

THEN AND NOW: A COMPARISON OF PATTERNS IN BLUE CRAB POST-LARVAL ABUNDANCE AND POST-SETTLEMENT MORTALITY DURING THE EARLY AND LATE 1990S IN THE MOBILE BAY SYSTEM

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ABSTRACT

Two independent, yet identical blue crab studies were conducted five years apart (1990–1991 and 1997–1998) within the Mobile Bay system, providing the rare opportunity to compare patterns in post-larval settlement and post-settlement mortality within the same system over time. Patterns from the previously published study in 1990–1991 (Heck and Coen, 1995; Morgan et al., 1996; Heck et al., 2001) and patterns from the 1997–1998 study that were compared included: correlation between physical factors and post-larval settlement, the relationship between megalopal abundance and juvenile abundance, the abundance of juveniles within the system, and the role of refuge on early juvenile mortality. In 1990–1991, recruitment of megalopae into the Mobile Bay System was greater than in 1997–1998; however, peak recruitment was in late August–early September during both time periods. Recruitment was compared with juvenile abundance using 1-, 3- and 7-day lags to determine if there was an immediate or delayed relationship between these two factors. There were few significant correlations between megalopal abundance and juvenile abundance in either study, and most of these occurred shortly after large recruitment events and disappeared within a few days. In both studies, juvenile abundance varied throughout the system, with most juveniles occurring in SAV (submerged aquatic vegetation) and in the lower portion of the bay. Early juvenile mortality was high ($>80\% \text{ d}^{-1}$) during both studies. Although some differences were found between the two studies, the overall patterns in post-larval settlement and post-settlement mortality from the 1990–1991 study were qualitatively similar to those of the 1997–1998 study. The relative importance of post-larval abundance and post-settlement mortality did not change between the two time periods, confirming that the Mobile Bay system seems to be limited by high levels of post-settlement mortality and not post-larval abundance.

The blue crab, *Callinectes sapidus*, is one of the most ecologically (e.g., Hines et al., 1990; Olmi and Orth, 1995) and commercially important species (e.g., NMFS, 1994) in estuaries of the Western Atlantic and Gulf of Mexico. Like many commercially important species, blue crabs have a complex life cycle in which individuals spend a portion of their lives in both offshore and estuarine habitats. In the Gulf of Mexico, ovigerous females migrate from oligohaline areas to the mouths of estuaries and release larvae from February to October (Daugherty, 1952; More, 1969; Adkins, 1972; Perry, 1975; Milliken and Williams, 1984). Larvae feed and develop up to 100 km offshore (Tagatz, 1968; Smyth, 1980; Truesdale and Andryszak, 1983) then metamorphose into postlarvae (megalopae) (Costlow and Bookhout, 1959). Megalopae then reenter estuaries and settle in “nursery habitats” (McConnaugha et al., 1983; Epifanio et al., 1989) such as submerged aquatic vegetation (SAV) or fringing marsh, where they molt into first crabs. Many estuarine organisms, including blue crabs, rely heavily upon “nursery habitats” for refuge and food. For example, up to 90% of the juvenile blue crabs [CW (carapace width) <25 mm] in a given area can be found in SAV or marsh habitats (Perry, 1975; Heck and Orth, 1980; Penry, 1982; Weinstein and Brooks, 1983; Heck and Thoman, 1984; Zimmerman and Minello, 1984; Orth and van Montfrans, 1987; Williams et al., 1990).

Variability in abundances of individuals in different life stages over both spatial

and temporal scales has complicated efforts to understand factors that control adult blue crab populations. Larval and post-larval supply, believed to be primary determinants of blue crab population size, vary spatially, with large differences in megalopal abundance existing between Gulf and Atlantic coast estuaries (Heck and Coen, 1995; Perry et al., 1995; Rabalais et al., 1995; van Montfrans et al., 1995; Morgan et al., 1996). Larval and post-larval supply also vary temporally on daily, seasonal and interannual scales (van Montfrans et al., 1990, 1995; Olmi, 1995; Rabalais et al., 1995).

Not only can the abundance of megalopae vary spatially, but the timing of megalopal invasion of the estuary can vary as well. Megalopae frequently enter shallow water habitats along the Atlantic coast of the U.S.A. on nocturnal flood tides during full or new moons or after strong onshore winds (Epifanio et al., 1984; van Montfrans et al., 1990). In the Gulf of Mexico, most megalopae are reported to enter bays in the middle of tidal passes when current velocities are highest (More, 1969; King, 1971). In Mobile Bay, however, megalopae have been reported to enter the estuary during nocturnal flood tides, although the largest settlement events occurred during minimum amplitude tides (Morgan et al., 1996). The timing of peak reinvasion of the estuary by megalopae relative to lunar phase or tidal amplitude fluctuations is incompletely understood (Rabalais et al., 1995); therefore, recruitment should be monitored daily to determine the timing of peak settlement events relative to physico-chemical factors.

Post-settlement mortality of early juveniles also varies spatially and temporally, with mortality apparently greatest at lower latitudes (Heck and Coen, 1995). The Gulf of Mexico has a multitude of juvenile blue crab predators, including mammals, birds, fishes and macroinvertebrates (Gunter, 1945; Darnell, 1959; Lambou, 1961; Bateman, 1965; Day et al., 1973; Evink, 1976; Overstreet and Heard, 1978a, 1978b). The reduced predation pressure on juvenile blue crabs within vegetated habitats (Heck and Wilson, 1987; Wilson et al., 1987; Thomas et al., 1990; Pile et al., 1996), has demonstrated the importance of SAV and marsh vegetation in juvenile blue crab survival. However, the variance in rates of predation in similar types of habitats (e.g., marshes or SAV beds) within an estuary remains incompletely understood.

In 1990–1991, an effort was made to determine the relative importance of post-larval supply and early post-settlement mortality in determining juvenile blue crab abundance in Mobile Bay, Alabama and adjacent coastal waters (Heck and Coen, 1995; Rabalais et al., 1995; Morgan et al., 1996, Heck et al., 2001). Results from this study showed that post-larval supply was much greater in the Northern Gulf of Mexico than that reported from mid-Atlantic estuaries (Rabalais et al., 1995), but despite frequent episodes of very large post-larval ingress to nursery habitats (Morgan et al., 1996), high post-settlement mortality quickly reduced early instar density to levels reported from mid-Atlantic estuaries (Heck and Coen, 1995; Heck et al., 2001) and seemed to be the primary determinant of juvenile blue crab abundance in the Mobile Bay system.

Although repeatability is a basic tenet of the scientific enterprise, ecologists infrequently repeat studies. In those rare instances when studies have been repeated, conclusions can vary substantially (Beck, 1998). Here, we compare the results of a 1997–1998 study on post-larval and juvenile abundance and post-settlement mortality with the results of our 1990–1991 study (Heck and Coen, 1995; Morgan et al., 1996; Heck et al., 2001). Our goal was to evaluate whether conclusions regarding the relative importance of post-larval supply and post-settlement mortality differed between these two very similar studies that were separated in time by five years.

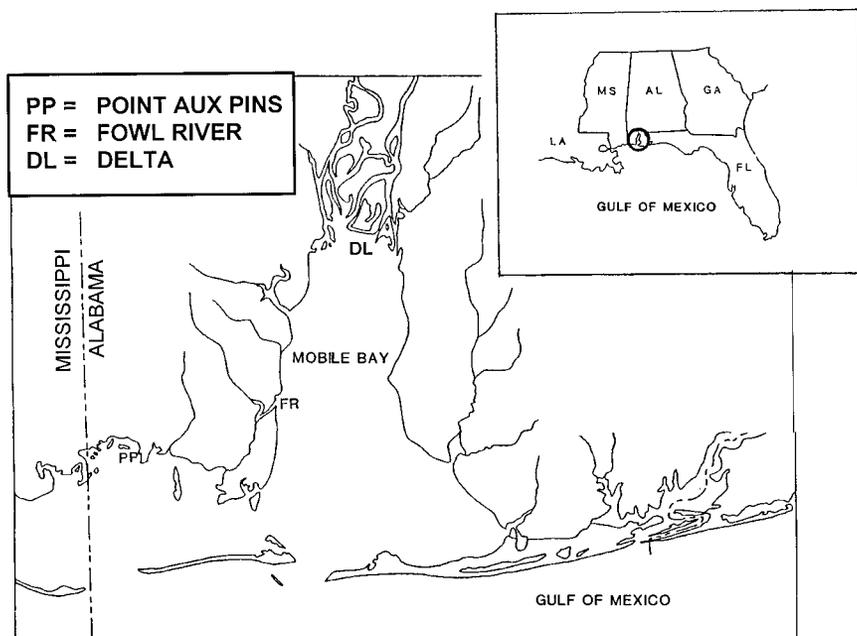


Figure 1. Map of study sites within the Mobile Bay system.

METHODS

STUDY SITES.—Approximately 4,500 acres of submerged aquatic vegetation (SAV) (mostly fresh water) (Zolczynski and Eubanks, 1990) in Mobile Bay and 25,000 acres of marshes (salt and fresh) along the coast of Alabama (Alexander et al., 1986) provide potential nursery habitats for blue crabs. Three sites that spanned the broad range of physical and biological environments within Mobile Bay and Mississippi Sound, Alabama (Fig. 1) were chosen for both megalopa and quantitative (suction sample) juvenile blue crab collections during the 1997–1998 study. The three sites, which were identical to those used in the 1990–1991 study, included: (1) Point aux Pins, a protected SAV-marsh dominated coastal area in Mississippi Sound; (2) Fowl River, an SAV-marsh area on a sub-estuary on the Bay's western shore; and (3) the Mobile Bay Delta at Meaher Park which was dominated by both freshwater marsh and SAV habitats.

Point aux Pins (PAP) had an average salinity of 23.6 PSU when averaged across all four years (1990, 1991, 1997 and 1998). Megalopal collectors were placed in a water depth of approximately 1.0 m, and samples of juvenile crabs were taken in SAV beds (*Ruppia maritima* and *Halodule wrightii*) at depths <1.0 m, as well as in fringing marsh (*Spartina alterniflora*).

The Fowl River site (FR) had an average salinity of 12.9 PSU when averaged across all four years. Megalopal collectors were placed in a water depth of 1.5 m and quantitative samples of juveniles were taken in SAV beds (*Ruppia maritima*) at depths <1.0 m, as well as in fringing marsh *Spartina alterniflora* (0.5–1.5 m water depth).

Sampling at the delta site (DL), where salinity averaged 3.3 PSU across all four years, was limited to the collection of juveniles during the 1997–1998 study. Megalopae were not collected from this site in 1997–1998 since the study in 1990–1991 (Morgan et al., 1996) found that very few megalopae recruit to the northern reaches of the bay. Juvenile abundance samples were taken in SAV beds (*Vallisneria americana*, with smaller amounts of *Myriophyllum spicatum*, *Heteranthera dubia* and *Potamogeton* sp.) where water depth ranged from 0.5 to 2.0 m, and also in fringing marsh vegetation (*Scirpus robustum*), at a depth less than 0.5 m.

Although the salinity values from the collection sites spanned a large range, they were all within the tolerance of juvenile blue crabs (see summary in Williams, 1984).

FIELD COLLECTIONS

ABUNDANCE OF MEGALOPAE (SUMMER/FALL).—In both the 1990–1991 and the 1997–1998 studies, larval recruitment at the PAP, FR and DL (1990 only) sites was estimated by placing passive collectors

in the surface waters immediately seaward of potential nursery habitats. Passive collectors have been used successfully in Atlantic coast estuaries from Delaware to Georgia (cf. Epifanio 1995; Mense et al., 1995; Metcalf et al., 1995; van Montfrans et al., 1995; Wrona et al., 1995), as well as in other areas of the northern Gulf of Mexico (Perry et al., 1995; Rabalais et al., 1995). The collectors were made of a 38×20 cm PVC support pipe wrapped with a 38×20 cm hoghair air conditioning filter that was held in place with bungee cords. Collectors were suspended in mid-water column using a polyethylene rope secured to automobile wheel rims placed on the sediment surface. The hoghair filters were removed every 24 hours and replaced with new filters. Collected megalopae were washed from both sides of each filter with fresh water.

Triplicate samples were collected daily from July–November during each year of both studies. Megalopae retrieved from the collectors were taken to the laboratory where they were identified and counted using a dissecting microscope. *Callinectes sapidus* megalopae can be readily distinguished from *C. similis* and other portunid megalopae by using existing larval descriptions (Stuck and Perry, 1982; unpubl. ms.). The data presented here are for *C. sapidus* only since they are the primary recruits during the summer/fall sampling period.

Previously, Morgan et al. (1996) hypothesized that physical factors were likely to play an important role in controlling the recruitment of blue crab larvae to the Mobile Bay estuary. As a result, meteorological and hydrographical data were recorded at the same time larval collections were made during the 1997–1998 study. Wind speed and direction, tidal amplitude, as well as, temperature and salinity were monitored daily at a National Oceanographic and Atmospheric Administration station located in Main Pass of Mobile Bay, while tidal amplitude was obtained from Corps of Engineers gauges at Bayou la Batre (Lat: $30^{\circ}23'55.22''$; Lon: $-88^{\circ}15'25.41''$), Cedar Point (Lat: $30^{\circ}18'38''$; Lon: $-88^{\circ}08'18''$) and Dauphin Island (Lat: $30^{\circ}15'04.41''$; Lon: $-88^{\circ}04'45.56''$). Peak wind (wind gust) for each 24-hour period was noted and wind speed and direction were converted into wind stress using vector mathematics (Hsu, 1972).

JUVENILE ABUNDANCE.—Using suction sampling techniques, which have been proven effective in Chesapeake Bay eelgrass habitats (Orth and van Montfrans, 1987; Pile et al., 1996), Texas salt marshes and seagrass beds (Zimmerman and Minello, 1984; Zimmerman et al., 1984; Thomas et al., 1990) and local grass beds in Mobile and Perdido Bays (Stout and Heck, 1991; Williams et al., 1991), juvenile abundance was estimated at each of the three sites. Each site had two potential nursery habitats (SAV and fringing marsh) that were sampled in triplicate on a biweekly basis from July–November of each year (1990, 1991, 1997 and 1998). Suction sampling has been shown to be a good quantitative method that was approximately 86% effective in capturing juvenile blue crabs in seagrass habitats (Wilson et al., 1990).

Samples were taken by placing a PVC cylinder (height = 1.524 m, diameter = 0.627 m), open at both ends, within the desired habitat (SAV or marsh). Care was taken not to disturb the sampling area prior to cylinder placement. Following placement, a tight seal was created by twisting the cylinder into the sediment, which prevented the escape of enclosed juvenile crabs. Once the seal was formed, the contents of the substrate enclosed by the cylinder (0.3084 m^2) were evacuated through a 0.5-mm mesh collecting bag. To ensure that the cylinder was empty, a dip net was used to remove any remaining juvenile blue crabs. Captured juvenile crabs were then identified, counted and measured (carapace width (CW)).

To determine if abundance of juvenile crabs was correlated with characteristics of vegetation, three 10 cm^2 vegetation samples were collected from the SAV surrounding the cylinder. Dry weights of each major plant species were quantified by drying in an oven for 24 hours at 80°C . For marsh samples, the number of shoots within the cylinder was recorded for each suction sample. The dry weights and shoot counts were then converted to values/ m^2 for data analysis. In 1998, a large amount of SAV detritus was found intermingled with the marsh habitats at PAP; therefore, samples of the SAV detritus were taken and dried to a constant weight for biomass determinations.

ESTIMATING POST SETTLEMENT MORTALITY (TETHERING).—Juvenile blue crabs are especially vulnerable to predation (Heck and Thoman, 1981; Wilson et al., 1987; Hines and Ruiz, 1995; Smith, 1995; Pile et al., 1996) because they are small and molt frequently. In 1997–1998, we estimated predation rates in the field on juvenile crabs (i.e., crabs with carapace widths between 5 and 20 mm) using tethering techniques similar to those used in 1990–1991 (Heck and Coen, 1995). Juveniles were collected with a beam plankton trawl (BPT) from vegetated habitats and returned to the laboratory. Tethers contained a loop with a slipknot at one end of a 0.5 m long monofilament line (8 lb test). The loop was then secured around the carapace between the last pair of walking legs and the swimming legs using cyanoacrylate cement. The other end of the line was secured to a one-foot j-shaped stake that was pushed into the ground in the desired habitat.

The habitats used for both the 1997–1998 and the 1990–1991 studies were: sand, low biomass SAV, high biomass SAV, low density marsh, and high density marsh. SAV biomass was determined by collecting all vegetation within a $10 \text{ cm} \times 10 \text{ cm}$ quadrat, drying the vegetation to a constant weight and then converting the dry weight to a dry weight/ m^2 . Ten measured crabs were placed in each of

the habitats at both DL and PAP study sites. After placement within the habitats, tethers were examined every 24 h to see whether the crabs were missing (i.e., molted, escaped or preyed upon). Results were recorded and missing crabs were replaced so that a full set of crabs was placed out for the next 24 hours. Experiments ran for five consecutive days in September during 1990, 1991, 1997 and 1998.

Molted crabs leave a complete carapace attached to the tether, whereas escaped crabs leave the complete loop and no carapace, and consumed crabs leave only fragments of a carapace. Therefore, it is unlikely that a molt or an escape would be classified as a predation event. However, in the event that a tether was found without any carapace attached, it was not included in the analysis. This occurred less than 5% of the time.

The reliability of data from tethering studies due to potential artifacts of the tethering technique has been questioned (Peterson and Black, 1994) and rebutted (Aronson and Heck, 1996). In addition, Pile et al. (1996) thoroughly tested for tethering artifacts on juvenile blue crabs in both vegetated and unvegetated habitats and found none. Therefore, tethering artifacts are not expected to significantly influence the conclusions of our studies.

STATISTICS.—Correlations between megalopal abundance and recorded physical factors (temperature, salinity, winds, tidal amplitude and lunar phase) were calculated to determine if recruitment was significantly related to any of the factors. Differences in abundance of juvenile blue crabs among sites and between vegetation types were examined using a One Way Analysis of Variance (ANOVA) and if significant differences were found a post hoc multiple comparison test was run. A priori tests were run to test for normality and heteroscedasticity (using the Kolmogorov-Smirnov test and checking variability about the group means, respectively) and if either failed, the data were transformed (arcsin square root or \log_{10}) to correct the violations. The relationship between juvenile abundance and vegetation biomass was examined using correlations at each site. An ANOVA was used to compare differences in vegetation biomass among sites during the 1997–1998 study and a post hoc multiple comparisons test was run if differences were found. Correlations were also calculated between juvenile abundance and larval recruitment samples taken 1, 3 and 7 days prior to suction sampling. Megalopae can metamorphose into first instars within 24 hours of settlement; therefore, a one day lag was used to determine if there was an immediate correspondence between post-larval supply and juvenile abundance. Three and seven day lags were also examined to determine how long an immediate response might last or to determine if the correspondence between post-larval supply and juvenile abundance was delayed. An ANOVA was also used to evaluate differences in predation rates between sites and among vegetation types. If significant differences were found, multiple comparison tests were used. Again, tests for ANOVA assumption violations were run and data were transformed if necessary prior to ANOVA analysis. Correlations between vegetation biomass and potential predation rates were used to determine the refuge value of SAV for juvenile blue crabs.

RESULTS

MEGALOPAL COLLECTIONS.—Recruitment patterns of blue crab megalopae into the Mobile Bay system during both 1990–1991 and 1997–1998 occurred in pulses that varied in magnitude. These pulses were usually weakly correlated with physical factors, although during 1990 recruitment was highly correlated with a five day lag of peak onshore winds, especially near minimum amplitude equatorial tides (Morgan et al., 1996). Recruitment of megalopae was highly variable over daily time scales but occurred throughout the sampling period (July–November) of each year (1990, 1991, 1997 and 1998). The greatest number of megalopae was collected during 1991 (Figs. 2, 3, 1991 > 1990 > 1997 > 1998). Recruitment was substantially higher in 1990–1991 (\bar{x} = 150 megalopae/collector) than in 1997–1998 (\bar{x} = 21.5 megalopae/collector). Peak recruitment occurred in late August to early September of each year [max number per collector = [410 (1990), 5,952 (1991), 2,400 (1997) and 906 (1998)]] (Figs. 2, 3).

JUVENILE ABUNDANCE.—Throughout both studies (1990–1991 and 1997–1998), juvenile abundance was inversely related to CW. Most crabs between 2–8 mm CW were found in SAV in the lower portion of Mobile Bay (i.e., PAP and FR). Juvenile abundance across habitats ranged from <5/m² at the Delta to 38/m² at PAP in 1990 (Fig. 4), and <5/m² at the Delta to 36/m² at PAP in 1991 (Fig. 4, Heck et al., 2001). FR SAV was not sampled during either 1990 or 1991, as submerged vegetation was not present. There were significantly ($P < 0.05$) more juveniles found in the lower bay (PAP) than any other sites in 1990 (Fig. 4), and

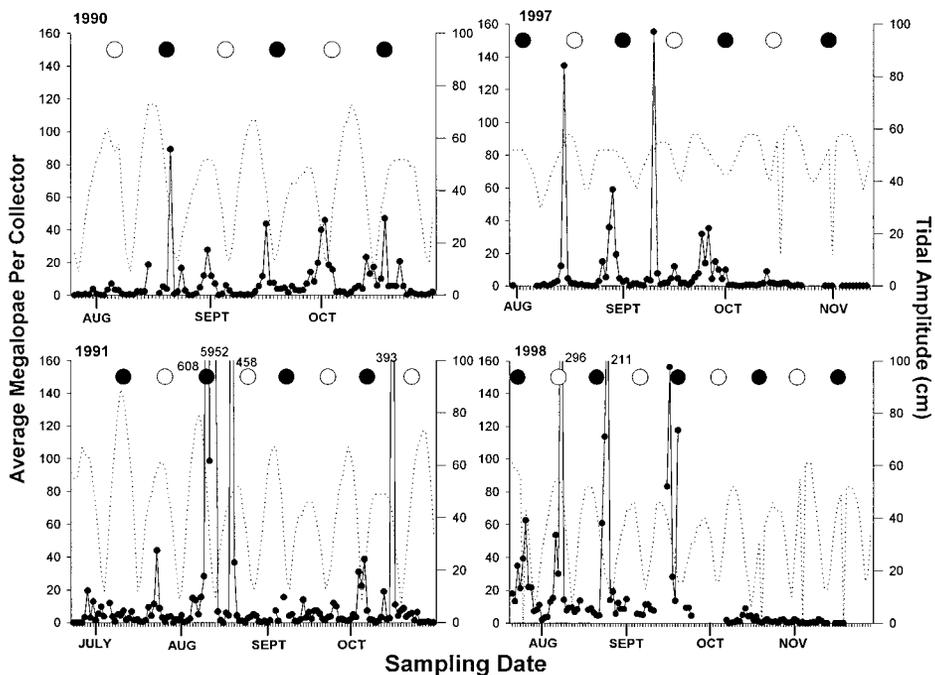


Figure 2. Average number of megalopae recruits per collector at Point aux Pins during 1990, 1991, 1997 and 1998. Gaps between points are due to missing samples from inclement weather. Dotted line indicates tidal amplitude, black circles indicate new moon and white circles indicate full moon. Long tick marks indicate first day of the month.

most of those juveniles were between 2–8 mm CW. Juvenile abundance was not significantly correlated with SAV biomass or marsh stem count in 1990. In 1991, juvenile abundance was also greater in the lower bay (PAP) with most crabs between 2–8 mm CW, although differences among sites was not significant (Heck et al., 2001). A greater number of juveniles was collected in PAP SAV than PAP marsh in 1990, although the difference was not significant (Fig. 4), while in 1991 there were significantly more crabs in PAP SAV than PAP marsh (Fig. 4, $P < 0.05$). The abundance of juvenile crabs decreased with size during both 1990 and 1991, and the smallest crabs occurred at PAP. Juvenile abundance was significantly correlated with SAV biomass at PAP ($P < 0.05$) and with marsh stem counts at FR ($P < 0.001$) in 1991 (Heck et al., 2001).

In 1997, SAV was present at FR, and FR SAV was therefore added to the sampling effort for both 1997 and 1998. Juvenile abundance across all habitats ranged from $<5/m^2$ at the Delta to $58/m^2$ at PAP in 1997 (Fig. 4), and from $<5/m^2$ at the Delta to $76/m^2$ at PAP in 1998 (Fig. 4). Data from both 1997 and 1998 failed the normality and heteroscedasticity assumptions of one way ANOVA and transformations did not correct these violations. Nevertheless, we present the results of the ANOVA rather than the non-parametric results for ease of comparison with earlier studies. However, results from non-parametric tests (Kruskal-Wallis and a Dunn's multiple comparison) showed similar results to those of the assumption-violated ANOVAs. Again in 1997 and 1998, there were significantly more juveniles in the lower (PAP) and middle bay (FR) sites than at the upper bay (DL) site (Fig. 4c, d, $P < 0.05$) and most of the crabs were within the 2–8

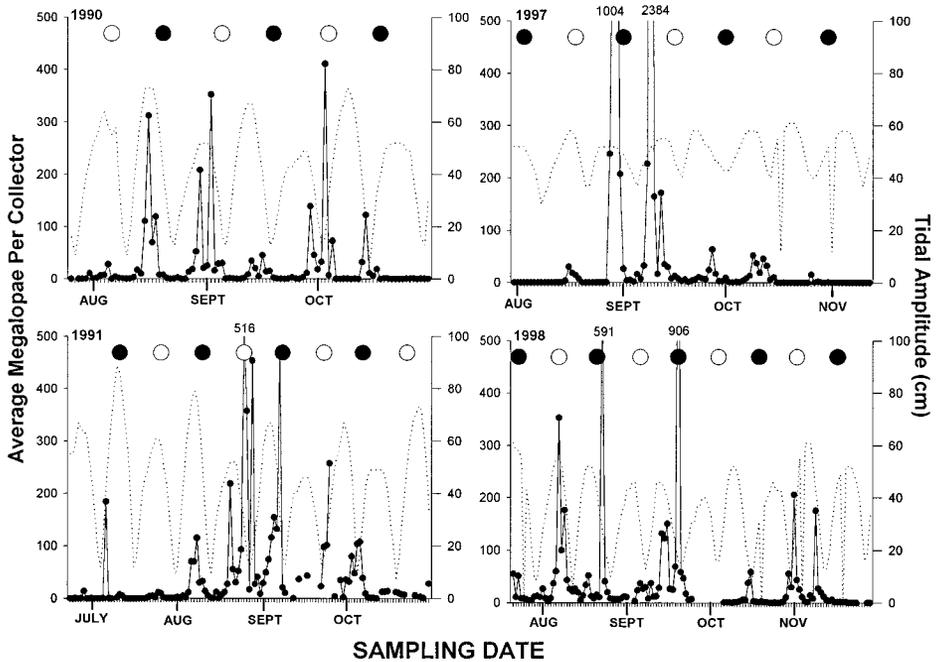


Figure 3. Average number of megalopae recruits per collector at Fowl River during 1990, 1991, 1997 and 1998. Gaps between points are due to missing samples from inclement weather. Dotted line indicates tidal amplitude, black circles indicate new moon and white circles indicate full moon. Long tick marks indicate first day of the month.

mm CW size class. More juveniles were found in SAV than marsh at FR and DL in 1997 and 1998 (Fig. 4c, d), although not significantly so ($P > 0.05$). Abundance of juvenile crabs was similar between PAP marsh and PAP SAV in 1997 (Fig. 4); however, significantly ($P < 0.05$) more juvenile crabs were found in PAP marsh than PAP SAV in 1998 (Fig. 4). During both 1997 and 1998, the abundance of juvenile crabs was inversely related to CW (i.e., abundance decreased as size increased) with newly settled crabs found at FR and PAP and no newly settled crabs found at DL.

There were no significant differences in SAV biomass (Fig. 5a) among sites during 1997 ($P = 0.454$) and 1998 ($P = 0.800$). However, there were significant differences in marsh stem counts (Fig. 5b) among sites in both 1997 ($P < 0.001$) and 1998 ($P < 0.001$). In 1997, all three sites were significantly different from one another, but in 1998 only DL was significantly different (less) from PAP and FR. Juvenile abundance was significantly correlated with SAV biomass at PAP ($P < 0.001$) in 1997 and SAV biomass at DL ($P < 0.05$) and FR ($P < 0.05$) in 1998, as well as with marsh stem count at FR ($P < 0.05$) in 1998.

MEGALOPAL-JUVENILE CORRELATIONS.—Few significant correlations between megalopal abundance and juvenile abundance were found during the 1990–1991 and the 1997–1998 studies; however, correlations that were significant coincided with large recruitment events and disappeared within a few days. In 1990, a significant positive correlation was found between megalopal abundance and juvenile abundance when lagged by one day at FR (Table 1, $r = 0.858$, $P < 0.05$), whereas in 1991 none of the correlations between megalopal abundance and juvenile abundance was significant (Table 1). When the data from both years were

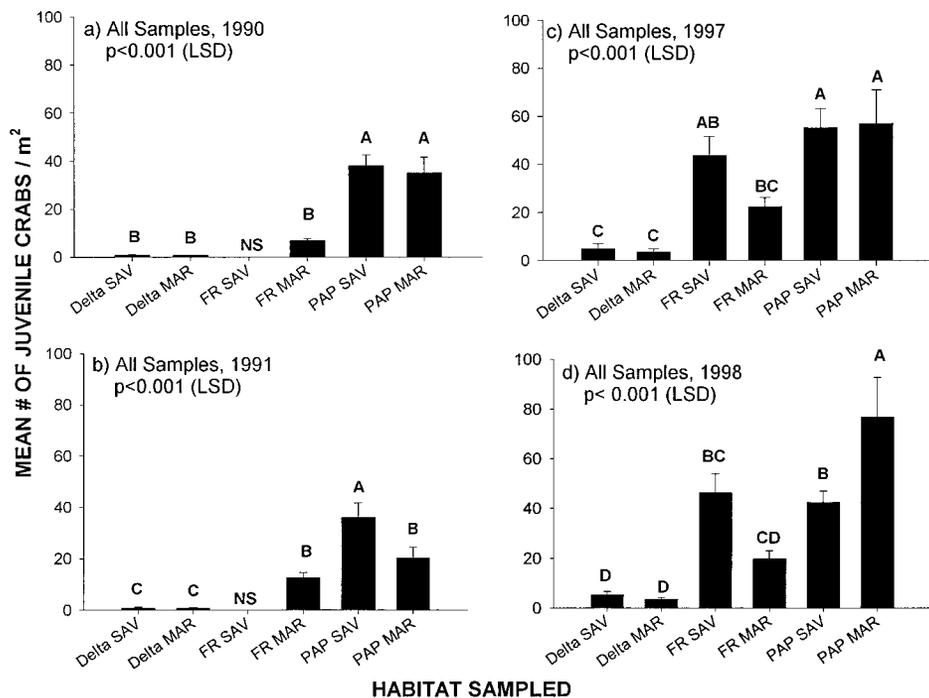


Figure 4. Mean abundance of juvenile blue crabs per m² in potential nursery habitats at all three sites (PAP, FR and Delta) during 1990, 1991, 1997 and 1998. Fisher's LSD post-hoc multiple comparison test was used to determine significant differences among habitats. Treatments with different letters are significantly different from one another. NS indicates that the habitat was not sampled.

combined, significant positive correlations were found for 1-, 3- and 7-day lags at FR (Table 1: $r = 0.7123$, $r = 0.6720$ and $r = 0.7077$, respectively; $P < 0.05$).

In 1997, no significant correlations were found between megalopal and juvenile abundance at any of the sites (Table 1). Yet in 1998 a significant positive correlation was found for a 3 day lag at PAP marsh (Table 1: $r = 0.8317$; $P < 0.05$). At FR, both the 3 and 7 day lags showed strong positive correlation ($r = 0.9987$, $r = 0.9999$, respectively) between megalopal abundance and juvenile abundance. However, the strong correlation should be interpreted cautiously due to the low sample size ($n = 3$; Table 1). When the 1997–1998 data were combined, a significant positive correlation was found for a 3 day lag at PAP marsh (Table 1: $r = 0.8113$; $P < 0.05$).

Closer examination of the significant correlations showed that they were usually associated with large recruitment events and only lasted a few days. When a significant correlation was found, most subsequent correlations showed either a lesser, positive correlation or a negative correlation, suggesting a decoupling of post-larval (megalopal) abundance and juvenile abundance within a few days.

POST SETTLEMENT MORTALITY (TETHERING).—Post-settlement mortality was very high (>80%) in the Mobile Bay system during both 1990–1991 and 1997–1998, with no apparent size refuge for the range of juveniles tested (7–21 mm CW) in these studies and no consistent habitat refuge. In 1990, the predation potential on juvenile blue crabs, as measured by tethering, across all tested habitats (sand, low grass, high grass, low marsh and high marsh) at both sites was extremely high (89.3% at PAP and 94.3% at DL; Heck et al., 2001). Although the

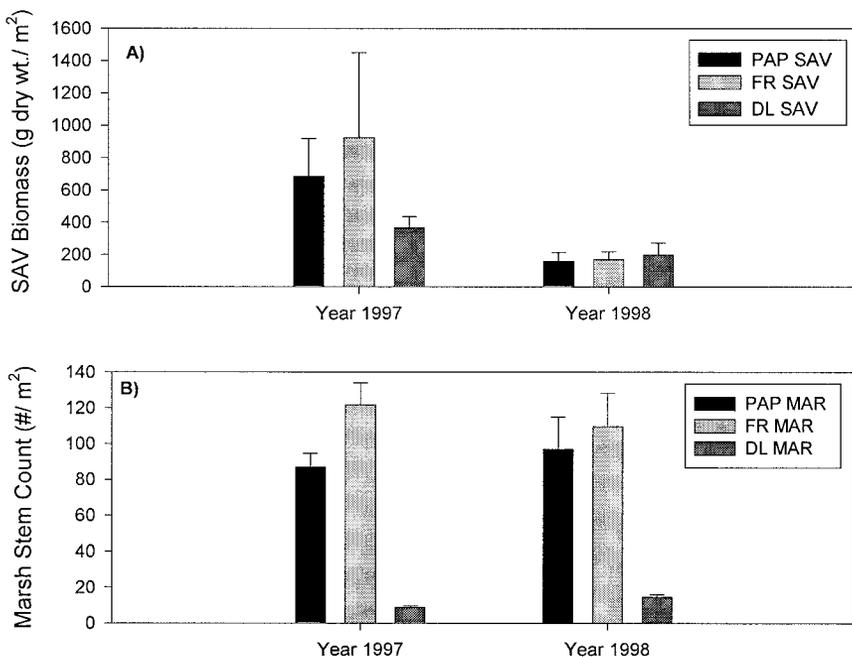


Figure 5. Mean a) biomass of SAV and b) marsh stem counts \pm SE at PAP (Point aux Pins), FR (Fowl River) and DL (Delta) during 1997 and 1998.

greatest survival at PAP was found in the high density grass habitat (Fig. 6), an ANOVA of arcsine square-root transformed data indicated no significant differences in predation potential ($P > 0.05$) among habitats (Heck et al., 2001). The greatest survival at DL was seen in the high marsh habitat (Fig. 8); however, an ANOVA found no significant differences among habitats (Heck et al., 2001). There were no significant correlations between SAV biomass or marsh stem counts and predation potential at either PAP or the Delta in 1990.

In 1991, post settlement mortality rates of juvenile blue crabs across all habitats at both PAP (68.4%) and DL (90.1%) were lower than in 1990. At PAP, the greatest survival was seen in the high marsh habitat (Fig. 6), although a one way ANOVA on arcsine square-root transformed data again found no significant ($P > 0.05$) differences in potential predation rates among treatments (Heck et al., 2001). Yet, at DL in 1991 there were marginally significant differences (ANOVA, $P = 0.06$) among potential predation rates in the various habitats (Fig. 8). A pairwise multiple comparison test indicated that there was a significant difference ($P < 0.05$) in the potential predation rates between the sand and the low density marsh habitats, with the greatest survival occurring in the low density marsh (Heck et al., 2001). There were no significant trends in mortality among the various size classes that were tested (Figs. 7, 9), although there did appear to be somewhat greater survivorship in the 20–21 mm class size at PAP (Fig. 7). This suggests that there is no size refuge for the range (7–21 mm CW) of juvenile blue crabs that were tested. There were no significant correlations between SAV biomass or marsh stem counts and predation potential at either PAP or the Delta in 1991.

In 1997, potential predation rates on juvenile blue crabs across habitats were also very high at both PAP (87.9%) and the Delta (91.5%). Significant differences

Table 1. Linear regression equations and correlation coefficients that define the relationship between megalopal abundance (x) and juvenile abundance (y) with 1-, 3-, and 7-day lags. Significant correlations are bolded and indicated by * ($P < 0.05$). (1990–1991 and 1997–1998 are the results from combining data from both years.)

	1-day lag		3-day lag		7-day lag	
	Slope	<i>r</i>	Slope	<i>r</i>	Slope	<i>r</i>
1990						
PAP SAV	-0.116	0.11667	-0.2722	0.26807	-0.5634	0.29527
PAP MAR	0.2443	0.1539	-0.3859	0.1717	-1.5674	0.3712
FR SAV	0.1937	0.8589*	0.0325	0.5066	0.0333	0.4798
1991						
PAP SAV	3.9957	0.4884	0.1598	0.6314	0.2546	0.6977
PAP MAR	0.8023	0.2015	-9.645	0.0783	0.0176	0.0989
FR SAV	0.0303	0.6798	0.056	0.7004	0.0844	0.7532
1997						
PAP SAV	1.2648	0.9383	3.7914	0.8057	0.9261	0.1367
PAP MAR	-0.07607	0.0489	0.2046	0.0562	-4.5816	0.341
FR SAV	-6.96	0.3393	-0.2511	0.1631	3.3176	0.6826
1998						
PAP SAV	-0.7172	0.2881	-0.2418	0.8057	0.4724	0.4319
PAP MAR	4.2634	0.3697	1.2755	0.8317*	-1.0899	0.223
FR SAV	0.2691	0.2159	0.7291	0.9987	-0.6358	0.9999
1990–1991						
PAP SAV	0.0936	0.4884	0.151	0.5533	0.2381	0.6107
PAP MAR	0.4766	0.1999	-0.0367	0.1196	-0.0366	0.0835
FR SAV	0.363	0.7123*	0.0604	0.672*	0.0856	0.7077*
1997–1998						
PAP SAV	1.2856	0.582	-0.2686	0.3624	-0.0104	0.01
PAP MAR	0.0096	0.0018	1.3808	0.8113*	-0.4151	0.0688
FR SAV	-1.6665	0.0831	0.5899	0.6326	-0.0169	0.0191

in predation potential were found among habitats at PAP (ANOVA, $P < 0.05$) (Fig. 6) and a multiple comparison test indicated a significant difference in predation potential between the low density grass habitat and the low density marsh habitat ($P < 0.05$), with greatest survivorship in the low density grass habitat. At the Delta there were also significant differences in predation potential among habitats (ANOVA, $P < 0.05$) (Fig. 8). A pairwise multiple comparison test revealed that the highest survivorship occurred in high density grass, where survivorship was significantly greater than in the sand ($P < 0.001$), low marsh ($P < 0.01$), or high marsh habitat ($P < 0.05$), and greater in the low grass habitat than in the sand habitat ($P < 0.01$). A significant negative correlation between potential predation rates and SAV biomass ($r = 0.975$; $P < 0.05$) was found at DL in 1997, suggesting that as vegetation increased, predation potential decreased. No significant correlation was found between SAV biomass and predation potential at PAP.

There was a reduction in predation potential across all habitats at PAP in 1998 (62.2%) and an increase at DL (97.1%) when compared to 1997. The greatest survival rates at PAP were seen in the low and high grass habitats (Fig. 6); however, a one way ANOVA found no significant differences among habitats. DL data violated both the normality and heteroscedasticity assumptions of ANOVA and transformation could not correct the violations. A non-parametric Krus-

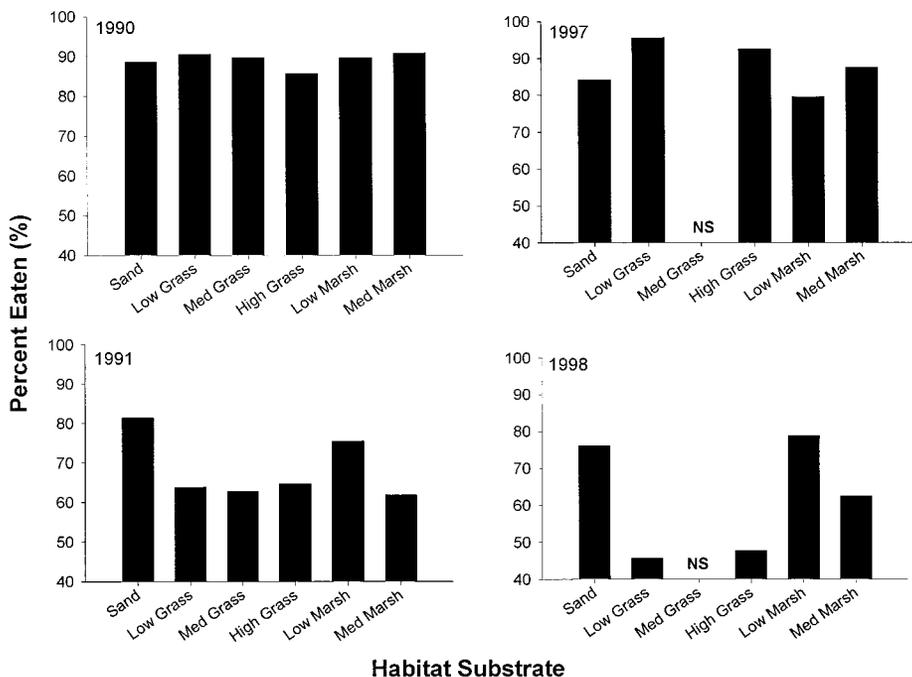


Figure 6. Percentage of juvenile blue crabs eaten during tethering studies at the Point aux Pins study site in 1990, 1991, 1997 and 1998. NS indicates that the habitat was not sampled.

kal-Wallis test found no significant differences in the predation potential among habitats (Fig. 8), although greater survivorship occurred in low density grass. There did not appear to be any trends in mortality rates among size classes (Figs. 7, 9), implying that there may not be a size refuge available for the range of juvenile blue crabs (7–21 mm CW) tested. There were no significant correlations between SAV biomass and predation potential at either PAP or the Delta in 1998.

DISCUSSION

When comparing these two independent, yet identical blue crab studies, some differences were found in post-larval settlement and post-settlement mortality; however, the overall patterns were qualitatively similar. Larval recruitment was lower during the latter study, yet recruitment still occurred in pulses with peak recruitment in late August–early September. Despite high levels of larval recruitment, juvenile abundance was relatively low with no significant correlation between larval recruitment and juvenile abundance, except immediately following large recruitment events. The decoupling between megalopae abundance and juvenile abundance seen in both of these studies may be caused by the high ($\approx 80\%$) rate of post-settlement mortality, as estimated by tethering techniques.

LARVAL RECRUITMENT.—Recruitment likely occurs year-round in our study area, as has been found elsewhere in the Gulf of Mexico (King, 1971), although peak recruitment in the Mobile Bay system occurred in late August–early September in all four years (1990, 1991, 1997 and 1998). More blue crab megalopae arrived at some inshore sites than others, but high rates of post-settlement mortality quickly dampened among-site differences in abundance of juveniles. Settlement of megalopae was lower at PAP in 1997 than in 1990 or 1991, whereas settlement

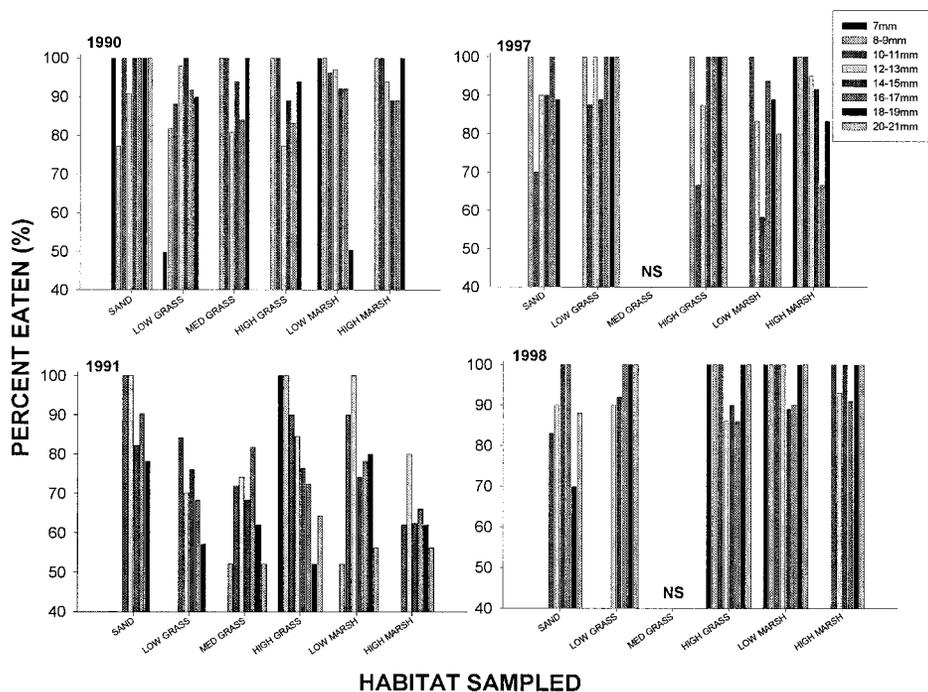


Figure 7. Size of juvenile blue crabs eaten during tethering studies at the Point aux Pins study site in 1990, 1991, 1997 and 1998. NS indicates that the habitat was not sampled.

increased by nearly 50% in 1997 at FR. One likely explanation for the increased settlement at FR is due to the appearance of SAV in 1997 that was not present during the 1990–1991 study, which may have enhanced megalopal settlement through chemical cues (Forward, 1996). In 1998, recruitment at PAP was similar to 1997, but recruitment at FR was only half that in 1997. The decreased recruitment at FR may have been due to the disruption of megalopal supply, or to the burial of SAV, both caused by the passage of two September hurricanes (Hurricanes Earl 9/2 and Georges 9/26) in 1998. Another possible cause of the decreased recruitment at lower salinities was also seen during the 1990–1991 study (Morgan et al., 1996). Finally, the large amounts of rain associated with hurricanes flowing downstream and out of Mobile Bay may have made it difficult for the ingress of megalopae, lowering recruitment numbers.

Larval recruitment occurred in pulses (cf. Rabalais et al., 1995; Morgan et al., 1996) during all four years, although the magnitude of the pulses varied greatly. Similar to results from a study in Mississippi (Perry et al., 1995), these pulses were not clearly related to any of the recorded physical factors. Since favorable onshore winds are present throughout most of the recruitment period, it is possible that these pulses are related to blue crab reproductive biology (i.e., spawning events) rather than physical factors. Recruitment averages between sampling periods did decrease substantially from 1990–1991 ($\bar{x} = 150$) to 1997–1998 ($\bar{x} = 21.5$); however, as suggested above, this decrease may be due in large part to hurricane effects during the time of peak recruitment (September) in 1998. Storm disturbance during the period of peak recruitment could have led to a significant reduction in megalopal recruitment, since settlement occurs predominately in

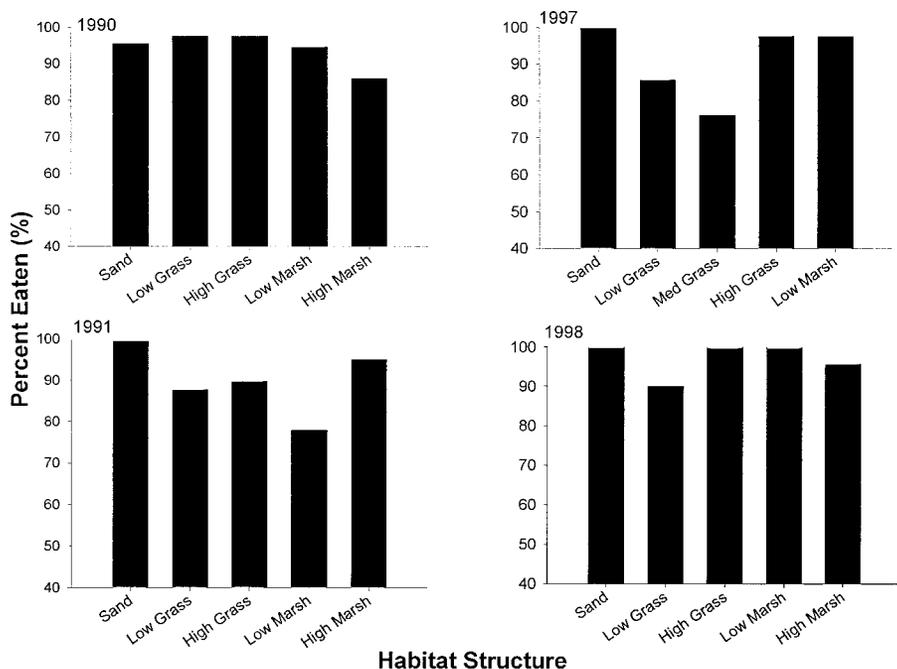


Figure 8. Percentage of juvenile blue crabs eaten during tethering studies at the Delta study site in 1990, 1991, 1997 and 1998.

small numbers interspersed with large peaks (Perry et al., 1995; van Montfrans et al., 1995). These large peaks can contribute up to 50% of the annual total of blue crab recruitment in a given area (van Montfrans et al., 1995). Since both storms and recruitment are episodic, the coincidence of a storm with a recruitment peak could potentially wipe out an entire “peak” of recruits, which could be a large percentage of the total recruitment during a season.

JUVENILE ABUNDANCE.—Studies in 1990–1991 clearly showed that megalopal settlement was confined to the lower parts of the Mobile Bay system and that megalopae settled preferentially on vegetated substrates (Morgan et al., 1996). Collections of juvenile blue crabs during both the 1990–1991 and 1997–1998 studies showed that small crab density was highest where megalopa density was highest (PAP & FR). Additionally, most of the juveniles found in the PAP and FR sites were within the 2–8 mm CW size range, whereas most of the juveniles at DL were larger (CW > 10 mm), indicating that settlement most likely occurs in the lower portions of the bay and then juveniles migrate into the upper bay.

More juveniles were located in SAV than marsh during the 1990–1991 study (Heck et al., 2001), while in the 1997–1998 study PAP marsh consistently had high abundances (equal to or greater than that of SAV) of juveniles. We attribute the increased density of juveniles in PAP marsh in 1998 to the large amount of SAV detritus (avg. dry wt. = 469.3 g dry wt/m²) found intermingled with the marsh plants. However, both of these studies (1990–1991 and 1997–1998) found that SAV and fringing marsh are primary nursery habitats for early juvenile blue crabs within the Mobile Bay system. These results agree with the findings of other studies conducted along the Mid Atlantic coast and elsewhere in the Gulf of Mexico (Orth and van Montfrans, 1987; Thomas et al., 1990; Williams et al.,

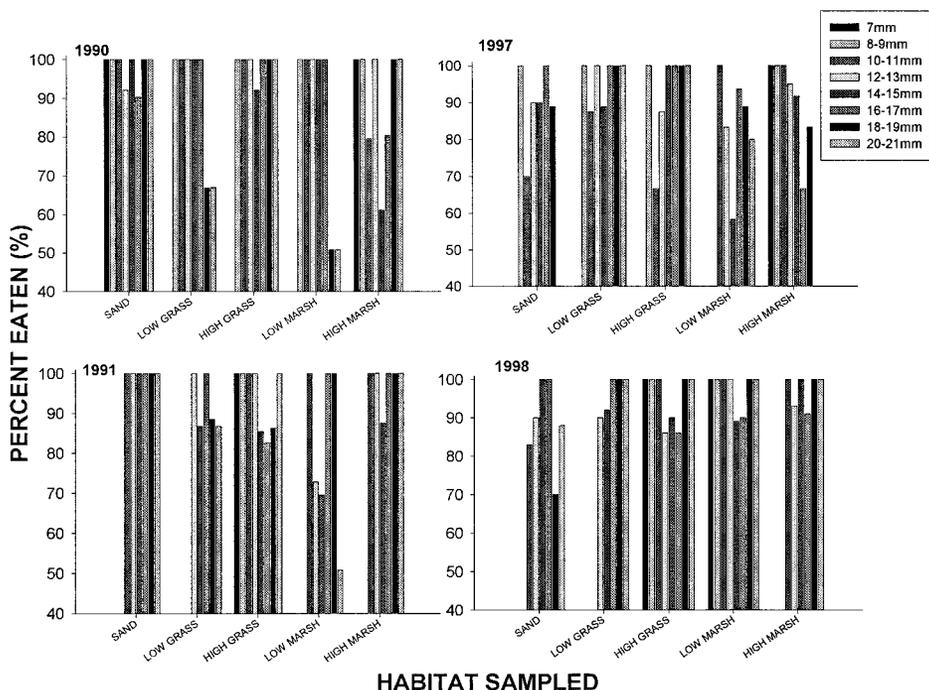


Figure 9. Size of juvenile blue crabs eaten during tethering studies at the Delta study site in 1990, 1991, 1997 and 1998.

1990), which also showed that SAV and marsh are important nursery habitats for young blue crabs.

Juvenile abundances were of the same order of magnitude as those reported previously from Chesapeake Bay (45–90/m²; Orth and van Montfrans, 1987). Given the exceedingly large numbers of megalopae reaching the Mobile Bay system (10–100 times more than seen in Chesapeake Bay; Heck et al., 1995), there must be exceptionally high post-settlement mortality in order to produce juvenile abundances of equal magnitude between Alabama waters and Chesapeake Bay (Heck and Coen, 1995). There was a decrease in average juvenile abundance between the 1990–1991 (range: 36–92/m²) and the 1997–1998 studies (range: 15–58/m²). This may be due to either reduced post-larval recruitment, a loss of nursery habitat due to hurricanes, or both, as discussed in the larval recruitment section. Although juvenile abundance differed between the studies, both showed that most juveniles were found in the lower bay in SAV and were in the 2–8 mm CW size. Both studies also found that juvenile abundance decreased as size increased.

Despite the notion that an increase in vegetation would lead to an increase in population size due to increases in refuge and food, there were no consistent relationships between juvenile abundance and SAV biomass or marsh stem counts during 1990, 1991, 1997 or 1998. The surprising lack of this relationship may be due to interactions between size dependent cannibalism and size dependent protection provided by different amounts of vegetation (see Heck and Spitzer, 2001, for detailed discussion).

MEGALOPA-JUVENILE CORRELATIONS.—One might have expected to find strong correlations between larval abundance and juvenile abundance, as seen for other decapod species such as the rock lobster (Pearse and Phillips, 1994) and the

American lobster (Incze et al., 1997; Wahle and Incze, 1997; Palma et al., 1998). However, this was not the case for the blue crab in the Mobile Bay system during either the 1990–1991 or the 1997–1998 study, as correlations between megalopal abundance and juvenile abundance were highly variable. Significant positive correlations were commonly associated with large recruitment events but were usually short lived, and lasted only a few days. Juvenile abundances usually returned to background levels within 7–14 days, leaving no evidence of the large episodic recruitment events. Density-dependent mortality (such as cannibalism) may explain the decoupling of megalopal and juvenile abundances in these and other studies. For example, Pile et al. (1996) found that early blue crab instars, like Dungeness crabs (Fernandez et al., 1993; Eggleston and Armstrong, 1996) and rock crabs (Palma et al., 1998) exhibit density dependent mortality, which may be a result of cannibalism by slightly larger crabs (Hines and Ruiz, 1995; Moksnes et al., 1997).

POST SETTLEMENT MORTALITY (TETHERING).—No size refuge was seen for any of the tested size classes during either study, and mortality rates were extremely high during both the 1990–1991 study (~86% consumed/day) and the 1997–1998 (~85% consumed/day) study when compared to mortality rates reported along the Atlantic coast in New Jersey (25%; Wilson et al., 1990) and Virginia (68%; Pile et al., 1996). These data suggest that the value of SAV and marsh as refuge from predators may be more important in lower latitudes (see Heck and Coen, 1995). Since many studies have found that increased structure may lead to increased survival rates by providing prey with partial refuge from predators, it was surprising that we did not find a consistent negative relationship between SAV biomass and predation potential. This relationship may not have been evident during our studies due to density-dependent cannibalism (as noted previously) that could negate the effects of SAV refuge and minimize differences in predation potential among habitats. Another reason for the seeming lack of refuge value, may be that the variation in biomass of SAV among study sites was insufficient to have a significant effect on predation rates.

Previously, Heck and Wilson (1987) found that predation losses of juvenile blue crabs and other crab species varied substantially from year to year both within and between habitats, as did the value of SAV as refuge from predators. Our findings also show that the value of SAV as refuge can vary greatly from year to year, possibly as a function of cannibalism or the recruitment success of blue crab predators. Despite variability in post-settlement mortality both within and between projects, post-settlement mortality within the Mobile Bay system is generally very high, with no apparent size refuge for the range of juveniles tested.

CONCLUSIONS

Despite notable differences between results of the two (1990–1991 and 1997–1998) studies, such as lower larval recruitment and juvenile abundance in 1997–1998, general conclusions from each were qualitatively similar. For example, both studies concluded that: larval recruitment occurs in pulses; peak recruitment occurred in late August–early September; no consistent relationship existed between megalopal abundance and juvenile abundance; juveniles were most abundant in SAV and in the lower part of the bay; and rates of mortality were very high for early juvenile blue crabs. Finally, the relative importance of post-larval abundance and post-settlement mortality did not differ between these two studies. Because we consistently find high levels of recruitment and lower levels of juveniles in

the Mobile Bay system, it appears that the blue crab population is not limited by larval supply, but by high levels of post-settlement mortality.

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