

EFFECTS OF SHALLOW WATER REFUGE ON BEHAVIOR AND DENSITY-DEPENDENT MORTALITY OF JUVENILE BLUE CRABS IN CHESAPEAKE BAY

*Ana I. Dittel, Anson H. Hines,
Gregory M. Ruiz and K. Keith Ruffin*

ABSTRACT

This study experimentally tested aspects of behavior and density-dependent mortality of juvenile blue crabs utilizing nearshore shallow water as a refuge from cannibalism by large blue crabs. In a large laboratory tank with a depth gradient, individual juvenile blue crabs shifted their depth utilization from deep and medium depths to shallow water in the presence of a large crab, but not in the absence of another crab or in the presence of another small crab. Survival of juvenile crabs preyed upon by large crabs was significantly higher in laboratory tanks with depth gradients providing a shallow refuge than in lab tanks without depth gradients. In the laboratory, proportional mortality of juvenile crabs was inversely density-dependent, indicating a type II functional response of large crabs irrespective of the presence or absence of a shallow water refuge. In a non-vegetated subestuary of Chesapeake Bay, survival of tethered juveniles was significantly higher in shallow (30 cm) than deep (70 cm) water of a nearshore zone, where cannibalistic large blue crabs were their major source of mortality. Proportional mortality in the field was also inversely density-dependent in both shallow and deep water. The persistence of a type II functional response of predators in our laboratory and field experiments indicates that shallow water provides a significant but partially effective refuge to juvenile blue crabs, although such inversely density-dependent mortality patterns indicate a potentially unstable predator-prey interaction. Under intense predation pressure from cannibalistic large crabs, this partially effective refuge in the nearshore shallows potentially grants juvenile crabs a crucial reduction in mortality during their first year of life until they grow to a size large enough to obtain an absolute refuge from predation.

Refuges provide prey means of escape from predation and thus are an important stabilizing factor in predator-prey interactions (Murdoch and Oaten, 1975). The stabilizing role of refuges from predation has received considerable theoretical and empirical attention (Cerri and Fraser, 1983; Werner et al., 1983; Schmitt and Holbrook, 1985; Abrams, 1987; Gilliam and Fraser, 1987; Murdoch and Bence, 1987). Most theoretical considerations have focused on "absolute refuges," where prey are completely invulnerable to predation (Murdoch and Oaten, 1975). Yet many field studies indicate that refuges provide "partial" escape from predation along a gradient of reduced predator access or efficiency (Werner et al., 1983; Mittelbach 1986; Dill, 1987; Dill and Lima, 1990).

The refuge function of a habitat often changes during ontogeny of prey and is a crucial component of nursery habitats that may limit juvenile survival (Werner and Gilliam, 1984). Estuaries serve as major nurseries for juveniles of many species of coastal fish and decapod crustaceans (McHugh, 1976; Heck and Thoman, 1984). In estuarine ecosystems, submerged aquatic vegetation (SAV) is a major habitat with structural complexity that provides critical refuge to early life stages and has profound effects on prey survival from mobile predators (Heck and Thoman, 1981; Penry, 1982; Wilson et al., 1987). However, little is known about the refuge function of estuarine habitats other than SAV beds. Coarse woody debris also can provide a significant source of habitat complexity and refuge for prey in estuarine ecosystems, but this structure is highly patchy in its distribution and has been reduced significantly in recent decades (Everett and Ruiz, 1993).

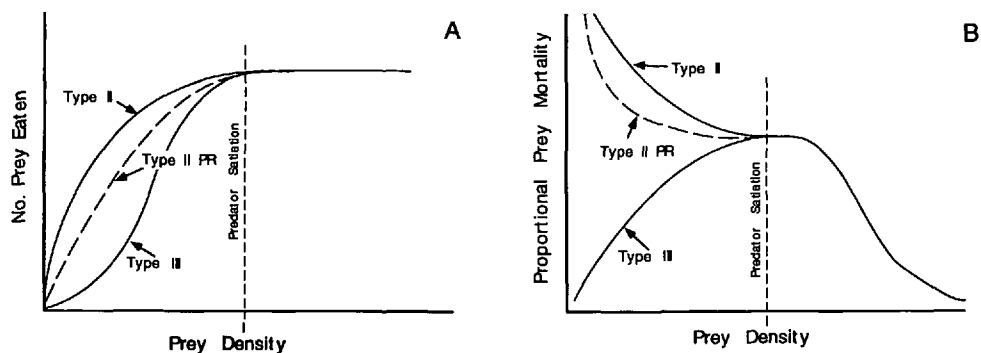


Figure 1. Functional response models depicting number of prey eaten (A) and proportional prey mortality (B) per predator per unit time as a function of prey density (modified from Holling, 1959). Type II response = inversely density-dependent mortality characteristic of habitats without refuge. Type II PR response = inversely density-dependent mortality at a lower rate that indicates a partially effective refuge. Type III response = sigmoidal mortality that indicates a fully effective refuge. Refuge effect is best tested by analyzing proportional mortality at densities below predator satiation.

With the demise of SAV in much of Chesapeake Bay (Orth and Moore, 1984), shallow water along the estuarine shoreline appears to provide an increasingly important refuge for small fish and crustaceans from large mobile predators residing in deeper water (Ruiz et al., 1993). Thus, even in the absence of any structural complexity within the nearshore zone, decreasing water depth (<70 cm deep) can enhance survival of small fish and decapod crustaceans, such as killifish (*Fundulus heteroclitus*), grass shrimp (*Palaemonetes pugio*), and juvenile blue crabs (*Callinectes sapidus*) (Ruiz et al., 1993; Hines and Ruiz, 1995).

Shallow water in the upper Chesapeake Bay provides juvenile blue crabs with a crucial refuge from cannibalistic large crabs, which are their major source of mortality (Hines and Ruiz, 1995). The size structure of blue crabs in shallow (<1 m), nearshore water includes predominantly small, 0+ year-class crabs and proportionately few large, 1+ year-class crabs compared to blue crabs sampled in deeper (2–4 m) water (Hines and Ruiz, 1995). The abundance of both juvenile and adult blue crabs varies greatly among years (Hines et al., 1987, 1990). Juvenile use of, and juvenile mortality rates in, the nearshore zone also exhibit large seasonal and annual variability (Ruiz et al., 1993; Hines and Ruiz, 1995). Even in very shallow (15 cm) nearshore water, mortality of experimental juvenile crabs is substantial (10–30 percent of tethered crabs consumed in 24 h), apparently due to intense predation pressure by large crabs. Both vulnerability of intermolt blue crabs to cannibalism and their utilization of the nearshore zone change ontogenetically, decreasing as the crabs grow (Ruiz et al., 1993; Hines and Ruiz, 1995; Hines et al., 1995). The behavioral basis for blue crab use of shallow water is unknown. However, for grass shrimp in this nearshore habitat, utilization of the shallow water refuge depends upon the presence of a predator, which induces rapid (and reversible) behavioral shifts in the depth distribution of shrimp from deep to shallow water (Posey and Hines, 1991). Thus, the refuge function of the depth gradient for juvenile crabs in the nearshore zone appears to be density dependent, partial and quite dynamic.

Under realistic conditions, a highly effective refuge can be distinguished from a partially effective refuge through analysis of the functional response by testing for a shift in density-dependent foraging efficiency of a predator in differing habitats (Fig. 1) (Holling, 1959; Murdoch and Oaten, 1975; Lipcius and Hines,

1986). In the absence of a refuge, prey suffer increasing proportional mortality with decreasing prey density, reflecting an inversely density-dependent (type II) functional response of predators (Fig. 1). Large blue crabs foraging on the clam *Mya arenaria* in muddy bottoms exhibit this functional response and repeatedly drive this prey to local extinction following recruitment in this habitat (Lipcius and Hines, 1986; Eggleston et al., 1992). By contrast, in habitats providing a fully effective refuge, prey suffer decreasing proportional mortality as prey density declines, reflecting a sigmoidal (type III) functional response of predators (Fig. 1) (Murdoch and Oaten, 1975; Hassell, 1978). Large blue crabs foraging on the clams *M. arenaria* in sandy bottoms and *Macoma balthica* in muddy and sandy bottoms exhibit this functional response, contributing to the persistence of these prey at low densities in these habitats to form their reproductive stocks (Lipcius and Hines, 1986; Eggleston et al., 1992). In a third, often overlooked possibility, prey utilizing a partially effective refuge suffer significantly reduced mortality compared to habitats lacking refuge; but proportional mortality does not decline with decreasing prey density, and density-dependent mortality still reflects a type II functional response (Fig. 1). Thus, refuge effectiveness is dependent on prey density, and by examining the functional response we can assess whether a refuge is: (1) not at all effective at reducing the risk of predation; (2) fully effective and allows prey persistence at low densities; or (3) partially effective but does not prevent local extinction of prey (Fig. 1) (Murdoch and Oaten, 1975; Katz, 1985; Lipcius and Hines, 1986; Abrams, 1987; Murdoch and Bence, 1987; Eggleston et al., 1992).

The purpose of this study was to examine behavior and density-dependent mortality of juvenile blue crabs in response to predation by adult blue crabs in the nearshore shallows in a non-vegetated subestuary of Chesapeake Bay. Our specific experimental goals were: (1) to determine the effect of cannibalistic large blue crabs on the depth distribution of juvenile blue crabs; and (2) to test for interactive effects of water depth and prey density upon prey mortality. Using the theoretical framework of predator functional response, we assess whether the nearshore shallows provide partially or fully effective refuge from predation. We then consider the potential significance of a partial refuge from intense predation pressure to blue crab population dynamics.

METHODS

Study Site.—This study was conducted in the Rhode River (38°51'N, 76°32'W), a 485 ha subestuary in the mesohaline zone of Chesapeake Bay (Fig. 2). Previous studies in this subestuary describe major aspects of its water quality (Jordan et al., 1991) and of blue crab biology (Hines et al., 1987, 1990). The subestuary is shallow (≤ 4 m), with about 80% of the bottom area composed of silt and clay and 20% composed of fine to medium sand. Monthly mean water temperatures fluctuate seasonally between 2–30°C, and salinity varies from 3–17‰. Tidal amplitude is approximately 0.5 m. Field experiments were conducted within the subestuary at Canning House Bay (Fig. 2), which is characterized by an unvegetated sandy beach and a nearshore bathymetry sloping gradually to depths >1 m about 40 m off from the water's edge.

Experimental Blue Crabs.—Juvenile (30–70 mm CW) and adult male (140–150 mm CW) blue crabs were collected by seining, trawling and trapping within the subestuary. These two size groups are representative of the 0+ and 1+ year classes of crabs (Hines et al., 1987, 1990; Hines and Ruiz, 1995). Because vulnerability to predation is size-dependent (Smith, 1990; Hines and Ruiz, 1995), juvenile crabs were assigned randomly by size within the size range and by sex to treatments to achieve interspersed in each trial of our experiments. During subsequent data analysis, we tested for effect of prey sex and size by arbitrarily partitioning the data into two size categories (30–50 mm and 51–70 mm) using log-linear models (SAS Institute, 1990) with size category and sex as factors and number of crabs killed as a response variable. We also determined whether the composition of treatment groups was independent of size or sex using log-linear models. Crabs were held in large aquaria

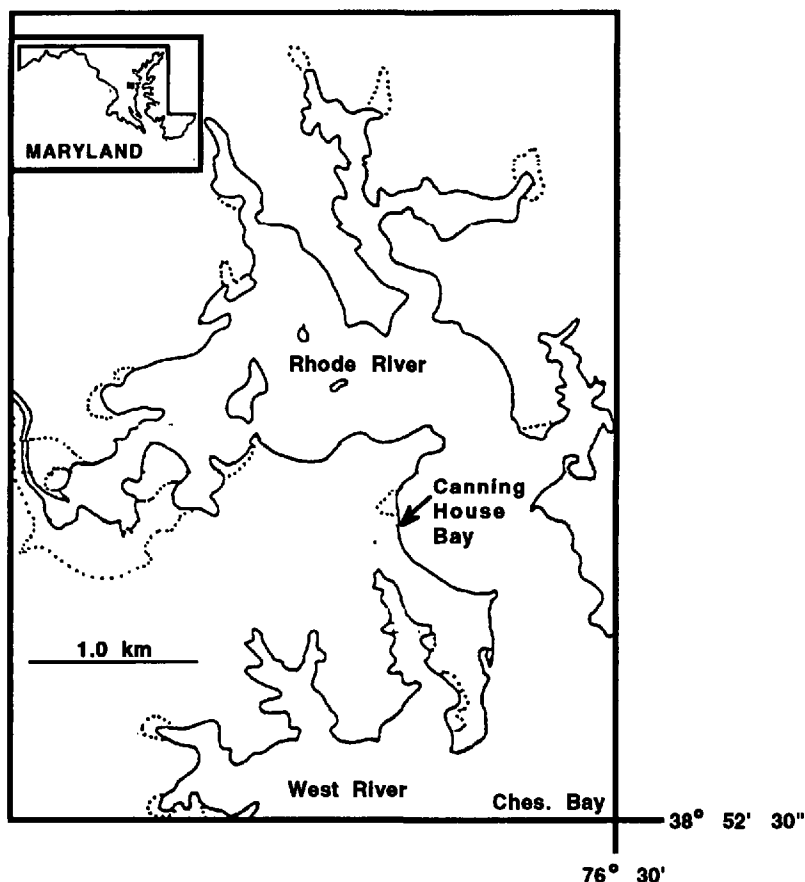


Figure 2. Map of Maryland portion of Chesapeake Bay (inset) and the Rhode River subestuary showing the location of the field experimental site in Canning House Bay.

and fed frozen fish (*Fundulus heteroclitus*) or clams (*Macoma balthica*) daily for 2–7 days. Only actively feeding, intermolt crabs were used in experiments. Less than 1% of test crabs underwent ecdysis during the experiments; these individuals were not included in subsequent data analyses. Crabs were used only once for experiments.

Effect of Predation Risk on Juvenile Crab Depth Distribution.—The effect of large (140–150 mm) blue crabs upon the depth distribution of juvenile blue crabs was tested from March to August 1990 in an indoor laboratory tank (2.4 m long, 0.8 m wide, 0.3 m deep), which allowed control of temperature (20–23°C) and salinity (8–14‰) to reflect the range of summer field conditions simulated by the experiment. The fiberglass tank was constructed with a sand-covered bottom that produced a depth gradient with shallow (7 cm), medium (18 cm), and deep (28 cm) zones (Fig. 3). The bottom sand was 3 cm deep, which was sufficient to allow small crabs to bury normally and completely, and large crabs to bury partially and restfully. During each experimental trial, a small juvenile blue crab was marked with a small dot of ink on the dorsal carapace and released into the tank in the deep depth zone. After a 24-hr acclimation period, we recorded the depth zone in which the marked crab was residing, and one of three treatments was initiated: (1) no crab was added to the tank; (2) a second juvenile crab was added to the deep zone; or (3) a large blue crab was added to the deep zone. Both small and large crabs added in these treatments were fed to satiation with fish just prior to release in the test tank, so as to minimize risk of actual predation upon the juvenile marked crab. After 24 h, the locations of the marked and second crabs were recorded by depth zone, and any mortality or damage (e.g., limb autotomy) was noted. Trials were replicated through time by alternating treatments systematically until 18 trials of each treatment were completed. Frequencies of the initial and final

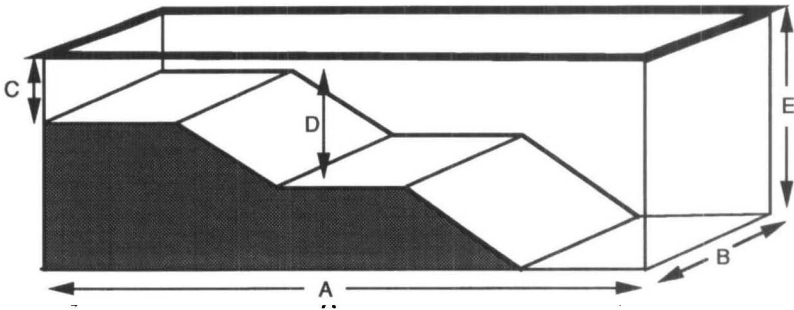


Figure 3. Schematic drawing of large tanks with depth gradients used in laboratory experiments. For the experiment testing the behavioral effect of a large blue crab on the depth distribution of juvenile blue crabs, A = 240 cm, B = 80 cm, C = 10 cm, D = 20 cm, and E = 30 cm. For the experiment testing the effects of shallow refuge and prey density on mortality of juvenile blue crabs, A = 220 cm, B = 110 cm, C = 10, D = 30 cm, and E = 50 cm.

depths of the juvenile test crabs were tested for independence of treatment using G-tests (Sokal and Rohlf, 1981).

Effect of Water Depth and Prey Density on Juvenile Crab Mortality.—LABORATORY EXPERIMENT. The interactive effects of shallow-water refuge and prey density upon mortality rates of juvenile blue crabs exposed to large cannibalistic blue crabs was tested outdoors in large (2.2 m long, 1.1 m wide, 0.5 m deep) fiberglass tanks. Six tanks were arranged in three pairs: one tank in each pair had a uniform water depth of 45 cm; the other tank had three depth zones (shallow, 5 cm; medium, 20 cm; and deep, 45 cm) that were similar to the indoor tank (Fig. 3). The bottom of each tank was covered with sand to a depth of 3 cm. Water temperature ranged from 20–25°C, and salinity varied from 10–14‰. Twenty-four hours prior to the start of a trial, juvenile crabs were added to both of the paired tanks at one of four test densities: 3, 6, 12, and 24 crabs per tank [densities = 1.5–12 crabs per m², which are within the range of juvenile blue crabs densities in the Chesapeake Bay (Orth and van Montfrans, 1987; Ruiz et al., 1993)]. Also during this 24-h acclimation period, six large adult crabs were starved to standardize hunger levels. After the 24-h starvation period, one large crab was added to each tank and allowed to forage. After a 24-h foraging period, the large crab was removed and the number of juvenile blue crabs consumed in each tank was recorded. Because we tested four densities of juvenile crabs but had only three pairs of tanks, we assigned treatments so as to intersperse density treatments randomly among locations of the paired tanks while also incorporating interspersions of densities as follows. Individual treatment combinations were replicated 9–21 times, with more replicates being performed at low densities where variability in mortality was higher than at high densities. Because more replicates were performed for low density than for high density treatments, we also maintained interspersions of low and high density trials throughout the temporal sequence of the experiment. In an additional component of experimental design, we also ran nine trials of each treatment without any large crab as a control for potential mortality or cannibalism among small crabs. These control trials were also interspersed randomly in space and time throughout the experiment.

The effects of juvenile density and refuge treatment upon juvenile crab mortality were assessed with an ANOVA model incorporating juvenile density (3, 6, 12, 24 crabs per tank) and refuge treatment (tank with uniform deep water versus tank with three water depths) as factors and proportional crab mortality as the response variable. Proportional mortality rates were angular transformed and tested for normality and homogeneity of variance before proceeding.

We used direct observation and time-lapse video recording to evaluate predator-prey behavior of large blue crabs foraging upon juvenile crabs in the laboratory tank fitted with a depth gradient (described above). Specifically, we observed movement of small and large crabs among depth zones, and we recorded whether attacks by large crabs upon small crabs occurred either when the large crab moved into shallow water or when small crabs moved into deeper water.

FIELD EXPERIMENT. The interactive effects of water depth and prey density upon relative mortality rates of juvenile blue crabs (30–70 mm CW) were also tested in the field using tethering techniques in the nearshore zone of Canning House Bay (Fig. 2). Tethering has been used successfully to assess relative predation risk in the field for crabs and other animals (Heck and Thoman, 1981; Wilson et al., 1987, 1990; Watanabe, 1984; Herrnkind and Butler, 1986; McIvor and Odum, 1988; Wilson, 1989; Barshaw and Able, 1990a; Ruiz et al., 1993; Barbeau and Scheibling, 1994; Heck and Coen, 1995; Hines and Ruiz, 1995). Although tethering can significantly alter animal behavior and absolute rates of predation (Barshaw and Able, 1990b; Smith, 1990, 1995), it allows comparison of relative rates of

mortality among treatments in the absence of tethering artifacts (Peterson and Black, 1994). When experimental manipulations, such as tethering, introduce artifacts which produce significant interaction effects with treatment variables, interpretation of results becomes problematic (Peterson and Black, 1994). For juvenile blue crabs, however, such interaction effects of tethering appear to be minimal in soft-bottom sediments lacking SAV. Our laboratory observations showed that tethered crabs displayed the full range of normal behaviors, including feeding, grooming, resting (including burying), and locomotory (including swimming) activities. Although crabs also rapidly moved and swam away from attacking predators, they were restricted in the extent of their escape by the tethers (Wilson et al., 1990; Hines and Ruiz, 1995). These qualitative observations are also supported by more detailed video analysis of juvenile blue crabs (Zimmer-Faust et al., 1994). Moreover, tethered 5–15 mm blue crabs in SAV in lower Chesapeake Bay did not show significant tethering artifacts (Pile, 1993), and mortality of tethered and untethered blue crabs (50 mm without missing limbs) did not differ when exposed to large blue crabs in large field enclosures in the Rhode River (Smith, 1995). In the Rhode River, there is only one major predator (large blue crabs) on small crabs (Smith, 1990; Ruiz et al., 1993; Hines and Ruiz, 1995), thus eliminating possible differences in tethering artifact among predators that could sometimes change if the species composition of predators varied along a depth gradient (Peterson and Black, 1994).

Tethering consisted of tying a loop of monofilament line (9 kg test) around the crabs' lateral spines to form a halter held in place with cyanoacrylate glue and attached to a coated steel leader (4.5 kg test). Each crab was tethered individually on a 0.5 m-long leader attached to a steel spike, which was also tied with a monofilament line attached to a small fishing float to locate the tether in the field. Following tethering and before deployment in the field, crabs were placed individually in small plastic containers of estuarine water and checked for 1–3 h to be sure they were not injured during tethering. During deployment, the spike was pushed into the sediment and the float line extended to the water surface, while the crab was allowed to move on the tether line.

Juvenile crabs were tethered in 3 m × 3 m patches at two water depths (shallow—30 cm; deep—70 cm) and three densities (3, 9, and 18 crabs per 9 m² patch). For each density, the crabs were placed into the patches with equal spacing that maximized the distance between adjacent crabs. The tether length and spacing prevented juvenile crabs from interacting in any of the treatments. Tethered crabs were placed into the field in early afternoon and checked after 48 h for survivorship, damage (autotomy or puncture), and body remains attached to the tether. Patterns of body damage provide strong indicators of predator species, especially large blue crabs (as determined by Hines and Ruiz, 1995). For example, large blue crabs accounted for 75–97% of the mortality of juvenile blue crabs in similar tethering experiments conducted in the same location and time periods (Hines and Ruiz, 1995). The block of six treatments (2 depths × 3 densities) was replicated seven times during July–September 1990 and July 1991. In each replicate block, the relative position of each density treatment was randomly located within a depth zone, and each patch was spaced 12 m (4 times the patch dimension) away from adjacent patches to minimize potential effects of other patches.

The effects of juvenile density and water depth upon juvenile crab survival were assessed using a randomized complete block ANOVA model with juvenile crab density (3, 9 and 18 crabs per patch) and water depth (shallow and deep) as factors and proportional crab mortality per 48 h as the response variable. Proportional mortality rates were angular transformed and tested for normality and homogeneity of variance before proceeding. We also employed a log linear model for categorical mortality data to assist in interpreting consistent mortality patterns with low statistical power in ANOVA models.

FUNCTIONAL RESPONSE ANALYSIS. Both the laboratory and the field experiments testing for the effect of juvenile crab density on predation rate were designed for analysis in the context of functional response theory (Holling, 1959). Rather than attempting to fit a functional response model to the data to determine the parameters of a particular equation (Hassell, 1978), our objective was to test density-dependent foraging rates for a shift between categories of functional response, especially a change from an inversely density-dependent response (type II) to a sigmoidal response (type III) that is indicative of a highly effective refuge (Murdoch and Oaten, 1975; Lipcius and Hines, 1986). In applications that include typical variability in predator feeding rates, it is often difficult to distinguish between type II and type III functional responses when testing numbers of prey consumed (Fig. 1A). However, the two types of functional response can be readily distinguished by testing whether proportional mortality increases (type II) or decreases (type III) as prey density decreases (Fig. 1B) (Lipcius and Hines, 1986). Thus, in contrast to model fitting that requires testing numerous prey densities, the distinction between functional response types can be made with relatively few tests at low prey densities, where proportional mortalities are predicted to diverge in habitats with and without effective refuge. We also considered an alternate possibility of significantly reduced prey mortality at low prey densities without producing a change in the type of functional response (Fig. 1). Lower prey mortality while still exhibiting a type II pattern of increasing rates of mortality as prey density decreased would reflect a significant but partially effective refuge from predation.

In practical considerations of experimental design for functional response analysis, we applied three

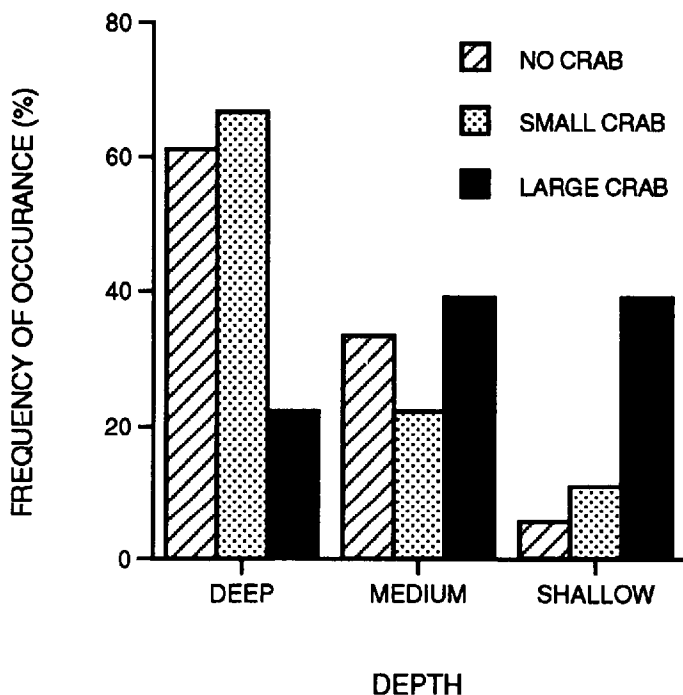


Figure 4. Depth distribution of marked juvenile blue crabs in laboratory tanks (see Fig. 3) as a function of three treatments: (1) no additional crab; (2) a second small blue crab; and (3) an additional, large blue crab. Histograms indicate percentages of marked juvenile crabs found in deep, medium and shallow zones after 24 h exposure to the three treatments. No mortality occurred during the experiment. $N = 18$ for each treatment.

criteria in selecting the range of prey densities for our experiments. First, we were interested in the range of prey densities observed in the field. Orth and van Montfrans (1987) and Ruiz et al. (1993) provide this range for juvenile blue crabs in Chesapeake Bay. Second, we set the area of the experimental unit (i.e., tank or patch size) to be large enough that the lowest test density would include no fewer than three juvenile crabs, because lower values inherently result in unacceptably high variances. Even so, we compensated for the inherently increasing variance by increasing the number of replicates at low densities. Third, the highest density of interest in these experiments was that which produced predator satiation. As predator satiation is approached, proportional mortality rates in habitats with and without refuge converge (and then rapidly diminish)(Fig. 1); and we tested our data for this convergence at higher experimental densities. Because functional response models indicate that refuge effectiveness should be evident only at low prey densities below satiation, we specifically tested for differences in juvenile mortality rates at prey densities below this convergence for the treatments.

RESULTS

Effect of Predation Risk on Juvenile Crab Depth Distribution.—No mortality occurred for either juvenile marked crabs or for large or juvenile treatment crabs during any of the experimental trials. Following the 24-h acclimation period, marked individual juvenile blue crabs occurred primarily in deep (60%) and medium (33%) zones of the experimental tank. After the subsequent 24-h test period, the depth distributions of marked juvenile crabs differed significantly among the three treatments (G-test, Chi-square = 11.625, $df = 4$, $P < 0.02$) (Fig. 4). Depth distributions of marked crabs did not change significantly in treatments in which no second crab was added or in which a second juvenile crab was added (G-test, Chi-square = 0.812, $df = 4$, $P > 0.5$); and these two treatments did not differ

significantly from each other (G-test, Chi-square = 0.786, $df = 2$, $P > 0.6$), with most (>90%) marked crabs occurring in deep and medium depths. However, for the treatment in which a large blue crab was added, the depth distribution of marked juvenile crabs shifted into shallow water, and marked crabs were found significantly more frequently in medium (ca. 40%) and shallow (ca. 40%) depth zones than they were in the other 2 treatments with either no crab or a second small crab added (G-test, Chi-square = 10.8, $df = 2$, $P < 0.005$) (Fig. 4). In the presence of a large crab, only 22% of marked juvenile crabs occurred in the deepest zone, contrasting sharply with the large crabs, which occurred in the deepest zone at a frequency of 90%.

Effects of Water Depth and Prey Density on Juvenile Crab Mortality.—LABORATORY EXPERIMENT. Juveniles in control treatments without a large crab suffered no mortality at any density or depth treatment, and subsequent analyses do not consider these controls. Less than 1% of the juvenile crabs died without any evidence of predation. Mortality of juvenile blue crabs in the laboratory tanks did not differ between sexes (log linear model, Chi-square = 2.31, $df = 1$, $P > 0.13$), and there was no significant interaction effects of sex with density or depth-refuge treatment (log linear models, P values > 0.5). Mortality also did not differ by size between 30–50 mm and 51–70 mm categories of crabs (log linear model, Chi-square = 0.84, $df = 1$, $P > 0.35$), and there were no significant interaction effects of size with density or depth-refuge treatment (log linear models, P values > 0.5).

When all densities are incorporated into the analysis, proportional mortality of juvenile crabs differed significantly among juvenile densities (ANOVA, $F_{(3,99)} = 6.70$, $P < 0.001$), but not between tanks with and without shallow refuge (ANOVA, $F_{(1,99)} = 0.107$, $P = 0.10$); and there was no significant interaction (ANOVA, density \times refuge, $F_{(3,99)} = 0.22$, $P > 0.8$) (Fig. 5). Proportional juvenile mortality increased significantly at low prey densities, averaging 42% at the lowest density of three prey per tank compared to 15% mortality at the highest density of 24 prey per tank. Consistent with the predicted pattern of predator satiation at high prey densities (see Methods), proportional mortalities in the two refuge treatments were similar in the highest prey density at about 15% (ANOVA, $F_{(1,8)} = 0.06$, $P > 0.9$), indicating that large blue crabs were satiated after consuming three to four juvenile crabs per 24 h (Fig. 5). At the lowest test density of three prey per tank, however, large crabs consumed an average of 1.25 juveniles per 24 h and thus were not satiated.

When only densities below that producing predator satiation are considered (i.e., 3, 6, and 12 prey per tank), as recommended by functional response models (see Methods), proportional juvenile mortality was significantly lower in tanks with than without shallow refuges (ANOVA, $F_{(1,83)} = 4.19$, $P < 0.05$), as well as differing significantly among prey densities (ANOVA, $F_{(2,83)} = 7.09$, $P < 0.002$); there was not a significant interaction (ANOVA, density \times refuge, $F_{(2,83)} = 0.04$, $P = 0.95$) (Fig. 5). At the lowest density of three prey per tank, proportional mortality in tanks with shallow refuges averaged 36%, compared to 46% in tanks without refuges. This pattern of increasing prey mortality at decreasing prey densities below predator satiation indicates that large cannibalistic blue crabs exhibited a type II functional response in tanks with and without shallow refuges (see Methods).

Out of 11 lethal attacks upon juvenile crabs observed in the laboratory, most occurred when juveniles moved out of shallow water and encountered the large crab in medium (6 cases) to deep (3 cases) zones, but also occasionally (2 cases)

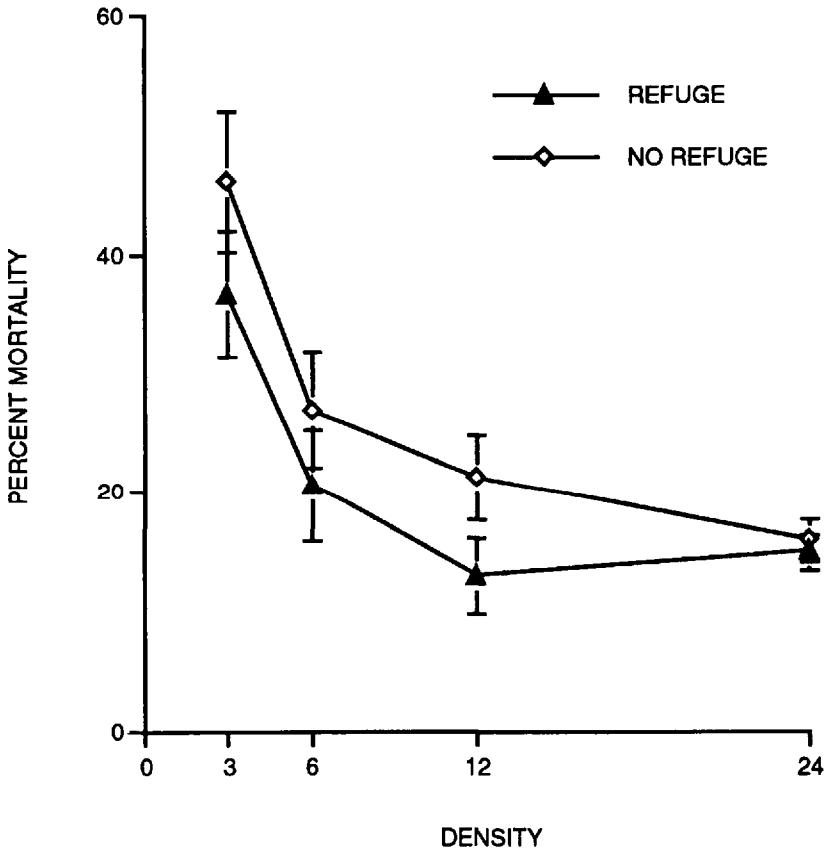


Figure 5. Proportional mortality of juvenile blue crabs preyed upon by large blue crabs in laboratory tanks with and without shallow refuges (Fig. 3) as a function of juvenile density (number of crabs per tank). Points plotted are means (\pm SE) of trials ranging from $N = 9$ at highest densities to $N = 21$ at lowest densities.

when large adult crabs moved briefly into shallow water, apparently to forage. Large crabs often consumed their prey at the location of the attack; but in more than 30% of the lethal attacks, the prey was moved to a different depth zone during consumption. Successful attacks occurred primarily (73%) when a small crab moved into a stationary large crab, but also when a large crab moved toward a juvenile (27%). Numerous other, non-lethal encounters between large and juvenile crabs were observed. However, since we did not run control observations between two juvenile crabs, it was often difficult to determine whether these involved predator-prey behavior or just chance encounter among two individuals moving within a finite space.

FIELD EXPERIMENT. Juvenile blue crabs tethered in the nearshore zone of the Rhode River exhibited an overall mortality rate of 56%. Of those juveniles which died, 61% exhibited direct characteristics of blue crab cannibalism (diagnostic shell fragments remaining attached to their tethers, dead crabs with punctures and limb loss), and another 38% had been removed entirely from their tethers, which is an indirect attribute of cannibalism by large blue crabs (Hines and Ruiz, 1995); <1% of juveniles were dead with no signs of predation. For juvenile crabs which were missing, killed or damaged, these frequencies of predation characteristics

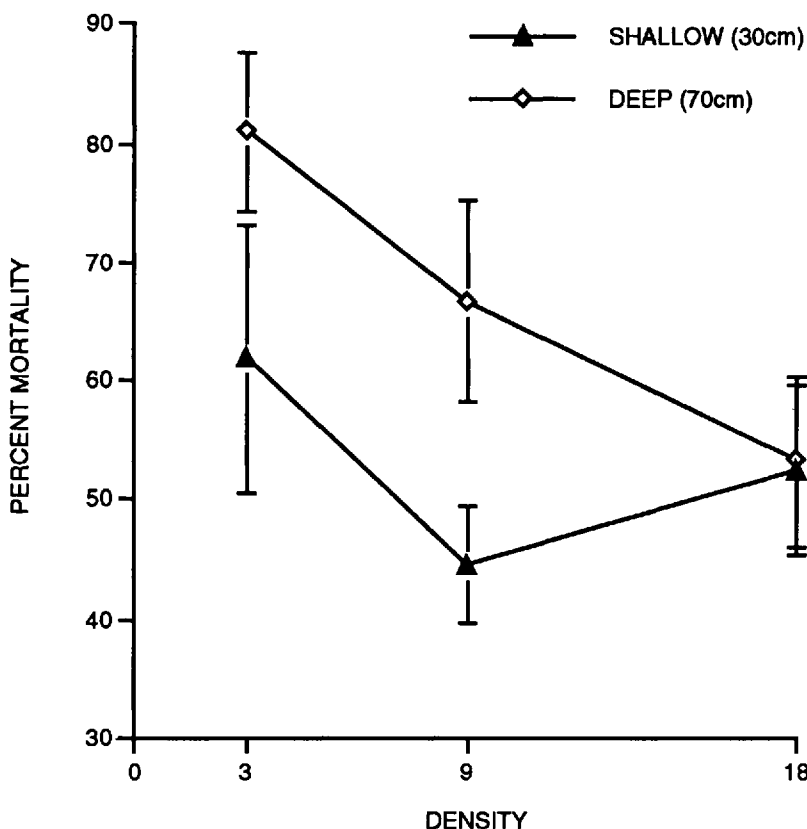


Figure 6. Proportional mortality of juvenile blue crabs tethered in 9 m² patches at densities of 3, 9, and 18 crabs per patch in shallow (30 cm) and in deep (70 cm) depths of the Rhode River subestuary. Points plotted are means (\pm SE) of 7 trials.

did not differ significantly between water depths (log linear model, Chi-square = 0.6, $df = 1$, $P > 0.7$) or among patch densities (log linear model, Chi-square = 0.03, $df = 2$, $P > 0.9$), and there was no significant interaction (log linear model, Chi-square = 0.4, $df = 2$, $P > 0.9$). Mortality of juvenile crabs did not differ significantly between sexes (log linear models, Chi-square = 2.31, $df = 1$, $P > 0.1$), and there were no significant interaction effects of depth, density, or depth \times density with sex (log linear models, P values > 0.6). Mortality did differ significantly by size (log linear models, Chi-square = 15.07, $df = 1$, $P < 0.001$), with 30–50 mm juveniles having higher mortality (64%) than 50–70 mm juveniles (39%). However, there were no significant interaction effects of size with depth, density or depth \times density (log-linear models, P values > 0.7); and size composition of tethered crabs did not differ among treatment groups (log linear models, Chi-square = 2.01, $df = 5$, $P > 0.4$), so the effect of size did not confound the experimental results. Mortality did not differ significantly between the two years of experimental runs (log linear model, Chi-square = 0.93, $df = 1$, $P > 0.7$), and subsequent analysis does not consider this factor.

When all densities are incorporated into the analysis, proportional mortality of juvenile crabs tethered in the nearshore zone of the Rhode River differed significantly among prey densities (ANOVA, $F_{(2,36)} = 4.60$, $P < 0.02$), but not between

water depths (ANOVA, $F_{(1,36)} = 3.78$, $P < 0.06$); and there was no significant interaction (ANOVA, density \times depth, $F_{(2,36)} = 0.79$, $P > 0.45$) (Fig. 6). Proportional juvenile mortality increased significantly at low prey densities, averaging 72% at three prey per patch compared to 52% at 18 prey per patch. Consistent with the predicted pattern of predator satiation at high prey densities (see Methods), proportional mortalities in the two depth zones were similar in high density patches at about 52% (ANOVA, $F_{(1,6)} = 0.04$, $P > 0.9$), indicating that the predators in the field were satiated after consuming about nine juvenile crabs per patch per 48 h (Fig. 6). At the low test density of three prey per patch, however, predators consumed an average of 2.2 juveniles per patch per 48 h and thus were not satiated.

When only densities below that producing predator satiation are considered (i.e., 3 and 9 prey per patch), as recommended by functional response models (see Methods), proportional juvenile mortality was significantly lower in shallow than deeper water (ANOVA, $F_{(1,24)} = 4.35$, $P < 0.05$), as well as differing significantly between prey densities (ANOVA, $F_{(1,24)} = 4.84$, $P < 0.04$) (Fig. 6). There was not a significant interaction (ANOVA, depth \times density, $F_{(1,24)} < 0.01$, $P > 0.95$). At the low density of three prey per patch, proportional mortality in shallow water averaged 61% compared to 81% in deeper water. This pattern of increasing prey mortality at decreasing prey densities below predator satiation indicates that predation exhibited a type II functional response in both shallow and deeper zones (see Methods).

DISCUSSION

The principal source of mortality of intermolt juvenile blue crabs in upper Chesapeake Bay is cannibalism by large blue crabs, which are abundant in water deeper than 1 m (Smith, 1990; Ruiz et al., 1993; Hines and Ruiz, 1995). The abundance of juvenile blue crabs is greater, and their mortality is significantly less, in shallow water of the nearshore zone than in deeper water of the Rhode River subestuary (Ruiz et al., 1993; Hines and Ruiz, 1995; this study). Our laboratory experiments indicated that the presence of a large blue crab induces a behavioral change in juvenile blue crabs to move from deep to shallow water, even in the absence of actual predation by a large crab. Our laboratory and field observations also indicate that large blue crabs do occasionally move into shallow water to prey upon juveniles; however, their feeding efficiency is apparently reduced in shallow water. For example, when tethered juveniles were attacked by large crabs in shallow water, there were proportionately higher frequencies of unsuccessful attacks (non-lethal attacks resulting in prey limb autotomy and/or body punctures) compared to attacks in deeper water (Hines and Ruiz, 1995). We do not know whether the reduced rate of successful attacks results from poorer performance of the predator or improved escape abilities of the prey. While utilization of shallow water habitat significantly reduces cannibalism upon juvenile crabs, the refuge is a partial one; and juveniles also suffered appreciable mortality rates in this refuge in both the laboratory and the field (see also Ruiz et al., 1993; Hines and Ruiz, 1995).

Structural complexity of a habitat provides a major source of refuge that stabilizes predator-prey interactions in many aquatic ecosystems by diminishing predator effectiveness and/or improving prey escape (Heck and Orth, 1980; Bell et al., 1991). Behavioral studies in freshwater habitats indicate that piscivorous predators often drive juvenile fish into refuges of the vegetation along shores (Werner et al., 1983; Mittelbach, 1986). Emergent vegetation, SAV, coarse woody

debris, and oyster reefs provide important sources of complexity and refuges in estuaries, but these habitats have undergone major declines within Chesapeake Bay in recent decades (Kneib, 1986; Orth and Moore, 1984; Mann et al., 1991; Everett and Ruiz, 1993). Growing evidence indicates that the nearshore shallows provides a crucial, non-structural refuge habitat for small fish and decapod crustaceans in Chesapeake Bay (Ruiz et al. 1993; Hines and Ruiz, 1995; this study). In contrast to the partial refuge provided to juvenile blue crabs, grass shrimp and killifish appear to be able to obtain an absolute refuge by moving into this near-shore habitat (Posey and Hines, 1991; Hines and Ruiz, pers. observ.). However, blue crabs eventually obtain a refuge in size by their second year of life (Smith, 1990; Moody, 1994; Hines and Ruiz, 1995), whereas grass shrimp and killifish do not (Everett and Ruiz, 1993; Hines and Ruiz, unpubl. data).

Considerations of density-dependent mortality rates of juvenile crabs in our experiments indicate that the functional response of cannibalistic large crabs is inversely density dependent in both shallow and deeper water. While a sigmoidal (type III) functional response produces a stable predator-prey interaction, an inversely density-dependent (type II) functional response often characterizes an unstable interaction where the predator can drive the prey to local extinction (Holling, 1959; 1965; Murdoch and Oaten, 1975; Hassel, 1978; Katz, 1985; Lipcius and Hines, 1986; Abrams, 1987; Murdoch and Bence, 1987; Eggleston et al., 1992). Our functional response analysis indicates that cannibalism by large blue crabs may be capable of driving juvenile crabs locally extinct throughout much of Chesapeake Bay, where juveniles must rely on the partially effective refuge of shallow water.

Although predator-prey interactions comprise only part of population dynamics, juvenile blue crabs' apparent reliance upon a partial refuge from intensely cannibalistic large crabs may be a major source of variability and potential instability in blue crab populations. Abundance of the blue crab population in Chesapeake Bay is markedly variable (Millikin and Williams, 1984; Hines et al., 1987; Lipcius and Van Engel, 1990; Hines et al., 1990). The Chesapeake blue crab population exhibits a significant recruit-stock relationship, which has been interpreted to reflect density-dependent cannibalism (Lipcius and Van Engel, 1990). Compounding an inherently variable pattern of larval recruitment (van Montfrans et al., 1990), intense cannibalism and the lack of an absolute refuge may effectively decouple recruitment of juveniles from survival to sizes forming the fishery and reproductive stock. Rates of cannibalism and juvenile mortality exhibit significant temporal mortality among years (Hines and Ruiz, 1995). A critical factor in these dynamics may be the shifting balance of available food resources and relative abundances of large and small crabs. Large blue crabs consume clams as their main prey, but small crabs appear to serve as an important supplement and alternate prey to clams (Hines et al., 1990; Mansour, 1992), so that predation pressure on small crabs may vary with availability of clams. For small crabs, since maximizing growth would confer improved survival, availability of the several food species they consumed (Laughlin, 1982; Mansour, 1992) may regulate the duration of exposure to intense cannibalism by limiting growth rate. While providing only a partial refuge, the nearshore shallows appears to provide a critical nursery habitat that significantly reduces juvenile mortality as blue crabs outgrow their vulnerability to intensely cannibalistic adults.

ACKNOWLEDGMENTS

We thank L. Nye, T. Steelman, M. Kramer, S. Godwin, G. Braun, R. Everett, and various SERC Interns for field assistance. L. Nye and D. Smith helped with data analysis. Two patient reviewers and

G. Olmi improved the manuscript. This work was supported by a Smithsonian Postdoctoral Fellowship to A.I. Dittel and by grants from the National Science Foundation (OCE-9000483) to A.H.H., Smithsonian Scholarly Studies Program to A.H.H. and G.M.R., and Smithsonian Environmental Sciences Program to A.H.H. and to GMR.

LITERATURE CITED

- Abrams, P. 1987. Indirect interactions between species that share a predator: varieties of indirect effects. Pages 38–54 in W. Kerfoot and A. Sih, eds. *Predation: direct and indirect impacts on aquatic communities*. Univ. Press of New England, Hanover, New Hampshire.
- Barbeau, M. A. and R. E. Scheibling. 1994. Procedural effects of prey tethering experiments: predation of juvenile scallops by crabs and sea stars. *Mar. Ecol. Prog. Ser.* 111: 305–310.
- Barshaw, D. E. and K. W. Able. 1990a. Deep burial as a refuge for lady crabs *Ovalipes ocellatus*: comparisons with blue crabs *Callinectes sapidus*. *Mar. Ecol. Prog. Ser.* 66: 75–79.
- and ———. 1990b. Tethering as a technique for assessing predation rates in different habitats: an evaluation using juvenile lobsters *Homarus americanus*. *Fish. Bull. U.S.* 88: 415–417.
- Bell, S. S., E. D. McCoy and H. R. Mushinsky. 1991. Habitat structure. The physical arrangement of objects in space. Chapman and Hall, New York, 438 pp.
- Cerri, R. D. and D. F. Fraser. 1983. Predation and risk in foraging minnows: balancing conflicting demands. *Am. Nat.* 121: 552–561.
- Dill, L. M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. *Can. J. Zool.* 65: 803–811.
- and L. M. Lima. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68: 619–640.
- Eggleston, D. B., R. N. Lipcius and A. H. Hines. 1992. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. *Mar. Ecol. Prog. Ser.* 85: 55–68.
- Everett, R. A. and G. M. Ruiz. 1993. Coarse woody debris as refuge from predation in aquatic communities: an experimental test. *Oecologia* 93: 475–486.
- Gilliam, J. and Fraser. 1987. Habitat selection when foraging under predation hazard: a model and a test with stream-dwelling minnows. *Ecology* 68: 1856–1862.
- Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. *Monogr. Pop. Biol.*, Princeton Univ. Press., Princeton, New Jersey.
- Heck, K. L., Jr. and L. D. Coen. 1995. Predation and the abundance of juvenile blue crabs: a comparison of selected east and Gulf coast (USA) studies. *Bull. Mar. Sci.* 57: 877–883.
- and R. J. Orth. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. Pages 449–464 in V. S. Kennedy, ed. *Estuarine perspective*, Academic Press, New York, New York.
- and T. A. Thoman. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Biol. Ecol.* 53: 125–134.
- and ———. 1984. The nursery role of seagrass meadows in the upper and lower Chesapeake Bay. *Estuaries* 7: 70–92.
- Herrnkind, W. F. and M. J. Butler. 1986. Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters *Panulirus argus*. *Mar. Ecol. Prog. Ser.* 34: 23–30.
- Hines, A. H., A. M. Haddon and L. A. Wiechert. 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 67: 105–126.
- , R. N. Lipcius and A. M. Haddon. 1987. Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 36: 55–64.
- and G. M. Ruiz. 1995. Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. *Bull. Mar. Sci.* 57: 884–901.
- , T. G. Wolcott, E. González-Gurriarán, J. L. González-Gurriarán, and J. Friere. 1995. Movement patterns and migrations in crabs: telemetry studies of juvenile and adult behavior in *Callinectes sapidus* and *Maja squinado*. *J. Mar. Biol. Assoc., U.K.* 75: 27–42.
- Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can. J. Ent.* 91: 293–320.
- . 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45: 1–60.
- Jordan, T. E., D. L. Correll, J. Miklas and D. E. Weller. 1991. Long-term trends in estuarine nutrients and chlorophyll, and short-term effects of variation in watershed discharge. *Mar. Ecol. Prog. Ser.* 36: 55–64.
- Katz, C. H. 1985. A nonequilibrium predator-prey interaction. *Ecology* 66: 1426–1438.

- Kneib, R. T. 1986. The role of *Fundulus heteroclitus* in salt marsh trophic dynamics. *Am. Zool.* 26: 259–269.
- Laughlin, R. A. 1982. Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Apalachicola estuary. *Fla. Bull. Mar. Sci.* 32: 807–822.
- Lipcius, R. N. and A. H. Hines. 1986. Variable functional responses of a marine predator in dissimilar homogeneous microhabitats. *Ecology* 67: 1361–1371.
- and W. A. Van Engel. 1990. Blue crab population dynamics in Chesapeake Bay: variation in abundance (York River, 1972–1988) and stock-recruit functions. *Bull. Mar. Sci.* 46: 180–194.
- Mann, R., E. M. Burreson and P. K. Baker. 1991. The decline of the Virginia oyster fishery in Chesapeake Bay: considerations for introduction of a non-endemic species, *Crassostrea gigas* (Thunberg, 1793). *J. Shell. Res.* 10: 379–388.
- Mansour, R. A. 1992. Foraging ecology of the blue crab in lower Chesapeake Bay. Ph.D. Dissertation, College of William and Mary, Williamsburg, Virginia. 297 pp.
- McHugh, J. L. 1976. Estuarine fisheries: are they doomed? Pages 15–27 in M. L. Wiley, ed. *Estuarine processes*. Vol. 1. Academic Press, New York, New York.
- McIvor, C. C. and W. E. Odum. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. *Ecology* 69: 1341–1351.
- Millikin, M. R. and A. B. Williams. 1984. Synopsis of biological data on the blue crab, *Callinectes sapidus* Rathbun. NOAA Tech. Rpt. NMFS 1, FAO Fisheries Synopsis No. 138., 39 pp.
- Mittelbach, G. 1986. Predator-mediated habitat use: some consequences for species interactions. *Environ. Biol. Fish.* 16: 159–169.
- Moody, K. 1994. Predation on juvenile blue crabs, *Callinectes sapidus* Rathbun, in lower Chesapeake Bay: the role of seasonality in patterns, predators, and potential impacts. Ph.D. Dissertation, College of William and Mary, Williamsburg, Virginia 94 pp.
- Murdoch, W. W. and J. Bence. 1987. General predators and unstable prey populations. Pages 17–30 in W. C. Kerfoot and A. Sih, eds. *Predation. Direct and indirect impacts in aquatic communities*. Univ. Press of New England, Hanover, New Hampshire.
- and A. Oaten. 1975. Predation and population stability. *Adv. in Ecol. Res.* 9: 1–131.
- Orth, R. J. and K. A. Moore. 1984. Distribution and abundance of submerged aquatic vegetation in Chesapeake Bay: an historical perspective. *Estuaries* 7: 531–540.
- and J. van Montfrans. 1987. Utilization of a seagrass meadow and tidal creek by blue crabs *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Mar. Ecol. Prog. Ser.* 41: 283–294.
- Penry, D. L. 1982. Utilization of a *Zostera marina* and *Ruppia maritima* habitat by four decapods with emphasis on *Callinectes sapidus*. M.Sc. Dissertation, College of William and Mary, 101 pp.
- Persson, L. 1993. Predator-mediated competition in prey refuges: the importance of habitat dependent prey resources. *Oikos* 68: 12–22.
- Peterson, C. H. and R. Black. 1994. An experimentalist's challenge: when artifacts of intervention interact with treatments. *Mar. Ecol. Prog. Ser.* 111: 289–297.
- Pile, A. J. 1993. Effects of habitat and size-specific predation on the ontogenetic shift in habitat use by newly settled blue crabs. M.Sc. Dissertation, College of William and Mary, Williamsburg, Virginia. 101 pp.
- Posey, M. H. and A. H. Hines. 1991. Complex predator-prey interactions within an estuarine benthic community. *Ecology* 72: 2155–2169.
- Ruiz, G. M., A. H. Hines and M. H. Posey. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 99: 1–16.
- SAS Institute. 1990. SAS user's guide: statistics. SAS Institute Inc., Box 8000, Cary, North Carolina. 895 pp.
- Schmitt, R. J. and S. J. Holbrook. 1985. Patch selection by juvenile black surfperch (*Embiotocidae*) under variable risk: interactive influence of food quality and structural complexity. *J. Exp. Mar. Biol. Ecol.* 85: 269–285.
- Smith, L. D. 1990. The frequency and ecological consequences of limb autotomy in the blue crab, *Callinectes sapidus* Rathbun. Ph.D. Dissertation, Univ. Maryland, College Park, 259 pp.
- . 1995. Effects of limb autotomy on juvenile blue crab survival from cannibalism. *Mar. Ecol. Prog. Ser.* 116: 65–74.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry. The principals and practice of statistics in biological research*. 2nd ed. W. H. Freeman Co., New York. 859 p.
- van Montfrans, J., C. H. Peery and R. J. Orth. 1990. Daily, monthly and annual settlement patterns by *Callinectes sapidus* and *Neopanope sayi* megalopae on artificial collectors deployed in the York River, Virginia: 1985–1988. *Bull. Mar. Sci.* 46: 214–229.
- Watanabe, J. M. 1984. The influence of recruitment, competition, and benthic predation on spatial distributions of three species of kelp forest gastropods (*Trochidae: Tegula*). *Ecology* 65: 920–936.

- Werner, E. E. and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.* 15: 393-425.
- , J. F. Gilliam, D. J. Hall and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64: 1540-1548.
- Wilson, K. A. 1989. Ecology of mangrove crabs: predation, physical factors and refuges. *Bull. Mar. Sci.* 44: 263-273.
- , K. W. Able and K. L. Heck, Jr. 1990. Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*). *Mar. Ecol. Prog. Ser.* 58: 243-251.
- , K. L. Heck, Jr. and K. W. Able. 1987. Juvenile blue crab, *Callinectes sapidus*, survival: an evaluation of eelgrass, *Zostera marina*, as a refuge. *Fish. Bull.* 85: 53-58.
- Zimmer-Faust, R. K., D. R. Fielder, K. L. Heck, Jr., L. D. Coen and S. G. Morgan. 1994. Effects of tethering on predatory escape by juvenile blue crabs. *Mar. Ecol. Prog. Ser.* 111: 299-303.

DATE ACCEPTED: April 24, 1995.

ADDRESS: *Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, Maryland 21037; (A.I.D.)* CURRENT ADDRESS: *College of Marine Studies, University of Delaware, Lewes, Delaware 19958-1298. Address correspondence to: A.H.H.*