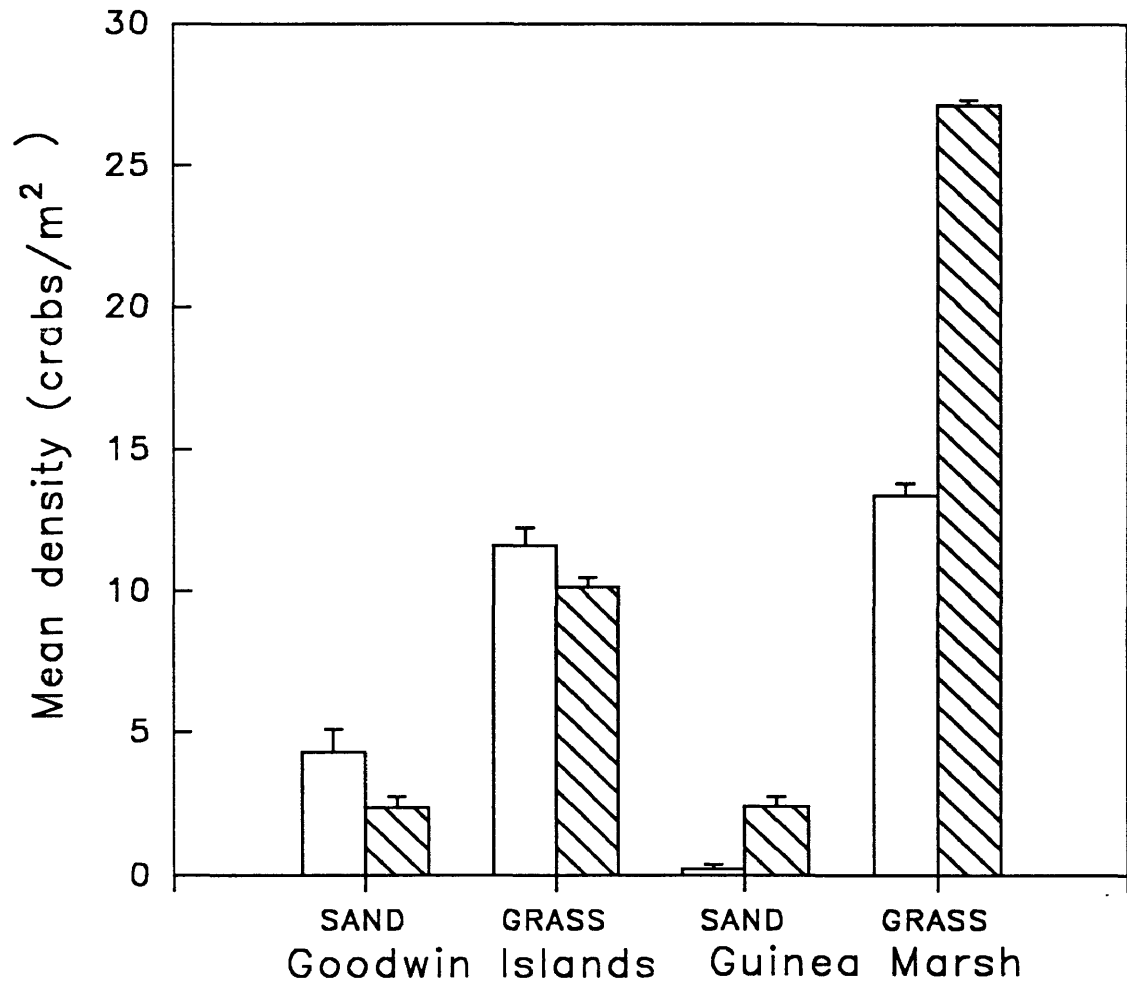
Table 10. G-test analysis of variance table for the size frequency of blue crabs during the field tethering experiment.

Source	df	X^2
Intercept	4	67.64^{****}
Date (D)	4	9.98^{*}
Location (L)	4	9.03^{ns}
Habitat (H)	4	6.73^{ns}
D*L	4	3.86^{ns}
D*H	4	6.77^{ns}
L*H	4	11.74^{**}
D*L*H	4	7.16^{ns}
Residual	0	-0.00^{ns}

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

(b) Lower level G-test for the Location x Habitat interaction effect. Treatment levels that are not significantly different are underlined.

	Interaction	
Location	Habitat	
Goodwin Islands	Sand	Grass
Guinea Marsh	Sand	Grass

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

Figure 19. Size frequencies of crabs during the field tethering study at the Guinea Marsh and Goodwin Islands. Frequencies of 1+ crabs was significantly higher at the Guinea Marsh location while frequencies of < 3.1 mm crabs was significantly higher on the post-storm date.
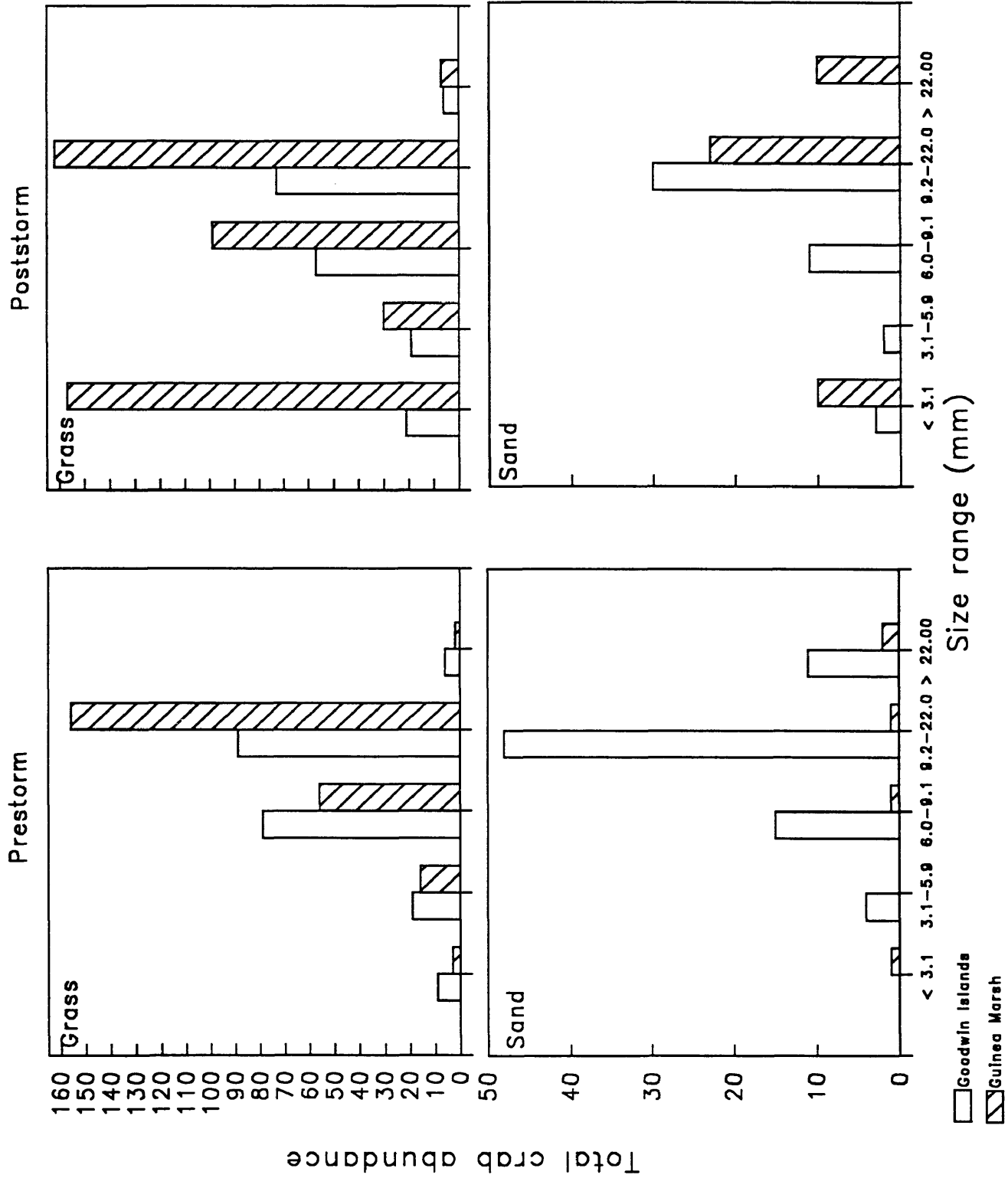
$X^2_2 = 2.13$, $P = 0.35$), location (lower level G-test, $X^2_2 = 2.05$, $P = 0.36$), or habitat (lower level G-test, $X^2_2 = 4.05$, $P = 0.13$) or had any significant interaction effects (Figure 19). The location habitat effect is due to significantly more 1^+ year-class blue crabs in sand habitats than grass habitats at the Guinea Marsh location (lower level G-test, $X^2_1 = 5.84$, $P = 0.0157$) before and after the storm.

Megalopae plankton abundance and settlement

Two significant peaks in blue crab megalopae planktonic abundance occurred while there were no significant peaks in megalopae settlement during 22-28 September 1992 (Figure 20). Peaks in blue crab megalopae planktonic abundance occurred on 22 and 27 September 1992. There was an increasing trend in blue crab megalopae settlement associated with the new moon on 26 September, it was not greater than two times the yearly mean settlement.

Figure 20. Mean blue crab megalopae planktonic abundance during maximum flood tide and mean nightly settlement from 15 August to 15 October 1992 at VIMS. The line through each graph represents two times the yearly mean abundance or settlement, above which peaks in abundance or settlement are considered significant. Dates marked with open circles represent the full moon, solid circles the new moon. Dotted vertical lines enclose period of field experiment.
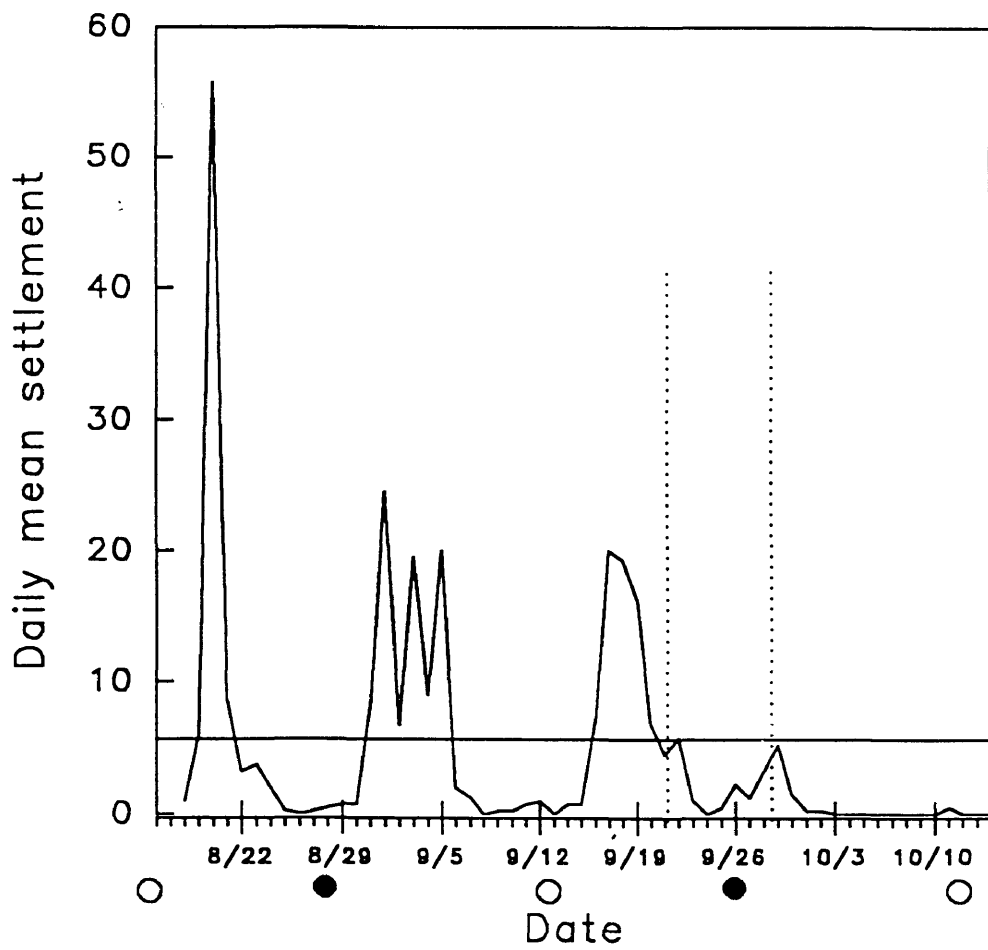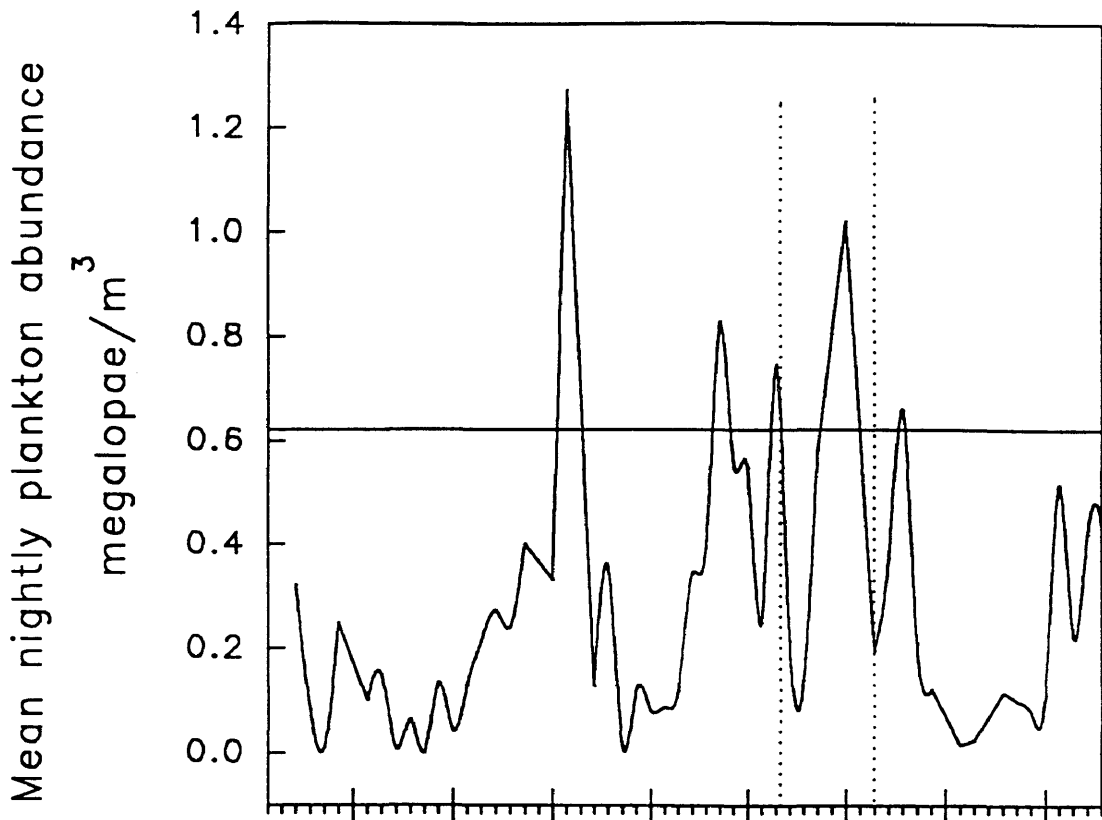
Discussion

Instar classification

There appears to be no difference between the Newcombe and the Newcombe-Van Engel classification systems. There were no differences in the cw for crabs smaller than the fifth instar, indicating that the sizes of the first five instars have low variability. Carapace width differs between the two classification systems after the fifth instar, with the Newcombe ranges smaller. However, there were differences between the annual mean densities of the fifth, seventh, and ninth instars as compared by 95% confidence intervals (Figures 5-7) the annual mean densities were highly correlated (Figures 5-7) indicating that yearly trends are adequately represented by both classification systems. Additionally, all statistical tests using frequencies or densities of crabs by instar were performed using both the Newcombe and Newcombe-Van Engel size ranges and were not different. While the Newcombe size ranges are smaller, either classification system will adequately represent the density or frequency of first through ninth instar crabs.

Loss of 0 year-class blue crabs in seagrass beds

The relationship of the mean annual densities of larger instar crabs to smaller instar crabs between the first seven instars was either a positive hyperbolic or parabolic function indicating a negative density-dependent relationship. Density-dependent losses were between the first and third, first and fifth, first and seventh, third and fifth, third and seventh, third and ninth, and fifth and seventh instars (Tables 3-5, Figures 9-11). While both of these functions are indicative of regulation by density-dependent processes

they have different end results on a population. The hyperbolic function indicates a constant maximum population level that is not effected by high values of the independent variable. The opposite is true of the parabolic function in that at once the maximum sustainable population is reached further increases in the independent variable result in decreases in the dependent variable. These decreases may result from increased predation or competition for resources resulting in increased natural mortality or emigration to other habitats (Menge and Sutherland 1987).

The relationship between instars within seagrass beds begins to decay once newly settled crabs start emigrating to unvegetated habitats; the fifth through ninth instars. Mean annual densities of seventh instars were dependent on fifth instars and regulated by density-dependent processes. Additionally, there was a possible linear relationship between seventh and ninth instars. This indicates that a different suite of processes are regulating the abundances of these larger instars.

Predation on juveniles is a major deterministic process characteristic of inverse density dependent relationships for many marine species. Previous studies on inverse density dependent relationships have been focused on typical predator-prey relationships (e.g. crab-clam Lipcius and Hines 1986, Mansour and Lipcius 1990, Eggleston et al. 1992) while this study considers newly settled blue crabs as prey. Density of tethered crabs did not significantly affect the survival of newly settled blue crabs in the field tethering study (Table 8). This may be due to selecting experimental densities that were on portions of the density dependent survival curve that resulted in the same proportional survival. The effect of crab density may be confounded by the profound effect that

Tropical Storm Danielle had on relative rates of predation. Further studies on the effects of newly settled crabs densities on survival are warranted before predation can be eliminated as a factor in density dependent loss to the nursery habitat.

Identification of predators

The observed predation event by a larger blue crab and foraging behavior of four larger blue crabs for the prey crab suggests that conspecifics are a major predator of newly settled blue crabs. Intra (Hines et al. 1990, Laughlin 1982, Mansour 1992, Moody and Lipcius unpublished data) and inter year class (Perry 1989, Moskas and van Montfrans unpublished data) cannibalism is common for blue crabs. Conspecifics can comprise between 2% (Hines et al. 1990) to 39% (Mansour 1992) of the diet of 1^+ year class blue crabs. Similarly, dungeness crabs (Botsford and Wickham, 1978, Fernandez et al. 1993) and the cape anchovy (Szeinfeld 1991) exhibit intra and inter year-class cannibalism. Cannibalism may function to regulate year class size or provide food of a higher nutritional content (Polis 1981).

The sub-lethal predation during the laboratory study and observed in the field is characteristic of agonistic behavior amongst blue crabs and attack behaviors when dealing with dangerous prey. The agonistic behavior between blue crabs is evident by the lack of limb loss for tethered crabs in the absence of predators (Figure 14). These crabs were far enough apart so that interaction was prevented. In contrast, 8% of untethered crabs in the absence of predators lost limbs (Figure 14). Agonistic behavior in a variety of laboratory studies (Mansour and Lipcius 1991, Lipcius and Moody unpublished data)

using larger blue crabs has similarly resulted in limb loss. Missing limbs are common in blue crabs, comprising 18-23% of natural populations (Smith 1990). The presence of predators resulted in a significantly higher percent of limb loss in both tethered and untethered treatments (Figure 14) and this study suggests that sub-lethal predation is responsible for a significant loss of limbs in newly settled blue crabs.

These results are consistent with attack patterns exhibited by diamondback terrapins (*Malaclemys terrapin*) on shore crabs (*Carcinus maenas*). When crabs were larger than could be consumed, turtles attacked crabs from the lateral or posterior aspects and frequently removed the 3rd and 4th pairs of legs while avoiding the anteriorly positioned claws (Davenport et al. 1992). Similarly, the attack behaviors of predatory blue crabs focused their initial effort on disabling the prey crab by removing the claws prior to consumption, whereas *Gobisoma (sp)* consumed walking legs when prey crabs were too large to eat whole.

Tethering accuracy and bias

Tethering was demonstrated to be an appropriate method to assess predator-induced mortality on newly settled blue crabs. The lack of any statistically significant interaction effects between habitat, crab size, and tethering (Figure 13, Table 6) indicates that the technique is unbiased. However, since crab survival was significantly lower for tethered crabs (Figure 13, Table 6) any results would not yield an accurate rate of predation. Yet just as untethered crabs, tethered crabs had significantly higher survival rates in vegetated habitats which increased with crab size (Figure 13). Thus, field

experiments using this experimental framework would measure relative rates of predation that assessed predator-induced mortality between treatments.

Previous field studies utilizing tethering to examine relative rates of predation for blue crabs (Heck and Thoman 1981, Wilson et al. 1987, 1990), spiny lobsters (Herrnkind and Butler 1986, Eggleston et al. 1990,, 1992, Mintz 1992, Smith and Herrnkind 1992, Lipcius et al. 1993 in review), American lobsters (Wahle and Steneck 1991, 1992), and dungeness crabs (Fernandez et al. 1993) have not quantitatively tested the accuracy of predation rate or for the presence of bias and assumed that the rate was an inaccurate and unbiased measure of the relative rates of predation. The quantitative method of indicating bias as the statistical interaction between treatments (Barshaw and Able 1990, Marshall 1992) is a more powerful method to determine bias and should be utilized in all tethering experiments.

The effects of habitat and size on crab survival

Crabs had significantly higher survival in vegetated habitats and with increasing crab size in both the laboratory (Figure 13, Table 6) and field (Figure 17, Table 8) experiments. During the field study crab survival was significantly higher in vegetated habitats and with increasing size regardless of the storm conditions (Figure 17, Table 8). The lack of statistically significant interactions between habitat, crab size and storm conditions indicates that where survival was significantly higher during and after the storm the main effects of habitat and size, while smaller during pre-storm conditions, are valid.

Habitat effects were different during pre-storm conditions as compared to storm and post-storm conditions (Figure 17). During pre-storm conditions there was significantly higher survival in vegetated habitats for first, third, fifth and seventh instar crabs while survival for ninth instar crabs was not significantly different by habitat. In contrast, survival was significantly higher in vegetated habitats during storm and post-storm conditions for all instars. There was of increasing survival as crab size increased in both vegetated and unvegetated habitats. Survival was significantly higher for fifth, seventh, and ninth instars than first and third instars in the field (Figure 17, Table 8). While in the laboratory survival increased with size from the first through the seventh instars with the survival of seventh and ninth instars not significantly different (Figure 13, Table 6). The laboratory study utilized a representative guild of small predators from both vegetated and unvegetated habitats. This is an inherent limitation of laboratory studies and the larger instar crabs reached a size refuge that is artificial for the field conditions.

The higher survival in vegetated habitats is consistent with previous studies for 1[+] year-class blue crabs (Heck and Thoman 1981, Wilson et al. 1987, 1990). However, previous studies indicated no increase in survival associated with increasing size (Heck and Thoman 1981, Wilson et al. 1987, 1990). These studies utilized crabs ranging from 12-80 mm cw and this study is unique in evaluating predation induced mortality in the field for 0 year-class blue crabs (Table 2). Survival increased with increasing size through the fifth instar (7.5-9.1 mm cw) and was not significantly different for crabs from the fifth through the ninth instar (7.5-16.1 mm cw) indicating that a size refuge

from predation for 0^+ year-class blue crabs is reached by the fifth instar. Similarly, increased habitat complexity and increasing size does provide a refuge from predation for 0 year-class spiny lobsters (Herrnkind and Butler 1986, Smith and Herrnkind 1992), American lobsters (Wahle and Steneck 1991, 1992), and dungeness crabs (Fernandez et al. 1993), other juvenile marine invertebrates (e.g. Paine 1966, Sousa 1992, Ugaccioni and Posey 1992) 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). While this is easy to conceptualize for obligate crevice dwellers (i.e. spiny and American lobsters, dungeness crabs) seagrass and algal habitats provide a structure that creates niches suitable 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). As the crabs grow, competition for larger crevices limits the effectiveness of the complex habitat as a refuge from predation and may create a bottleneck for the population. When predation risk is equal to that of other habitats emigration to less complex habitats occurs (Smith and Herrnkind 1992).

Effects of Tropical Storm Danielle

The close passage of Tropical Storm Danielle to the field location (Figure 2) had profound effects on the relative rates of predation and habitat utilization of the 0 year-class blue crabs. Survival of 0 year-class crabs was significantly higher during and immediately following the storm and relative rates of predation were 0 for a 17 h period

during the storm. There is little information available on the effects of storms on predation pressure and most researchers briefly mention the effects of a storm as an aside. This finding is opposite from that of Aronson (1992) who found no effect on arm loss of tethered star fish, *Ophiothrix oerstedi*, due to hurricanes in the Caribbean. However, Reiswig (1971) found that filter feeding tropical sponges stop filtering water during storm events with *in situ* experiments. Additionally, during a storm conditions in the southern Kattegat phytoplankton grazing by zooplankton ceased (Nielsen and Kioerboe 1991).

Decreased predation during the storm may be due to changes in a variety of physical factors that caused behavioral changes in predator and prey. There was a 5^0 C drop in mean temperature associated with the storm (Figure 15). Sharp decreases in temperature are associated with decreased activity level for a variety of crustaceans (Eggleston 1988, Lipcius unpublished data). Additionally, predators utilizing visual (e. g. Atlantic croaker (*Micropogonias undulatus*) and the naked gobi) and chemotacticle (blue crabs) search modes would have been severely 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 absence of spontaneous return of survival rates at both locations to those associated with pre-storm conditions is linked to the residual effect of the storm on the physical environment. Water levels did not recede to normal until 28 September (Figure 16), temperature did not rise to pre-storm levels until 27 September (Figure 15), and salinity increased after the storm. This is typical for storm events which create surges of water into the Chesapeake Bay. Time series analysis of water height to projected

water height during 1985 indicated that it takes three days for water heights to return to the projected levels after a storm surge (David Evans, The College of William and Mary, Virginia Institute of Marine Science, personal communication). The delay in the return of the physical environment to pre-storm levels prolongs the effect of the storm and contributes to the increased survival of newly settled blue crabs during post-storm conditions.

Storm events are common during the recruitment period of the blue crab (July - November) and are associated with peaks on megalopeal recruitment (Goodrich et al. 1989, Olmi unpublished data). These events are highly correlated with east winds which create surface Eckman Transport from offshore into the mouth of Chesapeake Bay facilitating the transport of blue crab megalopae from offshore into the initial nursery habitats of the Lower Chesapeake Bay (Goodrich et al. 1989, Olmi unpublished data). Settlement events are also associated with new and full moon periods (van Montfrans et al. 1990). A new moon occurred on September 26, 1992 and the increase in megalopae and first instar crabs frequencies at both locations (Figure 19, Table 10) is due to a post-storm new moon settlement event. This event coincided with an increase of blue crab megalopae in the nightly plankton samples (Figure 20). While increased blue crab megalopal settlement were not high enough to be considered a settlement event at VIMS, the field location is 12 km down stream from the monitoring point and VIMS may be projecting a lower record due to unusual flow regimes associated with the storm.

This study suggests that survival of newly settled blue crabs may be enhanced during storm events due to decreased predation pressure during and immediately

following a storm event. Caution should be used since evidence is limited by the sampling period and it is possible that the post-storm decreasing trend in survival may drop below non-storm conditions before returning to non-storm levels or a rebound effect. A rebound effect could have a net result on survival that would (1) be greater than the increased survival due to the storm resulting in a net decrease in survival, (2) be equal to the increase in survival due to the storm resulting in no net effect on survival or (3) be lower than the increase in survival due to the storm resulting in a net increase in survival. Further studies are necessary to determine the overall effects of storms on predation levels.

Additionally, there was an increase in blue crab densities at the Guinea Marsh location (Figure 18, Table 9) . Crab densities were significantly higher on the northern shore which was the lee side of the storm. This suggests that during the storm crabs found refuge in the lower energy regimes associated with the northern shore and were not moved with the storm surge to the southern shore. While a portion of this was due to the post-storm settlement event there was a proportional increase in the frequencies of crabs larger than the first instar (Figure 19). This may indicate that early benthic stages of blue crabs may have the capability to select a habitat associated with a lower energy regime during a storm event.

While storms of the magnitude of Tropical Storm Danielle are not frequent occurrences, storm of smaller magnitude do occur frequently within the Chesapeake Bay. The effects of these storms on blue crabs is unclear, yet they are reflected in the mean annual densities used to determine the inter-instar relationships. Storm events are a

portion of the dynamic environment that organisms live. However, it has not been determined if they are destructive or beneficial to marine communities. This study suggests that storms potentially enhance blue crab populations by increasing survival from predation.

Conclusions

The influences and controlling factors of populations vary during different life history stages (Paulik 1973, Fogarty and Idoine 1986, Lipcius and Cobb in press). The results of this study are novel in that they present evidence that density dependent processes are influencing loss of newly settled blue crabs to the initial nursery habitat and examine the effects of habitat complexity and size as refuges from predation, a density dependent process was examined.

This study is unique in demonstrating a density dependent loss within the 0-year-class of a decapod crustacean in the initial nursery habitat. Fogerty and Idoine (1986) by examining larval abundance and subsequent harvests for the American lobster concluded that the early benthic stages may be subject to density dependent controls . However, a density dependent relationship within the 0 year-class of lobsters has yet to be demonstrated. Phillips' (1990) re-evaluated the claim that density dependent processes on the juvenile western rock lobster (*Panulirus cygnus*) at nursery reefs were the determinant of year-class strengths of recruitment to the fishery. Now he suggests that density dependent processes are occurring at the extreme highs and lows of the populations and density independent processes at the intermediate levels.

Ontogenetic shifts in habitat utilization are common for other decapod crustaceans such as spiny lobsters (Hernnkind et al. 1975, Marx and Herrnkind 1985, Herrnkind and Butler 1986) and American lobsters (Cobb 1983, Botero and Atema 1982, Wahle and Steneck 1991) and remains uninvestigated for early benthic stages of the blue crab while juvenile and adult blue crabs partition themselves by habitats within the Chesapeake Bay (Van Engel 1958, Miliken and Williams 1984, Hines et al. 1987). The 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, Lipcius et al. 1993). 0 year-class blue crabs are not found outside of vegetated habitats until the third instar, and not at significant densities until the fifth instar (Orth and van Montfrans 1987, Lipcius et al. 1991). 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 (Figure 19, Table 10). The appearance of fifth instar crabs in unvegetated habitats is associated with a decrease in crab densities in seagrass habitats (Figure 8, years 1984, 1991, 1992) and the low variability in annual mean density associated with crabs larger than the seventh instar, suggesting an ontogenetic shift in habitat utilization.

Further evidence for an ontogenetic shift in habitat is provided by the inter-instar relationships. Since crabs smaller than the fifth instar are not found outside of vegetated habitats it is valid to assume that seagrass habitats are a closed system or that larger instars result from the growth of smaller instars. The densities of fifth, seventh, and ninth instars were dependent on third instars and regulated by density-dependent

processes. However, these inter-instar relationships change or become not significant beginning when subsequent densities depend on the fifth instar. This indicates that the densities of fifth, seventh, and ninth instars are not solely dependent on each other and that other processes are regulating these instars. Further, the size refuge associated with vegetated habitats is maximize between the fifth and ninth instar resulting in a predation risk may be similar in unvegetated habitats, as evident by the identical survival of ninth instar crabs in vegetated and unvegetated habitats during pre-storm conditions. If predation pressure is equal between habitats then other factors (e. g. food resources, increased size with ecdysis associated with lower salinities) may be controlling emigration to unvegetated habitats and further investigation is warranted.

This study provides evidence that seagrass beds are a crucial nursery habitat for newly settled blue crabs. Yet, the Chesapeake Bay has experienced an unprecedented decline in seagrass beds since the 1970's (Orth and Moore 1983). This loss of habitat has been associated with a decrease in the catch per unit effort in the blue crab fishery (Anderson 1989). Restoration of seagrass beds is warranted for the successful survival of the blue crab within Chesapeake Bay.

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