

TEMPORAL VARIATION IN JUVENILE BLUE CRAB MORTALITY: NEARSHORE SHALLOWS AND CANNIBALISM IN CHESAPEAKE BAY

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ABSTRACT

Adult abundance is determined by both recruitment and survival of juveniles. Blue crabs exhibit a distinct population size-structure reflecting seasonal cycles of recruitment and growth in the Rhode River, a subestuary lacking submerged vegetation in central Chesapeake Bay. Seasonally shifting modes in the size-structure, corresponding to juvenile, prepubertal and mature crabs, allowed trawl catches to be partitioned into 0+ and 1+ year classes of the crabs' 2-3 year life span. Fluctuations in the annual abundance of the year classes during 1988-1993 indicated that abundance of 0+ juveniles was not a good predictor of 1+ year-class abundance. We used tethering techniques to assess sources of, and temporal variation in, juvenile blue crab mortality as a function of water depth in the nearshore shallows of the subestuary. Laboratory experiments and analysis of remains of crabs tethered in the field indicated that cannibalism by large blue crabs was the source of 75-97% of mortality of juveniles. Crabs 30-50 mm CW suffered significantly higher mortality than 50-70 mm crabs. Mortality of tethered juveniles was significantly lower in shallow (15 cm) than deep (>70 cm) water. Mortality rates did not differ between day and night periods. Mortality of tethered juvenile blue crabs was high (40-90% per day) and exhibited significant seasonal and annual variation from 1989-1993; and water depth showed significant interaction effects with these components of temporal variability. Multiple regression analysis indicated that water temperature, abundance of 1+ year-class crabs in deep-water trawls, and abundance of 0+ year-class crabs in nearshore seines accounted for 82% of the annual variation in mortality of juveniles tethered at medium (40 cm) depth. Together, these results emphasize the importance of the nearshore shallows and body size as a crucial refuges for juvenile blue crabs encountering intense, but temporally variable cannibalism by large crabs. Juvenile mortality may be an important variable regulating population dynamics of blue crabs.

Variation in recruitment is a key component of population dynamics (Rothschild, 1986; Roughgarden et al., 1988). Fluctuations in abundance of adult populations reflect variation in both larval settlement (Phillips, 1986; Gaines and Roughgarden, 1987) and juvenile survival (Caputi and Brown, 1986; Herrnkind and Butler, 1986). Juvenile mortality may obscure the effects of variation in larval settlement through both density-independent and density-dependent mechanisms (Murdoch and Bence, 1987; Richards and Lindeman, 1987). Predation is often a dominant component of density-dependent mortality for juveniles (Beverton and Holt, 1957), and cannibalism can comprise a major source of predation upon juveniles (Elgar and Crespi, 1992) that regulates recruitment success in size-structured populations typical of many aquatic ecosystems (Tschumy, 1982; Werner and Gilliam, 1984; Ebenman and Persson, 1988; Stein et al., 1988). Predation rates are often mediated through prey utilization of refuges (Gilliam and Fraser, 1987; Persson, 1993), which may include spatial (habitat) and/or temporal (diurnal, seasonal, annual) components that reduce access or effectiveness of predator impact on prey. Spatial and temporal aspects of refuges may interact so that juvenile mortality may exhibit significant temporal variation within a refuge habitat (Heck and Wilson, 1987), especially when a critical habitat provides only partial refuge from predation (Eggleston et al., 1992; Dittel et al., 1995). Thus, temporal patterns of juvenile mortality within refuge habitats may provide insight into variation in recruitment success regulating population dynamics.

The blue crab (*Callinectes sapidus*) in Chesapeake Bay is characterized by marked fluctuations in population abundance, attributable to variability in recruitment success and a relatively short life span (2–3 years) (Millikin and Williams, 1984). Variation in adult crab abundance is often assumed to result from variation in larval settlement, which exhibits daily, seasonal and annual variation (van Montfrans et al., 1990, 1995; Olmi, 1995; Rabalais et al., 1995). However, there is little direct evidence that these settlement patterns are primarily responsible for variation in adult abundance, and there has been little effort to measure temporal patterns of juvenile mortality.

Juvenile mortality may contribute significantly to variation in, and regulation of, adult blue crab abundance in Chesapeake Bay for three reasons. First, the Chesapeake population is distinctly size-structured with 2 age classes (Hines et al., 1987, 1990). Following settlement and growth to about 20 mm carapace width in the submerged aquatic vegetation (SAV) beds of the lower Chesapeake Bay, small juveniles disperse into the subestuaries throughout the Bay to feed and grow to about 80 mm in their first year (Millikin and Williams, 1984; Hines et al., 1987, 1990; Pile, 1993). These juveniles forage extensively in the subestuaries, where they mature and mate in their second year (Millikin and Williams, 1984; Hines et al., 1987, 1990). Thus, juveniles 30–90 mm comprise a distinct mode of the 0+ year class, while prepubertal and adult crabs 110–170 mm form a second mode consisting of the 1+ year class. Second, blue crabs exhibit clear cannibalistic behavior, which is often size-dependent (Smith, 1990; Dittel et al., 1995), and cannibalism may be a major source of mortality for juveniles (Smith, 1990, 1995; Ruiz et al., 1993). Third, significant seasonal and long-term variation has occurred in habitats thought to provide potential structural refuge from predation for juvenile blue crabs, including the long-term declines in SAV (Orth and Moore, 1984), oyster reefs (Mann et al., 1991), and coarse woody debris (Everett and Ruiz, 1993).

This study presents evidence that variation in juvenile abundance over a 5-year period was not a good predictor of large blue crab abundance that comprises the fishable portion of the population in the Rhode River, a subestuary of Chesapeake Bay. We investigated patterns of variation in mortality of juvenile blue crabs, which may explain this apparent decoupling of variation in juvenile abundance from subsequent variation in adult abundance. Using tethering techniques (Heck and Thoman, 1981; Wilson et al., 1987), Smith (1990, 1995) showed that intermolt juvenile crabs <80 mm carapace width (0+ year class) suffer high levels of predation, whereas large crabs (1+ year class) suffered almost no mortality within the subestuary. Subsequently, we showed that juvenile blue crabs obtain refuge from predation by utilizing shallow water (<70 cm deep) but suffered high mortality rates in deeper (70–120 cm) water (Ruiz et al., 1993; Dittel et al., 1995). In the present study, we used tethering techniques to test for diel, seasonal, and annual variation in the mortality of 0+ juvenile blue crabs over a 5-year period; and we tested for interactions of these temporal components with the effects of water depth. We used stepwise multiple regression analysis to estimate the proportion of variation in juvenile mortality correlated with water temperature and abundances of large (1+ year-class) and small (0+ year-class) crabs. These variables potentially contribute to predation mortality by regulating seasonal and annual variation in activity levels of predators and prey (Hines et al., 1990), inter-year-class cannibalism (e.g., Botsford and Wickham, 1978), and within-year-class cannibalism (Fernandez et al., 1993).

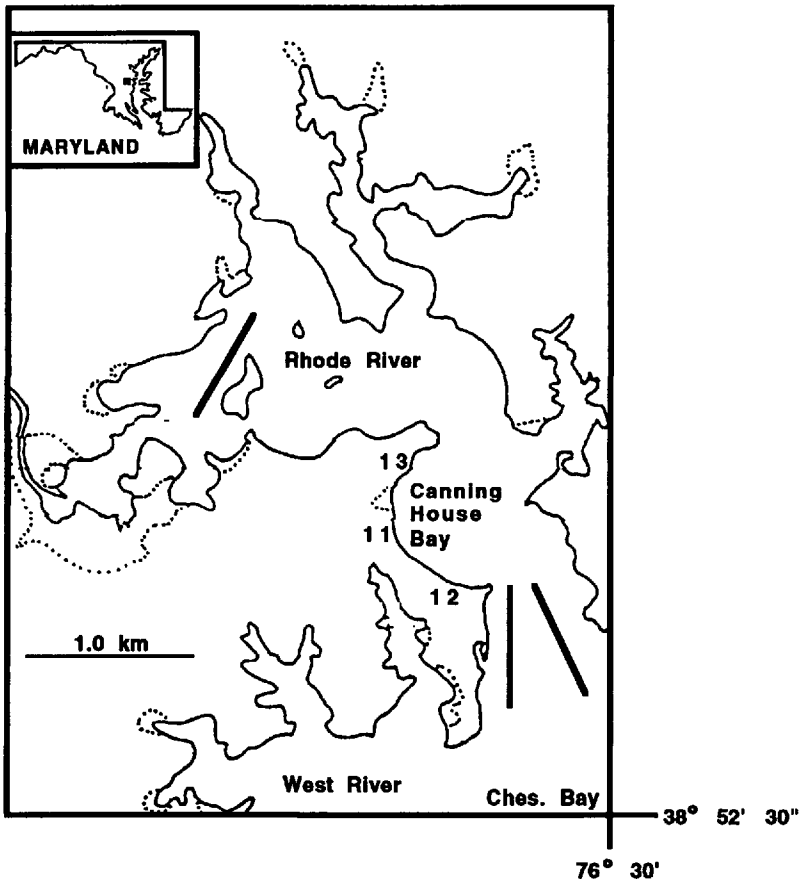


Figure 1. Map of Maryland portion of Chesapeake Bay (inset) and the Rhode River subestuary showing locations of trawling (3 dark lines), seining (11, 12, 13) and cylinder (11) sampling stations and locations of tethering experiments (11, 12, 13 for spatial variation, 11 for temporal variation) in Canning House Bay.

MATERIALS AND METHODS

Study Site.—This study was conducted in the Rhode River ($38^{\circ}51'N$, $76^{\circ}32'W$), a 485 ha subestuary of the mesohaline zone of Chesapeake Bay (Fig. 1). Previous studies describe major aspects of water quality (Jordan et al., 1991) and blue crab biology (Hines et al., 1987, 1990) in this subestuary. The Rhode River is shallow (max. depth = 4 m), with about 80% of the bottom area composed of fine silt and clay and 20% composed fine to medium sand. Monthly mean water temperatures fluctuate seasonally between 2 and $30^{\circ}C$, and salinity varies from 3 to 17‰; tidal amplitude is about 0.5 m. Beds of SAV disappeared from the study area in the 1970s and continued to be absent throughout our study period. Field experiments were conducted at Canning House Bay, which is characterized by an unvegetated sandy beach and a nearshore bathymetry which slopes gradually to depths >1 m about 50 m from the waters' edge. Water temperature 1 m below the surface was taken weekly in the channel off Canning House Bay using a Beckman temperature meter.

Population Size Structure.—We measured population size structure of blue crabs in deep (2–4 m) water with otter trawls and in the nearshore zone <70 cm deep with seines and drop cylinders. Monthly otter trawls during April to November of 1988–1993 were pulled for a fixed 900 m distance on three consecutive days at three stations (Fig. 1), as described in Hines et al. (1990). The trawl net had a 3-m-wide mouth, 5-cm-mesh net body, 7-mm-mesh cod end liner, and a tickler chain. Seines were pulled monthly during June, July and August 1989–1993 along 32 m of shoreline at three locations in Canning House Bay with a net 16 m long, 1.6 m high, and made of 7 mm mesh. Sampling with drop cylinders

occurred monthly during June, July and August 1989–1993 following methods of Ruiz et al. (1993) that employ an open ended sheet-metal cylinder (1.2 m high and 1.5 m diameter). The cylinder was suspended above the water on a boom extending over the bow of a boat, and it was dropped onto a sampling site by pulling a release cord that allowed personnel to remain > 15 m from the site, thereby minimizing disturbance to motile species before the drop. The cylinder trapped crabs as it fell quickly through the water column and became embedded in the bottom, while the upper edge remained above the water surface. Water in the cylinder was then pumped out completely using a suction dredge fitted with a 3-mm-mesh bag to capture entrained animals. Crabs remaining within the cylinder were collected from the sediment surface, which was probed thoroughly for buried individuals. All blue crabs in trawls, seines and cylinder samples were counted and measured to the nearest mm in carapace width including spines (CW).

Tethering Experiments.—We used tethering to compare the relative risks of predation upon juvenile blue crabs among water depth zones in Canning House Bay (Fig. 1). Tethering has been used successfully to assess relative predation risk in the field for crabs and other animals (Heck and Thoman, 1981; Watanabe, 1984; Herrnkind and Butler, 1986; McIvor and Odum, 1988; Wilson et al., 1987, 1990; Ruiz et al., 1993; Barbeau and Scheibling, 1994; Dittel et al., 1995). Although tethering can significantly alter animal behavior and absolute rates of predation (Barshaw and Able, 1990a; Smith, 1990, 1995), it allows comparison of relative rates 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 are likely to be minimal in soft-bottom systems lacking SAV. Our laboratory observations showed that tethered crabs displayed the full range of normal behaviors, including feeding, grooming, resting (including burying) (see also Barshaw and Able, 1990b), and locomotory (including swimming) activities. Although crabs rapidly moved and swam away from attacking predators, they were restricted in the extent of their escape by the tethers (see also Wilson et al., 1990). 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, 1994). In the Rhode River, there is only one major predator (large blue crabs) on small crabs (see Results below; Smith, 1990; Ruiz et al., 1993), thus eliminating possible differences in tethering artifact among predator species that could sometimes change if the species composition of predators varied along a depth gradient (Peterson and Black, 1994).

Blue crabs 30–70 mm CW were collected with seines and trawls and were held and fed in the laboratory for 1–3 days prior to use in field experiments. This size range was selected to represent the 0+ year class. Crabs in the laboratory were fed pieces of fish (*Fundulus heteroclitus*) daily. We selected active, intermolt crabs for experiments, and checked for molting and limb loss during every run. Tethering consisted of tying a loop of monofilament (9 kg test) around the crabs' lateral spines to form a halter held in place on the carapace with cyanoacrylate glue and attached to a coated steel leader (4.5 kg test). Each crab was tethered individually on a 0.75 m 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 laboratory or 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 pressed below the sediment surface and the float line extended to the water surface, while the test crab was allowed to move on the tether line.

We conducted laboratory experiments during July–August 1990 to test the vulnerability of juvenile blue crabs to potential estuarine predators, that are common in the subestuary and have been reported to consume crabs. Four species, which were present in the Rhode River (Hines et al., 1990; Ruiz et al., 1993) and known to consume blue crabs (Millikin and Williams, 1984) were tested as potential predators: *Callinectes sapidus* of large (140–160 mm CW) and small (30–70 mm CW) size classes; *Anguilla americana* (American eel) 90–115 cm total length (TW); *Opsanus tau* (oyster toadfish) 20–30 cm TW; and *Morone americana* (white perch) 25–30 cm TW. Other predators known to consume blue crabs, including *Morone saxatilis* (striped bass) and *Ardea herodias* (Great Blue Heron), were present in the study area at such low abundances that we judged them to have negligible potential impact on juvenile crab abundance. Individuals of each predator species were acclimated to laboratory conditions for 5 days and tested in large (2 m long × 1 m wide × 0.6 m deep) tanks with flowing estuarine water and muddy sand substrate (10 cm deep) collected from the field experimental site. The predators were not fed for 24 h prior to testing. Four intermolt juvenile blue crabs (30–70 mm CW) were tethered as described above and placed into each test tank. Mortality of the crabs was scored daily for 72 h, and characteristics of prey remains were noted. The test was replicated five times in blocks of six tanks for different individuals of each predator and a control tank lacking

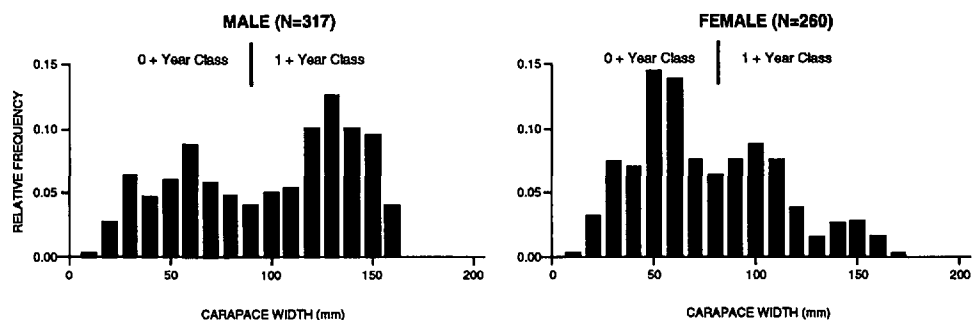


Figure 2. Population size structure of blue crabs captured in trawls within the Rhode River subestuary during June 1989–1993. Size breaks for juvenile, prepupal and mature males and females are indicated for the 0+ and 1+ year classes. Shaded bars indicate mature females.

predators to test for escape or other mortality. We also made laboratory observations on predation success of the five predators upon free-ranging (untethered) juvenile blue crabs in the tanks.

In field experiments, we tested the mortality rate of tethered juvenile (30–70 mm CW) blue crabs placed at shallow (15 cm), medium (40 cm), and deep (80 cm) water in the nearshore zone of Canning House Bay from 1989–1993. Tethered individuals were spaced along shore at intervals >2 m to ensure that there was no interaction among test crabs. Mortality and characteristics of tethered crab remains were scored at 24 and 48 h, except for diel tests (see below) which were scored at about 12-h intervals. For each sample period, we tethered individual juvenile crabs at each depth in two groups of about 12 or 13 crabs; the second group was deployed 2 days after the first. This design resulted in a sample size of about 25 individuals at each of three depths, for a total of about 75 crabs for each sample period. A sample size of 25 is the recommended minimum per test cell in log-linear models employed in our data analysis (below). To test for spatial variation in juvenile mortality, we conducted tethering experiments simultaneously at three locations separated by >0.5 km within Canning House Bay in August 1990. To test for diel variation in mortality we deployed half of each group of tethered crabs at alternating times of the day (early morning or late afternoon–evening) during 1990 to avoid biasing the results by potential diel variation in mortality. Since results indicated no diel variation in mortality, later temporal tests began in early afternoon. To test for seasonal and annual variation in juvenile mortality, we conducted tethering experiments repeatedly during 1989–1993 at three depths at a single location in the middle of the study area. Although we randomly distributed the test crabs among the tethering treatments, we recorded CW and sex of each crab during deployment so that we could perform a posteriori tests for differences in mortality by size and gender.

Data Analysis.—Size frequency distributions of blue crabs were compared among trawl, seine and cylinder samples using Kolmogorov-Smirnov tests (Sokal and Rohlf, 1981).

Annual estimates of the abundance of 0+ and 1+ year classes of crabs were computed from trawl catches using sine-cosine functions as covariates in ANCOVA to partition the strong seasonal variation in catch (Hines et al., 1990). We used least-square means per year as an estimate of abundance of each year class.

We used log-linear models (SAS, 1990) to test for independence of juvenile blue crab mortality among depths, locations, sampling periods, and sex-size categories of individuals. To assess spatial variation, we compared mortality among three stations and tested for interaction with water depth. Diel variation compared mortality rates (adjusted for hours of exposure to predators) between day and night exposure periods. A test of seasonal variation compared mortality among months from April–September 1990. Interaction among months of the summer and year was tested for tethered crabs in June, July, and August from 1990–1993. Variation in mortality among years compared tethering experiments conducted in August of 1989–1993.

We used multiple regression analysis to test for the contribution of water temperature (an indicator or predator activity), abundance of the 1+ year class in trawls (an index of between year-class cannibalism), and abundance of the 0+ year class in nearshore seines (an index of within year-class cannibalism) in explaining the variance in mortality of juvenile blue crabs.

RESULTS

Population Size-Structure and Variation in Abundance.—A distinct size structure characterized the population of blue crabs captured in monthly trawls in the Rhode

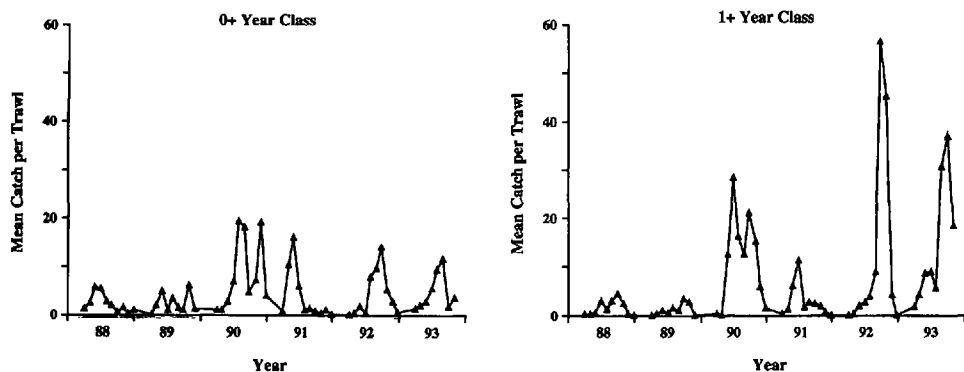


Figure 3. Abundance of 0+ and 1+ year classes of blue crabs in trawls during 1988–1993. Trawls were pulled at stations within the Rhode River subestuary shown in Figure 1.

River (Fig. 2). Both sexes exhibited modes in size-frequency distributions which reflected 0+ year-class juveniles and 1+ year-old prepubertal and adult crabs. The modal size of the 0+ juveniles increased as these crabs grew during the seasonal cycle (Hines et al., 1987, 1990). Juvenile crabs grew to prepubertal instars and matured in their second summer. Thus, the distinct size structure of the population allowed us to partition the contribution of each of the 2 year-classes to the population samples (after we adjusted the size used to separate the year classes in each monthly sample to account for seasonal growth of the cohorts).

Abundance of blue crabs in the trawl catches ranged six-fold among years from a low in 1989, with mean catch of two crabs per trawl and peak catch of eight crabs per trawl, to a high in 1992, with mean catch of 11.6 crabs per trawl and a peak catch of 71 crabs per trawl (Fig. 3). Abundances of both year classes in the blue crab population caught in monthly trawls fluctuated in a consistent seasonal cycle (Fig. 3), which we partitioned from annual variation (ANCOVA, sine-cosine function, $F_{(1,480)} = 74.5$, $P < 0.001$). Both year classes exhibited significant variation among years (ANCOVA on the residuals of trawl catch by year class after the average seasonal cycle was partitioned from the data, i.e., the “seasonally-partitioned catch”; 0+ YearClass: $F_{(5,480)} = 10.79$, $P < 0.001$; 1+ YearClass: $F_{(5,480)} = 39.58$, $P < 0.001$). During the 5 years of this study, however, the abundance of the 0+ year-class recruits was not a significant predictor of the abundance of the 1+ year class of crabs in the subsequent year and explained less than 5% of the variance (ANOVA: dependent variable = least-squared mean of seasonally-partitioned catch of 1+ year-class lagged by 1 year; independent variable = least-squared mean seasonally-partitioned catch of 0+ year class catch; $P > 0.8$) (Fig. 4).

Size Structure by Water Depth.—The size structure of blue crabs in the subestuary differed significantly among samples caught with trawls, seines and cylinder sampling (Fig. 5). The crabs caught by cylinders and seines in shallow, nearshore water <1 m deep included proportionately more small, 0+ year class crabs and less large, 1+ year-class crabs than crabs sampled in deeper water of the channel (Kolmogorov-Smirnov test, $G = 47.77$, $P < 0.001$).

Sources of Juvenile Mortality.—Juvenile blue crabs in laboratory experiments suffered no mortality in the absence of predators, and none escaped from their tethers. Our laboratory observations of tethered crabs showed that they appeared

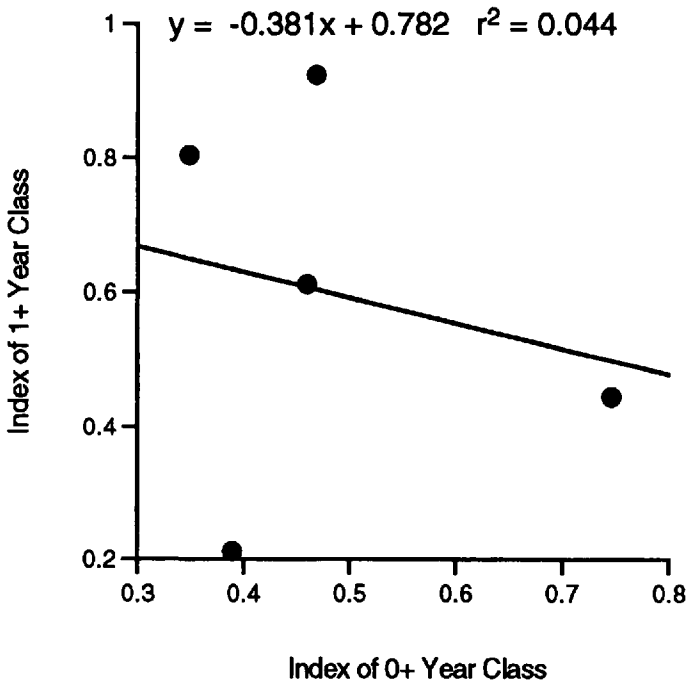


Figure 4. Regression of lagged annual index of 1+ year-class abundance versus annual index of 0+ year-class abundance. See text for explanation of indices. The regression is not significant ($P > 0.8$).

to behave normally, exhibiting the full range of activities, including moving rapidly and swimming away from attacking predators; however, they were obviously restricted by the tethers in the extent of their escape.

Mortality of the intermolt juveniles tethered in the laboratory differed significantly among the five potential predators (Chi-square = 19.05, $df = 4$, $P < 0.001$). Large blue crabs readily attacked and consumed 65 percent (11 of 20) of tethered juvenile blue crabs in laboratory tanks. Whereas small untethered blue crabs occasionally fought with tethered juveniles, these encounters only resulted in 5% (1 of 20) mortality of tethered individuals. Attacks by large blue crabs produced characteristic remains of tethered crabs. If an attack did not produce immediate mortality, the tethered crabs often suffered limb loss or punctured carapaces. Punctured juveniles soon died and were attacked again with invariable consumption by the large crab. Successful capture of juveniles by large crabs invariably led to immediate dismemberment and consumption of the juvenile, leaving two types of remains: usually pieces of dorsal carapace remained glued to the monofilament halter; other times (20%, 4 of 20) only a clean halter remained. Oyster toad fish consumed 15% (3 of 20) of tethered crabs, but all of these were eaten on the third day of the trials. In each of these cases of predation, the oyster toad fish swallowed the whole juvenile blue crab and the fish remained attached to the tether leader as a clear indicator of predation. Neither American eels ($N = 20$) nor white perch ($N = 20$) consumed any tethered crabs, nor did these predators inflict any damage or limb loss on the juveniles. Our laboratory observations of untethered crabs revealed similar patterns of vulnerability to these predators, although untethered crabs suffered 29% lower mortality than tethered crabs. Our

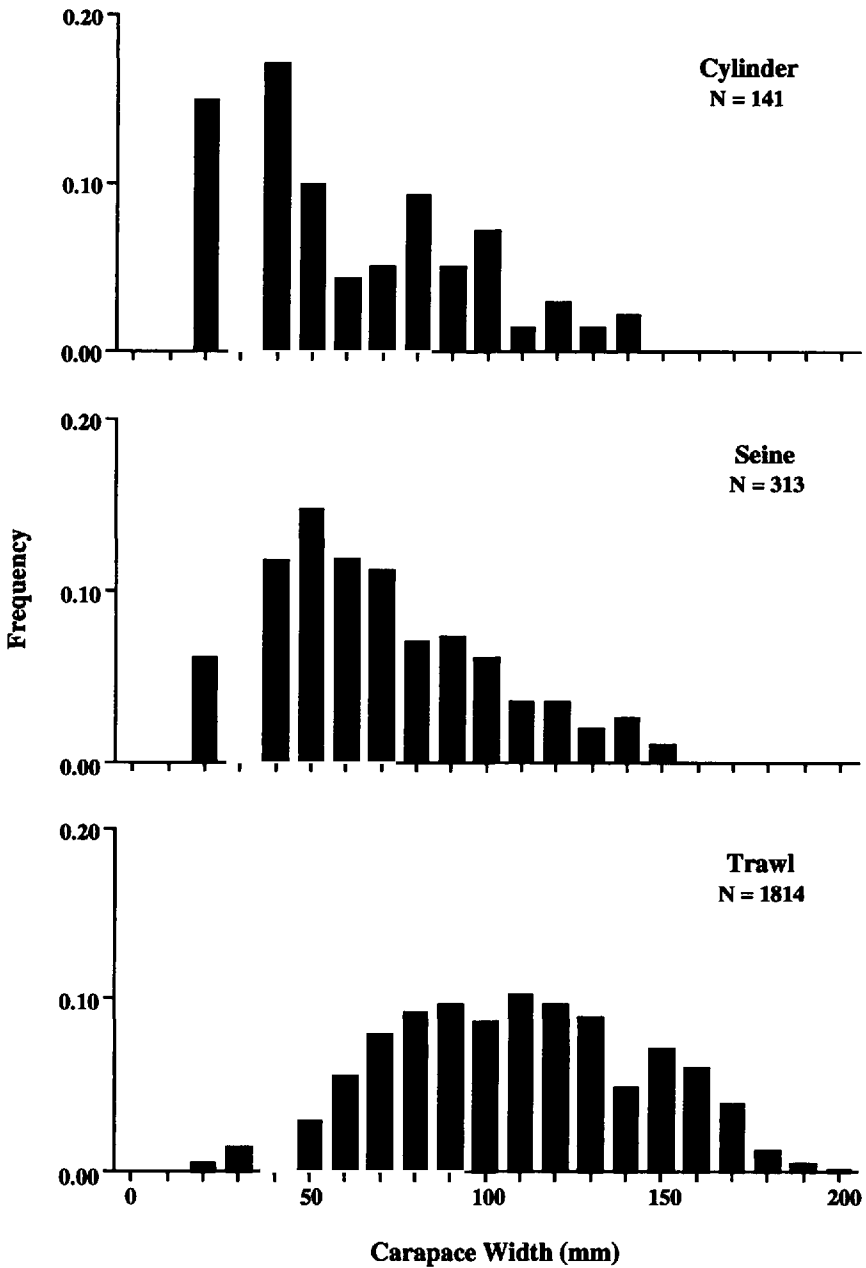


Figure 5. Population size structures of blue crabs sampled by drop cylinders and seines in shallow (<90 cm) water, and otter trawls in deep (2–4 m) water. N = number of crabs in sample.

study did not test mortality of molting crabs, which we have observed to be vulnerable to all five of the tested predators.

We evaluated the remains of juvenile blue crabs tethered in field experiments to deduce sources of mortality based on the characteristic remains of tethered crabs in the laboratory (Table 1). Of the 1,039 juvenile blue crabs tethered in the

Table 1. Frequencies of remains of juvenile blue crabs tethered at 3 water depths in the Rhode River subestuary during June, July and August of 1990–1993. Values in body of table are percentages of sample at that depth which had remains in the category of the column heading. N = number of tethered crabs for the column or row. See text for interpretive description of categories.

	Lost or molted	Alive, intact	Carapace fragment	No remains	Alive with damage	Dead with damage	Dead, no damage	N
Shallow	<1	62	9	4	17	3	5	346
Medium	<1	44	23	10	15	6	1	345
Deep	<1	34	29	20	11	4	1	348
All depths	<1	46	21	11	15	4	2	1,039
N	8	482	213	118	153	42	23	1,039

field during June, July, and August 1990–1993, less than 1% molted or were lost with their entire tether apparatus. About 46% across all depth zones were recovered alive and intact (i.e., no limbs lost); the remaining 53% of tethered crabs suffered death or exhibited significant injury (puncture and/or limb loss). Whereas only about 2% of the juveniles died from causes other than apparent predation, about 51% of crabs exhibited loss or injury attributable to predation. Of these cases, 40% (21% of the total experimental sample) were killed with shell fragments attached to the tether, which is characteristic of cannibalism by large blue crabs. An additional 35% of these cases (19% of the total sample) were either dead with punctures and/or missing limbs or alive with punctures and/or missing limbs, which is indicative of attacks by large blue crabs. Another 22% of these cases (11% of the total) had all remains missing from the tether, which is equivocally indicative of cannibalism by large blue crabs. We surmise cannibalism by large crabs in these additional cases, because there were no other potential predators present in sufficient numbers and with comparable depth distribution (Ruiz et al., 1993), and because we observed similar frequency of removal of the entire remains by large crabs in the laboratory (above). Thus, about 97% of the mortality and trauma suffered by juvenile blue crabs tethered in the field was clearly (75%) or equivocally (22%) attributable to cannibalism by large blue crabs.

The categories of remains of tethered juvenile blue crabs (Table 1) differed significantly by depth (log-linear models, Chi-square = 110.41, df = 12, $P < 0.001$). Juveniles in water >70 cm deep suffered 1.4 times as much mortality as those in shallow water <15 cm deep. Mortality at medium depth was intermediate between deep and shallow depths. Within the subset of categories comprising mortality and injury (carapace fragment, no remains, alive damage, dead damage), those categories which indicated immediately successful predation-cannibalism (carapace fragments remaining or entire crab missing) comprised a significantly higher proportion of the mortality and injury in deep (77%) than in shallow (39%) water (Chi-square = 103.43, df = 2, $P < 0.001$). These data are recalculated from Table 1 after excluding intact surviving and intact dead crabs. Conversely, within the same subset of mortality and injury categories, those categories which indicated unsuccessful attacks (alive or dead crabs with punctures and/or missing limbs) comprised a higher proportion in shallow (60%) than in deep (23%) water (Chi-square = 14.34, df = 2, $P < 0.02$). The proportion of the combined mortality and injury attributable to large blue crabs was not statistically different in shallow water (87%) than in deeper water (97%) (Chi-square = 2.56, df = 2, $P = 0.37$).

Effects of Size and Sex on Juvenile Mortality.—Crabs utilized in tethering experiments were selected to represent the size range of the 0+ year class and assigned randomly to treatments. Within this range, we tested for effect of body size upon

Table 2. Log-linear model tests for effects of water depth (shallow, medium, deep), sex (male, female), and size (< or > 50 mm CW) or mortality of 1,095 juvenile blue crabs tethered in the Rhode River subestuary during 1989–1993

	df	Chi-square	P value
Depth	2	87.00	0.001
Sex	1	0.13	0.717
Size	1	29.99	0.001
Depth × sex	2	1.13	0.569
Depth × size	2	9.80	0.007
Sex × size	1	1.91	0.167
Depth × sex × size	2	1.56	0.458

mortality of juvenile crabs by arbitrarily dividing the 30–70 mm test crabs into 2 groups: small = 30–50 mm CW; and large = 50–70 mm CW. Mortality of juvenile blue crabs tethered in the Rhode River during June, July and August of 1990–1993 differed significantly by size but not sex, and there was a significant interaction effect between water depth and size but not sex (log-linear models, Table 2). Small (<50 mm) crabs suffered nearly twice as much mortality as larger (>50 mm CW) crabs: 46% versus 25% respectively. Both size categories of crabs suffered about the same, relatively low levels of mortality in shallow water and exhibited increasing mortality in deep water (Fig. 6). However, small crabs had disproportionately higher mortality in deeper water than larger crabs (Fig. 6). Because all treatment groups for tethering were homogenous for crab size (Chi-square = 0.135, df = 1, $P > 0.90$), this factor did not bias any of our tethering experiments.

Variation in Juvenile Mortality among Sites.—Mortality of tethered juvenile blue crabs did not differ significantly among three sites in Canning House Bay during July–August 1991 (Fig. 7) (log-linear model, Chi-square = 0.18, df = 2, $P > 0.90$). However, mortality rates in deep (>70 cm) water were significantly higher

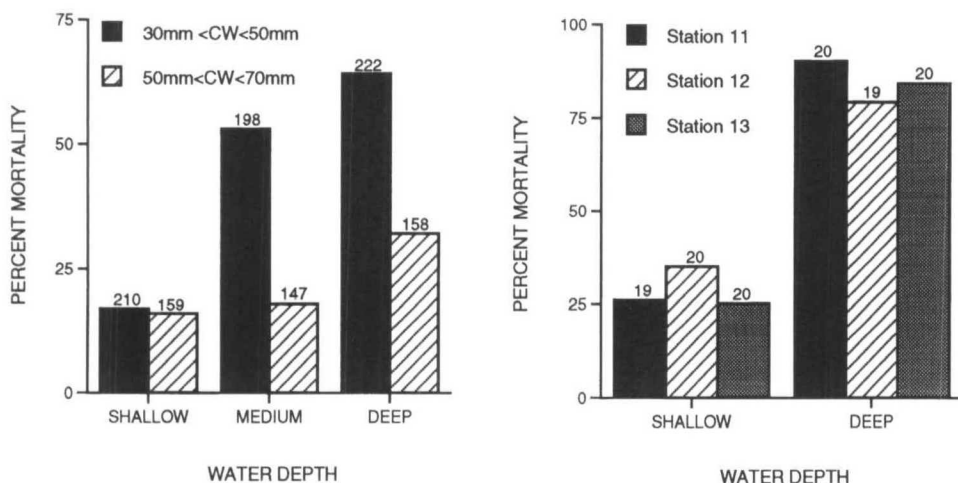


Figure 6 (left). Mortality of 30–50 mm and 50–70 mm CW blue crabs tethered in shallow, medium and deep water of the Rhode River subestuary during June, July, and August of 1990–1993.

Figure 7 (right). Mortality of juvenile blue crabs tethered in shallow and deep water at three stations within Canning House Bay of the Rhode River subestuary.

Table 3. Diel comparison of mortality of juvenile blue crabs tethered at three water depths in the Rhode River subestuary during 1990. Values under day and night are percent mortalities; values under N are numbers of crabs tethered. Frequencies of mortality differed significantly by depth ($P < 0.001$) but did not differ significantly by diel period ($P > 0.5$) (log-linear models).

Water depth	Percent mortality		N
	Day	Night	
Shallow	6	8	261
Medium	13	14	253
Deep	16	23	245
All depths	12	15	759

than mortality in shallow (15 cm) water (log-linear model, Chi-square = 30.96, $df = 1$, $P < 0.001$). There was no significant interaction of site \times water depth (log-linear model, Chi-square = 1.23, $df = 2$, $P > 0.50$).

Diel Variation in Juvenile Mortality.—Mortality of juvenile blue crabs tethered in the field (Table 3) did not differ significantly between day-time and night-time periods during 1990 (log-linear models, Chi-square = 1.41, $df = 1$, $P = 0.23$). Mortality differed significantly among water depths (log-linear models, Chi-square = 15.00, $df = 2$, $P < 0.001$), and there was no significant interaction between water depth and diel period (log-linear models, Chi-square = 0.61, $df = 2$, $P = 0.74$).

Seasonal Variation in Juvenile Mortality.—Mortality of juvenile blue crabs tethered in the field differed significantly among months during April–September 1990 and exhibited a distinct seasonal cycle (Fig. 8), with peak overall mortality in July and little overall mortality of tethered crabs early and late in the warm season (log-linear models, Chi-square = 21.96, $df = 5$, $P < 0.001$). Mortality

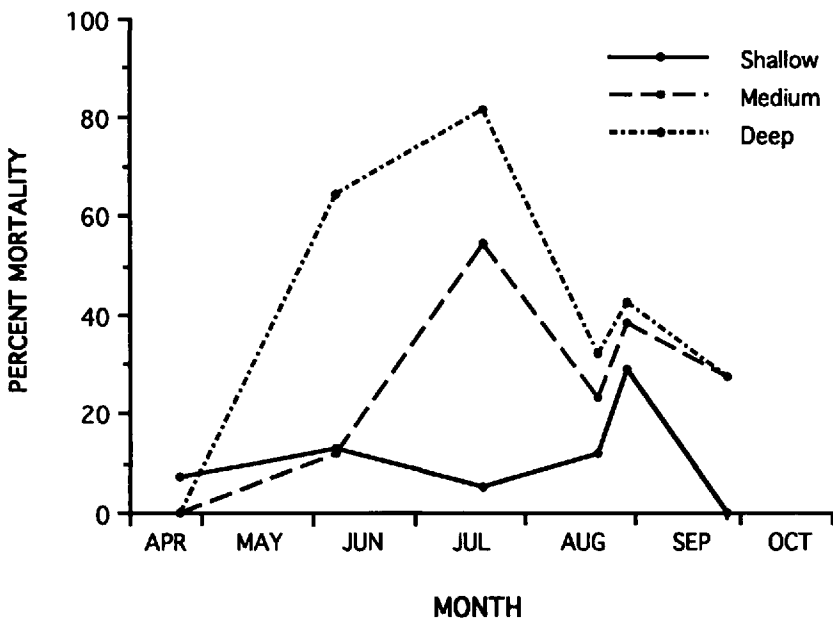


Figure 8. Seasonal fluctuation in mortality of juvenile blue crabs tethered in shallow, medium and deep water of the Rhode River subestuary during 1990.

also differed significantly among water depths (log-linear models, Chi-square = 9.92, $df = 2$, $P < 0.01$); however, there was a significant depth \times month interaction (log-linear models, Chi-square = 21.92, $df = 10$, $P < 0.02$). In April mortality was very low at all depths. Mortality was greatest in deep water throughout the summer and showed the greatest seasonal fluctuation (up to about 80% in July); at medium depth mortality increased markedly in July but was similar to mortality in shallow depth at other times; while mortality in shallow water was significantly lower and showed comparatively less seasonal variation but peaked in September (Fig. 8).

Interaction among Month, Year and Depth.—Mortality of the 1,044 juvenile blue crabs tethered in the field during June, July and August 1990–1993 exhibited significant variation among water depths and years, and marginally significant variation among months (Fig. 9) (log-linear models, Table 4). Overall, mortality varied with depth (Fig. 9), with the lowest mortality (17%) in shallow depth, intermediate mortality (40%) in medium depth, and highest mortality (54%) in deeper water. Averaged for all years, mortality across all depths peaked in July (48%), with lower rates early and later in the summer (33% and 34% mortality in June and August, respectively). Across all three summer months, the lowest mortality (31%) occurred in 1992 and highest mortality occurred in 1991 (48%). However, there was a significant depth \times month interaction (Table 4), in which mortality at medium depth increased disproportionately during July (Fig. 9). Month \times year also exhibited a significant interaction (Table 4), with highest mortality occurring in August in 1992 but during July in the other years (Fig. 9).

Variation in Juvenile Mortality among Years.—Mortality of the 470 juvenile blue crabs tethered in the field during August of the years 1989 to 1993 differed significantly among the 5 years and among the three depths (Fig. 10), but there was no significant year \times depth interaction effect (log-linear models, Chi-squares = 34.15, $df = 4$ for year and 34.15, $df = 2$ for depth, $P < 0.001$; Chi-square = 8.47, $df = 8$ for year \times depth, $P > 0.38$). Across all years, mortality was always least in shallow water (average = 17 percent and nearly always (except for 1993) intermediate in medium water (average = 41%) and greatest in deep water (average = 58%). Across all depths, mortality was lowest in 1990 (29%) and highest in 1989 (68%).

Correlates of Juvenile Mortality.—We performed multiple regression analysis of juvenile mortality at mid-depth because: mortality exhibited a graded response with depth; mid-depth is where most juvenile crabs occur (Ruiz et al., 1993); and this is where interactions with cannibalistic adult crabs were most likely to occur. Small crabs were uncommon at the deep zone, unless we tethered them there; while the shallow zone functioned as an effective refuge, such that mortality there was comparatively unresponsive to fluctuations in adults. The combination of water temperature, abundance of the 1+ year class, and abundance of 0+ year class crabs explained about 53% of the variance in mortality of juvenile blue crabs tethered at medium water depths: $\arcsine(\text{Mortality})^{-2} = 0.037\text{Temp} - 0.208\text{YrClassOne} + 0.343\text{YrClassZero}$. Temperature, as a measure of strong seasonal variation in mortality, was a significant factor in the regression ($F = 17.18$, $P < 0.03$), explaining 39% of the variation; 1+ year-class trawl catch (explaining 9% of variation) and 0+ year-class abundance in the nearshore seines (explaining 4% of variation) were not significant variables individually ($P = 0.14$ and 0.34 , respectively), but combined they improved the multiple regression significantly ($F = 6.65$, $P < 0.03$).

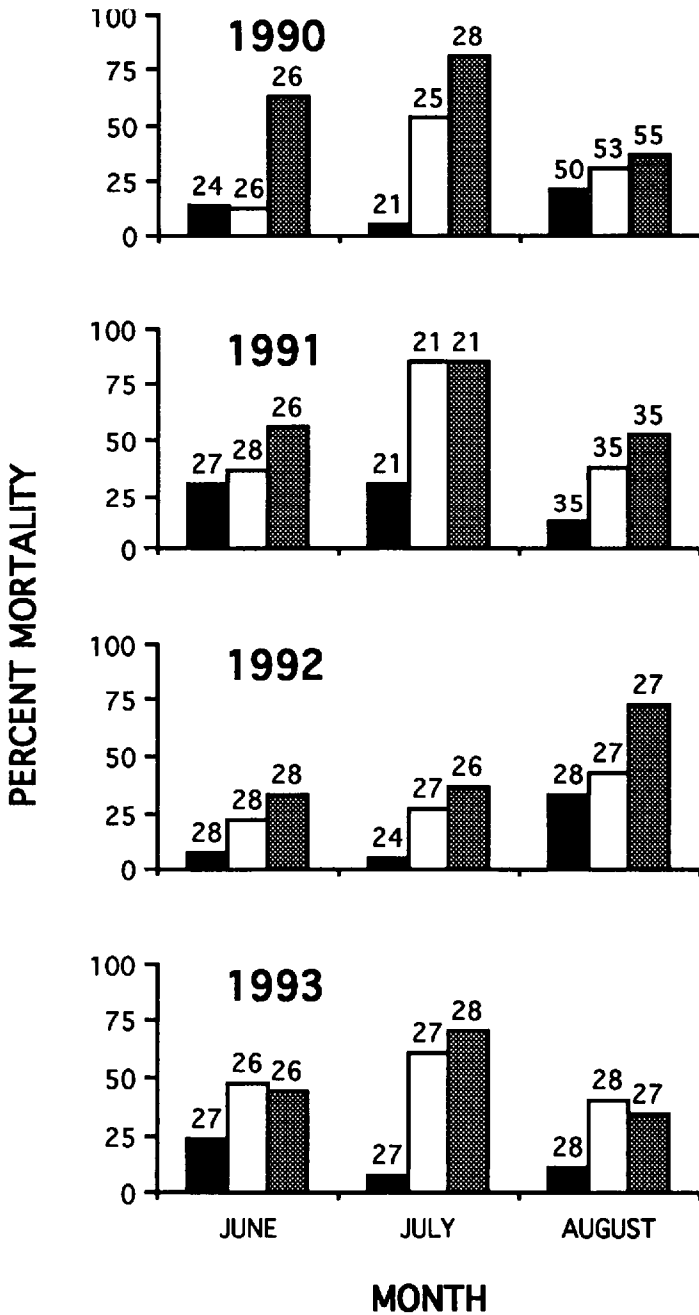


Figure 9. Monthly and annual variation in mortality of juvenile blue crabs tethered in shallow, medium and deep water in the Rhode River subestuary during June, July and August of 1990-1993. Solid bars = shallow; open bars = medium; stipled bars = deep. Numbers on top of bars indicate numbers of individual crabs tethered.

Table 4. Log-linear model tests for effects of water depth (shallow, medium, deep), month, and year on mortality of 1,044 juvenile blue crabs tethered in the Rhode River subestuary during June, July, and August of 1990–1993

	df	Chi-square	P value
Depth	2	88.21	0.001
Month	2	5.60	0.060
Year	3	15.23	0.001
Depth × month	4	12.95	0.020
Depth × year	6	8.69	0.200
Month × year	6	34.52	0.001
Depth × month × year	12	13.53	0.350

DISCUSSION

Juvenile blue crabs tethered in the Rhode River suffered high mortality in water deeper than 70 cm, with 40–90% of crabs being killed per day during summer months. This level of mortality is higher than mortality rates of equal or smaller sized juvenile blue crabs tethered similarly on unvegetated bottoms: 45% for 30–60 mm crabs in New Jersey (Wilson et al., 1987); 15–40% for 12–64 mm crabs in New Jersey (Wilson et al., 1990); 25% for 20 mm crabs in lower Chesapeake Bay (Pile, 1993); and 38% for 11–20 mm crabs in New Jersey (Heck and Coen, 1995). High mortality rates for tethered blue crabs have also been reported for other locations, but these are generally for smaller crabs in subtropical waters: 14–86% for 18–25 mm crabs in Florida (Heck and Thoman, 1981); and 85–91% for 5–20 mm crabs in Alabama (Heck and Coen, 1995). Because juvenile (0+

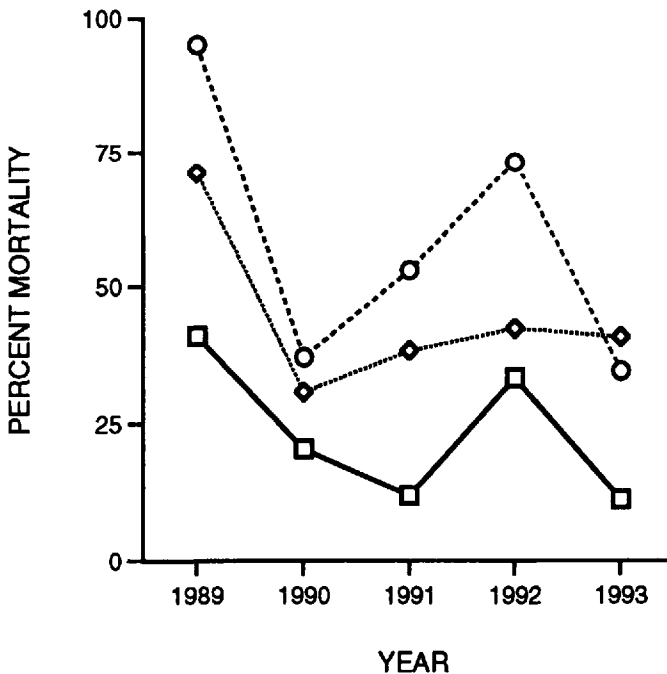


Figure 10. Annual variation in mortality of juvenile blue crabs tethered in shallow, medium and deep water in the Rhode River subestuary during August of 1989–1993. Squares = shallow; diamonds = medium; circles = deep.

year-class) abundance was not correlated with variation in adult (1+ year-class) abundance 1 year later in the Rhode River, we suggest that high juvenile mortality was at least as important as recruitment of juveniles from the lower Bay in determining adult population fluctuations within the subestuary.

Predation, especially cannibalism by large blue crabs, was the major cause of this juvenile mortality and accounted for 75 to 97% of the loss of the 0+ year class, as indicated by the remains of juveniles in our tethering experiments. Although other subtidal predators (e.g., oyster toad fish) may have taken juvenile blue crabs within the Rhode River, their abundances were so low (Hines et al., 1990; Ruiz et al., 1993) that it is unlikely that they were significant sources of mortality. The pattern of increasing mortality of tethered crabs in deeper water indicates that not only were large blue crabs the predominant predator in this system, but also that terrestrial predators (e.g., great blue herons, raccoons) entering the nearshore shallows to feed were relatively unimportant, probably because they also were not abundant. Even at the shallowest depths, the damage patterns indicated that most juvenile mortality was caused by large blue crabs. The lack of diel variation in juvenile mortality is also consistent with the major source of mortality being large blue crabs, which are well adapted for chemotactile foraging and do not exhibit a strong day-night pattern of foraging (Pearson and Olla, 1977; Nye, 1989). Thus, cannibalism may be an important negative feed-back mechanism of population regulation in blue crabs, just as it is common in size-structured populations of other aquatic species (Werner and Gilliam, 1984).

The nearshore shallows provide a critical refuge from this intense cannibalism in central Chesapeake Bay (Ruiz et al., 1993). In this ecosystem, habitats which historically provided structural refuge from predation (SAV, oyster reefs, coarse woody debris) have essentially disappeared or are significantly reduced (Orth and Moore, 1984; Mann et al., 1991; Everett and Ruiz, 1993). It is difficult to assess the impact of the historical loss of these refuge habitats upon the survival of blue crabs at the scale of the ecosystem. However, two observations point to the historic as well as the present significance of the nearshore shallow refuge. First, even where SAV remains commonly available to blue crabs, juveniles appear to move out of this habitat and into non-vegetated habitats once they grow to about 20 mm CW (Penry, 1982; Orth and van Montfrans, 1987; Pile, 1993; Heck et al., 1995). Second, the difference in relative mortality of juvenile blue crabs in shallow versus deep water in our tethering experiments is greater than the difference in mortality of similarly tethered juveniles in vegetated versus non-vegetated habitats (Heck and Thoman, 1981; Heck and Wilson, 1987; Pile, 1993; Heck and Coen, 1995). Thus, the unvegetated nearshore shallow zone may have provided crucial refuge habitat for 30–70 mm CW juveniles both before the historical demise of key structured habitats and into the present, when it is of especially high refuge value.

The mechanism by which shallow water provides the refuge from predation-cannibalism is not clear. The depth distribution of large crabs shows that they spend more time in deep water than shallow (Fig. 5; Ruiz et al., 1993). Small blue crabs move into shallow water in response to the presence of large crabs (Dittel et al., 1995). Moreover, the attack success of large blue crabs appears to be lower in shallow than deep water, as indicated by the damage-mortality ratios of our tethered juveniles (Table 1). However, large crabs can and do forage into shallow water to attack small crabs (personal observations; Dittel et al., 1995). Therefore, while significantly reducing mortality, the refuge of shallow water is only partial (Dittel et al., 1995). The effectiveness of the shallow-water refuge may vary with steepness of the bottom slope, affecting the distance of forays

made by large predators (Lin, 1989). Thus, human modifications of the nearshore bathymetry (e.g., by bulkheads built to prevent shoreline erosion) may have significant impacts on refuge value.

Increased body size also provides juvenile blue crabs a refuge from predation. Vulnerability of intermolt blue crabs decreased significantly with increasing juvenile size within the 0+ year class (Fig. 6), and Smith (1990) showed that large (1+ year-class) intermolt crabs suffer essentially no mortality when tethered in the Rhode River. Variation in temperature and food availability for rapid growth probably will determine both the rate of juvenile attainment of large, invulnerable size, and the rate of cannibalistic activity of large adults.

Prediction of variation in strength of the 1+ year-class of blue crabs remains a complex problem. Mortality of juvenile (0+ year-class) blue crabs in our tethering experiments exhibited significant seasonal and annual variation, which could add considerable complexity to the recruitment-stock dynamics of the blue crab population (Lipcius and van Engel, 1990). Our data indicate that variation in cannibalism by large crabs, mediated by the shallow water refuge in the nearshore zone, is an important regulator of adult abundance, with more than a two-fold range in mortality of tethered crabs among the 5 years of our study. Our study focused upon mortality of intermolt juveniles; but sequential ecdysis presents crabs with periods of extreme vulnerability to a larger suite of predators, which may create special additional bottlenecks requiring further refuge habitats (Hines et al., 1987; Shirley et al., 1990). However, the 5 years of data that we present here are limited to a time span of only two life cycles for blue crabs. Longer-term measures of blue crab population dynamics in the Rhode River (Hines et al., 1990) indicate that our study encompassed a period of relatively low crab recruitment and abundance compared to the mid-1980s, when trawl catches were five times the maximum abundance reported here. During such years of much higher abundance, juvenile recruitment may be more important than juvenile mortality in determining abundance of adults (Hines et al., 1990), perhaps by "swamping" the predatory capacity of cannibalistic 1+ year-class crabs. Once grown, a strong year class will have a major negative impact on the subsequent year's juveniles.

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